Climate warming and biomass accumulation of terrestrial plants: a meta-analysis

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Summary

- Growth of terrestrial plant species and functional types (PFTs) in response to climate warming determines future dynamics of terrestrial vegetation.
- Here, a meta-analysis was conducted with data collected from 127 publications to reveal general patterns of biomass responses of terrestrial plants to warming.
- Warming significantly increased biomass by 12.3% (with a 95% confidence interval of 8.4–16.3%) across all the terrestrial plants included. However, biomass responses were dependent upon PFTs, with significantly greater stimulation of woody (+26.7%) than herbaceous species (+5.2%). Warming effects on biomass showed quadratic relationships with both latitude and mean annual temperature, but did not change with mean annual precipitation or experimental duration. In addition, the other treatments, including CO_2 enrichment, nitrogen addition, drought and water addition, did not alter warming responses of plant biomass.
- Dependence of the terrestrial plant biomass responses to warming upon PFTs, geographic and climatic factors as well as warming magnitudes will have consequent influences on community composition and structure, vegetation dynamics, biodiversity and ecosystem functioning in a warmer world. Our findings of functional type-specific responses of terrestrial plants are critical for improving predictions of climate-terrestrial carbon feedbacks.

Introduction

Most models predict that climate warming will increase the release of carbon dioxide (CO_2) from the terrestrial biosphere into the atmosphere, thus triggering positive climate-terrestrial carbon (C) feedback which lead to a warmer climate (Cox *et al.*, 2000; Luo, 2007). However, stimulation of biomass accumulation and net primary productivity (NPP) of terrestrial ecosystems under rising temperature (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009) may enhance C sequestration and attenuate the positive feedback between climate warming and the terrestrial biosphere. Nevertheless, given that there are > 300 000 terrestrial plant species and great variations in the environments in which they grow, a lack of a general pattern in relation to how and to what extent warming impacts terrestrial plant growth and biomass accumulation limits the credible projection of climate-terrestrial C feedback.

Increasing research efforts using field manipulative experiments across the world have investigated the potential impacts of climate warming on terrestrial plants and ecosystems (Rustad, 2008). However, the observed responses of plant biomass and/or NPP of terrestrial ecosystems to experimental warming have been reported as increases (Shaver *et al.*, 1998; Rustad *et al.*, 2001; Wan *et al.*, 2005; Sullivan *et al.*, 2008), decreases (Klein *et al.*, 2007), and even no change (Saleska *et al.*, 2002). Many factors contribute to the highly variable warming responses of terrestrial plants. First, experiments conducted in various ecosystems inevitably involve different plant species and/or functional types (PFTs), which vary in their responses to climate warming (Van Wijk *et al.*, 2004; Luo, 2007). Second, warming-induced alterations of interspecific interactions among coexisting plant species can change growth of different plant species or PFTs even under the same warming conditions (Cowling & Shin, 2006; Niu & Wan, 2008). Third, climate warming can impact plant growth by

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reducing soil moisture (Wan *et al.*, 2005) and/or increasing soil nitrogen (N) mineralization and availability (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Miller *et al.*, 2007). Changes in soil water and N availability can also differentially affect growth of plant species and functional types that vary in water/N use efficiency or strategy.

Differences in the initial environmental conditions among the diverse terrestrial ecosystems may also exert strong influences on the plant response to climate warming (Shaver *et al.*, 2000). Plants in ecosystems at the higher latitudes (especially in the northern hemisphere) would be more positively affected than those at the lower latitudes (Root *et al.*, 2003; Parmesan, 2007) because of greater warming rates and stronger low-temperature limitation for plant growth in the former regions. For example, a declining trend of plant above-ground biomass in response to warming along an increasing temperature gradient has been observed in European shrublands (Peñuelas *et al.*, 2004). However, the assumption has never been tested for terrestrial plants on a global scale. Biomass responses of terrestrial plants to climate warming may also show temporal variability under climate warming (Rustad *et al.*, 2001) because of changes in growth rate and/or sensitivity of plants to environmental factors at different growth stages (Day *et al.*, 2002; Escudero & Mediavilla, 2003); and interannual fluctuations in abiotic factors (e.g. temperature, precipitation, and soil N mineralization and availability). Moreover, concurrent changes in atmospheric CO_2 concentration, N deposition, and global and regional precipitation regimes may affect growth responses of terrestrial plants to climate warming (Rustad *et al.*, 2001; Norby & Luo, 2004).

In order to improve the understanding of climate-warming influences on the terrestrial biosphere, several syntheses have been conducted to explore general patterns of the warming responses of terrestrial plant growth or NPP (Arft *et al.*, 1999; Cornelissen *et al.*, 2001; Rustad *et al.*, 2001; Dormann & Woodin, 2002; Van Wijk *et al.*, 2004; Walker *et al.*, 2006). However, there are still many uncertainties in the growth responses of terrestrial plants (especially at functional type level) to climate warming. For example, most data in previous studies have been collected from the Arctic regions or tundra ecosystems, which restricts extrapolation from their findings. With the increasing availability of reports from various ecosystems across the world, we conducted a meta-analysis using updated data from 127 publications (see Supporting Information, Tables S1, S2, Notes S1). In analyzing the general response patterns of terrestrial plant biomass to climate warming, terrestrial plants were separated into different PFTs, above-ground vs below-ground parts, and different tissues. The responses were then plotted against geographic (latitude) and climatic (mean annual temperature (MAT) and precipitation (MAP)) factors, warming magnitude, and experimental duration. Finally, warming effects on plant growth were examined, regardless of whether other climate change factors (CO_2 enrichment, N addition, drought, and water addition) were manipulated.

Given that low temperature is more critical in limiting plant growth and its warming response at higher than at lower latitudes (Shaver *et al.*, 2000; Peñuelas *et al.*, 2004) and that the ratio of plant respiration to photosynthesis is greater at higher (27°C) than at moderate (20°C) and low temperatures (13°C; Atkin *et al.*, 2007), we first hypothesize that climate warming may have a positive impact on plants at high latitudes and a negative impact on tropical plants. As one of the essential resources for plant growth, water availability not only limits biomass accumulation of terrestrial plants but also has an impact on its response to elevated temperature because climate warming can exacerbate water limitation by stimulating evapotranspiration and reducing soil water availability (Harte & Shaw, 1995; Wan *et al.*, 2005; Niu *et al.*, 2008). Therefore, we propose a second hypothesis that biomass responses of terrestrial plants to increased temperature will increase with MAP. In addition to soil water availability, other resources, for example, atmospheric CO_2 concentration and soil N availability, also constrain plant growth. Under the concurrence of multiple global change factors (rising atmospheric CO_2 concentration and Earth surface temperature, changing precipitation regimes, and increasing atmospheric N deposition), we hypothesize that enrichment of atmospheric CO_2 concentration and N will positively affect the biomass responses of terrestrial plants to warming.

Materials and Methods

Data collection

We conducted study searches in Web of Science and retrieved the references cited in papers we found to build a database. Plant biomass, plant growth, plant productivity, warming, increased temperature, and elevated temperature were used as keywords in the searching process. We used the following criteria to include papers in our analysis: responses of terrestrial plant biomass, growth, and/or productivity to warming with and/or without other treatments (such as N addition) were reported; means (X), standard errors (SE), standard deviations (SD) or confidence intervals (CI), and sample sizes (n) of both the control and warming treatments were provided. In addition, there was no study involving both warming treatments and invasive species. As a result, 127 individual publications before June 2009 were included in our analysis.

We extracted data of biomass responses directly from tables or text in original papers, or indirectly from figures using SigmaScan (Systat Software Inc., San Jose, CA, USA). Units of plant biomass were unified into g, g m^{-2}, g m^{-2} yr^{-1}, g per plant or other analogous ones. Other variables, if

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provided, such as latitude, MAT, and MAP of the experimental sites, warming magnitude, experimental duration, and other treatments were also extracted for further analysis. In addition, each variable was divided into six classes to reveal general patterns of biomass responses to warming (Table 1). Moreover, we separated terrestrial plant species into different PFTs based on biological realms (seed plants vs spore plants), growth forms (woody vs herbaceous plants, grasses, forbs, shrubs, and trees), and other functional traits (leguminous vs nonleguminous forbs, deciduous vs evergreen shrubs, and deciduous vs evergreen trees). In order to ensure the data were independent, we made great efforts to exclude duplicate results in different publications. However, our analyses were not completely independent because individual papers often provided data with more than one treatment (e.g. different warming magnitudes) and/or different above- and below-ground tissues (leaf, root, shoot and stem). To examine the influence of nonindependence of data, we first averaged those data from the same published study by PFTs in order to make sure that only one comparison was used from a published study for each PFT. We then conducted the analyses on the response patterns of each PFT using only one comparison from one study. Nonetheless, we found that the response pattern was unchanged but with larger 95% CIs as a result of smaller sample sizes (Fig. S1) when compared with the results using all data. Thus, all data obtained, including data from different growing seasons, were used in our study.

Since both field and pot experiments were included in our analysis, we first divided our database into two datasets: data from field experiments and pot experiments. However, only biomass responses to warming in deciduous trees were significantly different between the two experimental types as a result of the small observation number ($n = 4$ for deciduous trees in field experiments; Fig. S2, Table S3). Therefore, we combined the two datasets in the analysis; the only exception to this was that we examined the effects of the initial conditions (i.e. latitude, MAT and MAP) on biomass responses in field experiments only. Moreover, we pooled all plant parts (i.e. above-ground parts, below-ground parts, and whole plants) in our database because of the similar response patterns between above- and below-ground parts in most PFTs (Fig. 2). In order to examine the effects of warming facilities, we grouped warming facilities by chamber (i.e. environment-controlled chamber), free air (including electric heating cable, infrared (IR) heater, lightbulb heating, and passive heating), glasshouse (including temperature-gradient glasshouse), and open-top chamber (OTC). However, no impact of warming facility on biomass responses of terrestrial plants to warming was detected (Fig. S4). Consequently, experiments using different warming facilities were combined in this analysis.

Meta-analysis

We followed the techniques described in detail by Wan *et al.* (2001). Briefly, the natural log-transformed response ratio ($\log_e r$) of plant biomass at elevated temperature (X_e) to that at ambient temperature (X_c), with or without other treatments, was used to calculate the effect size of warming treatments. When the warming treatment was combined with other treatments (for example, N addition), the warming plus other treatment (for example, warming plus N addition) was used as X_e. SE and CI were transformed to SD before calculation. Weighted log response ratio ($\log_e$RR) and its 95% CI were calculated using MetaWin 2.1 (Sinauer Associates Inc., Sunderland, MA, USA). We used the homogeneity test to determine whether different groups of independent variables resulted in different responses, as the total heterogeneity (Q_T) was partitioned into within-group (Q_w) and between-group (Q_b) heterogeneities. According to Gurevitch & Hedges (1999), Q_b rather than Q_w may be of considerable scientific interest. An independent variable had a significant impact on the response ratio when Q_b was larger than a critical value (Gurevitch & Hedges, 1993). Warming effects were estimated as a percentage change relative to the control (%), using the equation (exp ($\log_e$RR) − 1) × 100%. The warming effects were considered as significant if the 95% CI did not overlap with zero, while the warming effects of different groups or under different conditions were considered to be significantly different from each other if their 95% CIs did not overlap (Wan *et al.*, 2001). Statistical differences were considered as significant when $P < 0.05$. All calculations (except for the effects of other treatments) were

Table 1 Class levels of independent variables in the meta-analysis

Variables	Class levels					
Latitude (°)	0–15	15–30	30–45	45–60	60–75	75–90
MAT (°C)	≤ −2	−2 to 3	3–8	8–13	13–18	> 18
MAP (mm)	≤ 300	300–450	450–600	600–750	750–900	> 900
Warming magnitude (°C)	≤ 1	1–2	2–3	3–4	4–5	> 5
Experimental duration (months)	≤ 12	12–24	24–36	36–48	48–60	> 60

MAT, mean annual temperature; MAP, mean annual precipitation.

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conducted using data with warming treatment only (Table S1).

Results

Warming effects on biomass were dependent on PFTs

Experimental warming significantly increased biomass by 12.3% (with a 95% CI of 8.4–16.3%; Fig. 1) across all the terrestrial plants included (Table S2). However, warming effects showed strong dependence upon PFTs (Fig. 1, Table 2). For example, warming stimulated biomass of seed plants (+13.6%, $P < 0.05$) but suppressed biomass of spore plants (−13.6%, $P > 0.05$; Fig. 1, Table 2). Biomass responses to warming of woody plants (+26.7%, $P < 0.05$) were significantly greater than those of herbaceous plants (+5.2%), whose 95% CI overlapped with zero (Fig. 1, Table 2). For herbaceous plants, grass biomass was enhanced by 12.3% ($P < 0.05$), but forb biomass did not change and no difference in the biomass response was detected between these two categories (Q_b = 2.0, P = 0.16; Fig. 1, Table 2). For woody plants, both trees and shrubs showed significant biomass increases under the warming treatment. In addition, enhancement of tree biomass (+34.4%, $P < 0.05$) was significantly higher (Q_b = 21.3, $P < 0.001$; Table 2) than that of shrub biomass (+13.3%, $P < 0.05$; Fig. 1). When PFTs were divided further, biomass response of leguminous and nonleguminous forbs to warming was not different from each other or from zero (Fig. 1, Table 2). The positive responses of evergreen shrubs (+21.8%, $P < 0.05$) were significantly greater (Q_b = 11.9, $P < 0.001$; Table 2) than those of deciduous shrubs (+1.9%, $P > 0.05$; Fig. 1). By contrast, the biomass stimulation induced by experimental warming did not differ (Q_b = 0.9, P = 0.35; Table 2) between deciduous (+38.7%, $P < 0.05$) and evergreen trees (+32.0%, $P < 0.05$; Fig. 1).

Biomass responses to warming varied among plant parts and tissue types

There was no difference in the warming responses between above- (+12.7%, $P < 0.05$) and below-ground biomass (+13.0%, $P < 0.05$) across all the terrestrial plants (Q_b = 0.0, P = 0.95, Fig. 2, Table 3). When compared within each PFT, warming responses of below-ground biomass (+33.4%, $P < 0.05$) were significantly greater than those of above-ground biomass (+4.7%, $P > 0.05$) in grasses only (Q_b = 8.8, $P < 0.01$, Fig. 2, Table 3). By contrast, above-ground biomass was stimulated more than below-ground biomass in trees (+44.9 vs + 14.9%; Q_b = 9.2, $P < 0.01$) under experimental warming (Fig. 2, Table 3). There was no difference in the above- and below-ground biomass responses to warming for other PFTs (Fig. 2, Table 3).

When plant biomass was further divided into different plant tissue types (leaf, root, shoot, and stem), no difference in the biomass responses to warming was detected among these tissue types (Q_b = 4.3, P = 0.23), irrespective of the significant enhancement of all the four tissue types (Fig. 3, Table 3). When compared within each PFT, woody plants, forbs, grasses, trees, nonleguminous forbs, and deciduous trees showed significant differences in the warming responses among tissue types (Fig. S3, Table 3). Specifically, the greatest warming-induced biomass stimulations occurred in shoots for woody plants (+51.0%), trees (+60.0%) and deciduous trees (+112.1%), stems for forbs (+93.2%) and nonleguminous forbs (+107.4%), and roots for grasses (+33.7%; Fig. S3).

Impacts of latitude, MAT, and MAP on biomass responses to warming

The impacts of latitude, MAT, and MAP on the biomass responses to warming were examined in field experiments

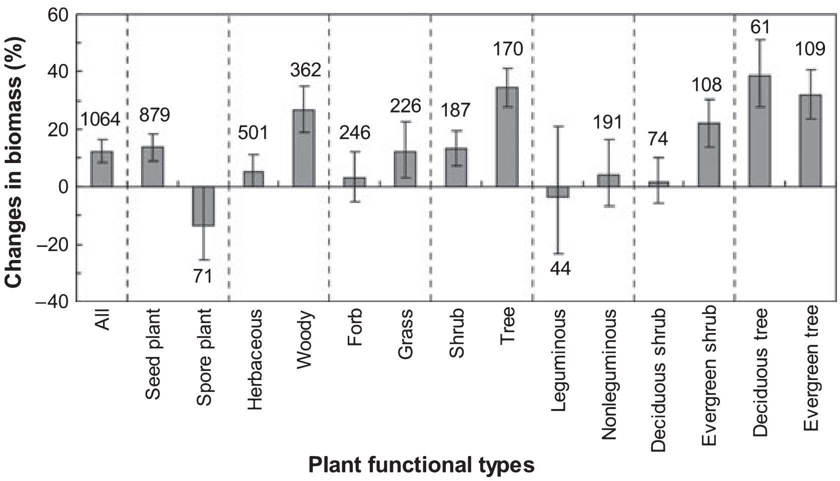

Fig. 1 Responses of terrestrial plant biomass to warming as a percentage change relative to control (%) for all plant functional types (PFTs) included in the meta-analysis. Values are means ± 95% CI and numbers of observations are shown near the bar. Because some observations in broader PFTs (e.g. woody species) cannot be divided into narrow ones (e.g. shrubs and trees), the sum numbers of observations in narrow PFTs are smaller than those in wider PFTs.

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Table 2 Between-group heterogeneity (Q_b) and probability (*P*) of warming effects on biomass across different biological realms and functional types

	Categories	Q_b	*P*
Biological realms	Seed, spore plants	12.5	< 0.001
Growth forms	Herbaceous, woody plants	20.2	< 0.001
	Forbs, grasses	2.0	0.16
	Shrubs, trees	21.3	< 0.001
Other functional types	Leguminous, nonleguminous forbs	0.4	0.53
	Deciduous, evergreen shrubs	11.9	< 0.001
	Deciduous, evergreen trees	0.9	0.35

only. Warming-induced changes in plant biomass showed quadratic relationships with both latitude (Fig. 4a) and MAT (Fig. 4b) across all the terrestrial plants. Stimulations of biomass under warming were statistically significant at the mid-latitude regions (30–45°, 45–60°, 60–75°; Fig. 4a). When biomass changes were plotted against MAT, significant increases in plant biomass were observed at all except for the highest temperature range (> 18°C; Fig. 4b). No clear relationship of biomass changes with MAP was found across all the MAP ranges (Fig. 4c). However, biomass responses were significantly greater than zero in four (300–450, 450–600, 750–900, and > 900 mm) out of the six MAP ranges. In addition, increases in plant biomass at MAP of 750–900 mm (+33.8%) were significantly higher than those at 300–450 and 600–750 mm (Fig. 4c).

When analyzed by PFTs, warming effects on biomass of herbaceous plants increased linearly with latitude (warming effect (%) = 0.55 × latitude – 24.11, $r^2 = 0.91$, $P < 0.05$; Fig. S5a), whereas the warming responses of woody plants did not change with latitude (Fig. S5a, Table 4). Warming effects on biomass of herbaceous plants were statistically significant only when MAT was lower than −2°C (+11.8%; Fig. S5b). Similarly to the patterns across all the terrestrial plants, warming responses of woody plants showed a quadratic relationship with MAT, with significant biomass increases at the two MAT ranges of −2 to 3 and 3–8°C (Fig. S5b). Neither herbaceous ($Q_b = 2.1$, $P = 0.71$) nor woody plants ($Q_b = 14.8$, $P < 0.05$; but with 95% CIs overlapped between any two MAP ranges) showed any significant difference in warming responses among all the MAP ranges (Fig. S5c, Table 4).

Biomass response changes with warming magnitudes but not experimental duration

All the magnitudes of temperature increases, except for the 3–4°C increase, caused significant stimulation of plant biomass. However, there was no difference in the biomass responses among the warming magnitudes ($Q_b = 6.5$, $P = 0.26$; Fig. 5a, Table 4). Biomass of herbaceous plants significantly increased only at the lowest warming magnitude (≤ 1°C, +40.7%; Fig. 5b). By contrast, warming-induced stimulations of biomass of woody plants were statistically significant across all warming magnitudes except of 3–4°C. The greatest biomass enhancement (+57.3%) of woody plants occurred when the warming magnitude was > 5°C, which was also significantly higher than those at the other four warming magnitudes (≤ 1, 1–2, 2–3, 3–4°C; Fig. 5b). Furthermore, warming-induced stimulation of woody plant biomass did not differ from that of herbaceous plants under the relatively small warming magnitude (≤ 4°C), whereas it was significantly higher under the relatively large warming magnitude (> 4°C; Fig. 5b).

Warming manipulations caused significant increments of plant biomass at experimental durations < 24 and > 48 months, but not between 24 and 48 months, irrespective of the insignificant difference in the biomass responses between any two durations ($Q_b = 9.2$, $P = 0.10$; Fig. 5c, Table 4). When analyzed by PFTs, herbaceous plants did not show significant enhancement across all the experimental durations or difference in biomass responses to warming

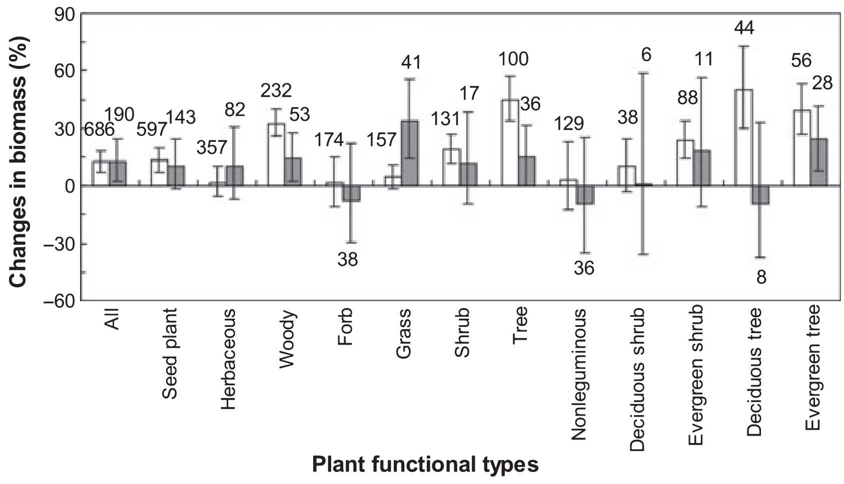

Fig. 2 Comparisons between above- (open bars) and below-ground (closed bars) biomass responses to warming within each plant functional type (PFT). Values are means ± 95% CI. Numbers of observations are shown near the bar.

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Table 3 Between-group heterogeneity (Q_b) and probability (P) of warming effects on biomass across different plant parts and tissue types within each plant functional type (PFT)

	Above- vs below-ground		Tissue types[1]	
PFTs	Q_b	P	Q_b	P
All	0.0	0.95	4.3	0.23
Seed plant	0.2	0.68	5.3	0.15
Herbaceous	0.7	0.39	0.6	0.91
Woody	5.9	< 0.05	10.6	< 0.05
Forb	0.4	0.54	11.0	< 0.05
Grass	8.8	< 0.01	13.6	< 0.01
Shrub	0.4	0.55	4.7	0.19
Tree	9.2	< 0.01	13.8	< 0.01
Nonleguminous	0.6	0.45	11.3	< 0.05
Deciduous shrub	0.2	0.65	3.2	0.37
Evergreen shrub	0.1	0.73	3.1	0.38
Deciduous tree	8.1	< 0.01	31.9	< 0.001
Evergreen tree	2.1	0.15	3.5	0.32

[1]Tissues types include leaf, root, shoot, and stem.

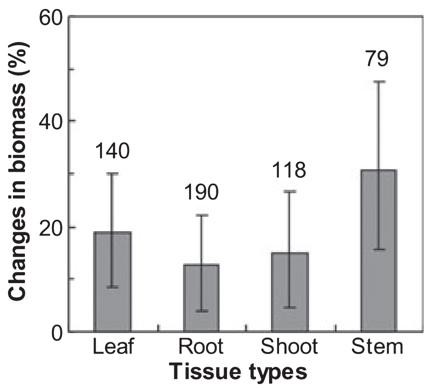

Fig. 3 Percentage changes in biomass as a result of warming for different tissue types across all the terrestrial plants. Values are means ± 95% CI. Numbers of observations are shown above the bar.

between any two experimental durations (Q_b = 5.1, P = 0.40; Fig. 5d, Table 4). Woody plants positively responded to the warming treatments at experimental durations of ≤ 12, 12–24, 24–36, and 48–60 months, with significant differences only between the durations of ≤ 12 and 36–48 months (Fig. 5d). Moreover, warming effects on biomass did not differ between herbaceous and woody plants when experimental duration was > 12 months, but woody plants were simulated more than herbaceous plants when the duration was < 12 months (Fig. 5d).

Effects of other treatments on plant biomass responses to warming

We examined the effects of other treatments (including CO_2 enrichment, N addition, drought, and water addition) on the biomass responses of terrestrial plants to experimental warming. Across all the terrestrial plants, the additional treatments did not affect biomass responses to warming (Fig. 6, Table 4). Although the homogeneity test of the warming effects on biomass between with and without N addition shows significant differences (Q_b = 4.5, P < 0.05; Table 4), biomass responses to warming with and without N addition did not differ from each other, with their 95% CIs overlapping (Fig. 6).

Discussion

The overall warming effects on terrestrial plant biomass

The overall warming-induced stimulation of terrestrial plant biomass (+12.3%, with a 95% CI of 8.4–16.3%) in this study is smaller than the stimulation (+19%) of plant community productivity in a previous meta-analysis (Rustad *et al.*, 2001). The latitude range of experimental sites in our analysis was from 64.78°S to 78.93°N, which is similar to that of Rustad *et al.* (2001). However, more studies, especially at the low latitudes, were included in our analysis. The smaller warming effects at the lower than at the higher latitudes (Fig. 4a) might partially explain the relatively low plant biomass response illustrated in this study.

Plant biomass responses to warming varied with PFTs

The biomass responses of terrestrial plants to warming were strongly dependent upon PFTs in spite of the overall positive warming effects on biomass across all the terrestrial plants included (Fig. 1). The positive biomass responses to warming in most PFTs revealed in this study are consistent with the conclusions of Dormann & Woodin (2002). Our findings that climate warming stimulated seed plant biomass but suppressed the growth of spore plants (Fig. 1) provide further support for the hypothesis that decline in lichen biomass and/or abundance is a function of the increases in vascular plants (Cornelissen *et al.*, 2001). The negative warming effects on spore plants could have been attributable to warming-induced decreases in relative humidity and/or soil moisture (Potter *et al.*, 1995; Day *et al.*, 2009); and negative impacts imposed by vascular plants on the growth of nonvascular plants (e.g. lichen; Cornelissen *et al.*, 2001).

In seed plants, biomass responses to warming still varied among PFTs (Fig. 1). Our findings that greater warming-induced stimulation occurred in woody biomass than in herbaceous biomass are inconsistent with those in a previous meta-analysis, in which no difference in the warming effect on plant biomass was detected between herbaceous and woody plants (Dormann & Woodin, 2002). The positive response of grasses and herbaceous plants to warming (Fig. 1) found in this study is also smaller to the stimulation

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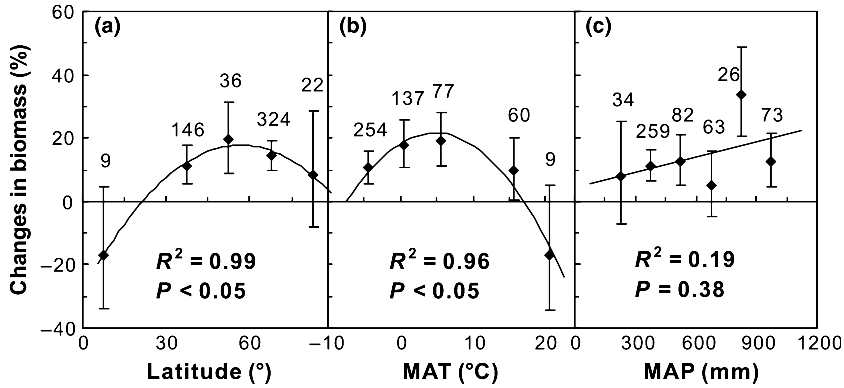

Fig. 4 Relationships between terrestrial plant biomass responses to climate warming and latitude (a), mean annual temperature (MAT) (b), and mean annual precipitation (MAP) (c). Values are means ± 95% CI. Numbers of observations are shown above each point. The equations for the relationships of warming effects (%) with latitude and MAT are $y = -0.0144x^2 + 1.6265x - 28.368$ and $y = -0.1452x^2 + 1.3903x + 18.268$, respectively.

Table 4 Between-group heterogeneity (Q_b) and probability (*P*) of warming effects on biomass across levels of different independent variables and other treatments for all plants, herbaceous and woody species

		All plants		Herbaceous species		Woody species	
Variables[1]		Q_b	*P*	Q_b	*P*	Q_b	*P*
Latitude		12.1	< 0.05	29.0	< 0.001	3.1	0.21
MAT		14.3	< 0.01	17.6	< 0.01	17.8	< 0.001
MAP		22.9	< 0.001	2.1	0.71	14.8	< 0.05
Warming magnitude		6.5	0.26	9.4	0.09	57.3	< 0.001
Experimental duration		9.2	0.10	5.1	0.40	11.8	< 0.05
Other treatments[2]	CO_2	0.2	0.67				
	N addition	4.5	< 0.05				
	Drought	2.0	0.16				
	Water	0.7	0.40				

MAT, mean annual temperature; MAP, mean annual precipitation.
[1]See class levels of each variable except other treatments in Table 1.
[2]There were no enough data for further division into herbaceous and woody species.

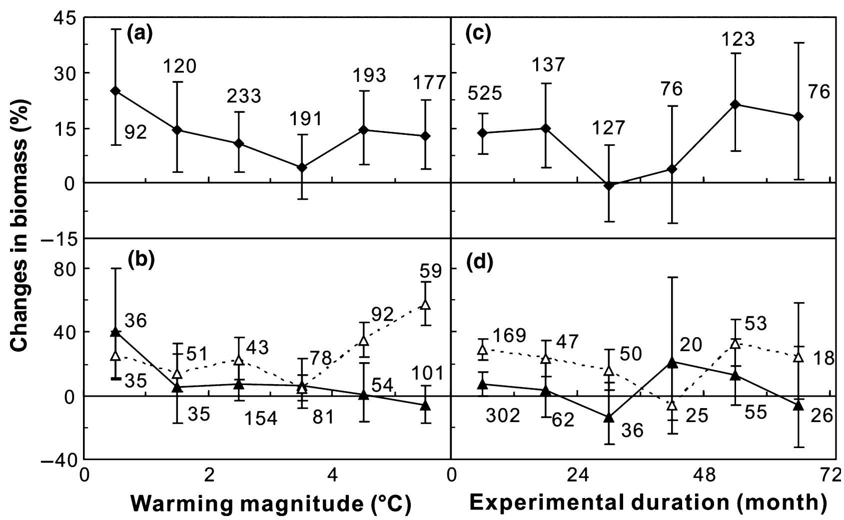

Fig. 5 Percentage changes in biomass as a result of warming for all terrestrial plants (a, c) and herbaceous (closed triangles) and woody plants (open triangles) (b, d) under different warming magnitudes (a, b) and experimental durations (c, d). Values are means ± 95% CI. Numbers of observations are shown near each point.

of grass biomass (*c.* 50%) in the Arctic region reported in Dormann & Woodin (2002). In our analysis, we included more individual studies at the lower latitudes, where biomass of herbaceous plants was reduced by warming (Fig. S5a). This may partially explain the disparity because there are similar response magnitudes in Dormann & Woodin (2002) and at the higher latitudes in our study (Fig. S5a).

Woody plants were more favored than herbaceous plants under climate warming, with trees benefiting most among the four functional groups of woody and herbaceous plants (Fig. 1). Although litter decomposition may also be

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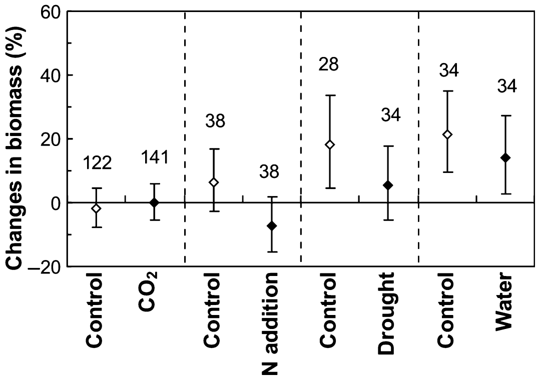

Fig. 6 Plant biomass responses to warming with (CO_2 enrichment [CO_2], nitrogen [N] addition, drought, and water addition) and without (control) other treatments for all terrestrial plants. Values are means ± 95% CI. Numbers of observations are shown near each point. In our analysis, CO_2 concentrations under CO_2 enrichment treatments ranged from 480 to 800 ppm. In addition, because of different levels of treatments (e.g. CO_2 enrichments), observation numbers without other treatments (control) might be smaller than those with other treatments.

accelerated by elevated temperature, litter of woody plants is more recalcitrant and therefore has a longer resident time than that of herbaceous plants (Hobbie, 1996). Consequently, more C will be sequestered in woody plant biomass and lasts for a longer time, suggesting that woody vegetation plays a more important role than herbaceous vegetation in mitigating the rising concentrations of atmospheric CO_2 under climate warming (Cornelissen *et al.*, 2007).

Suding *et al.* (2005) have predicted that the advantage of leguminous over nonleguminous species will be lost when N availability increases as a result of accelerated rates of N mineralization under climate warming (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Miller *et al.*, 2007). Our findings of a tendency for leguminous forb biomass to reduce and nonleguminous forb biomass to increase under warming (Fig. 1) partially support the prediction. However, no difference from zero or from each other in the biomass responses to warming between leguminous and nonleguminous forbs was detected (Fig. 1, Table 2). Biomass (Dormann & Woodin, 2002) and canopy height and cover (Walker *et al.*, 2006) of deciduous and evergreen shrubs have been reported to increase significantly under warming irrespective of a nonsignificant difference between the two PFTs. A recent study also suggests that cover and biomass of deciduous shrubs, but not other shrubs, will be increased by warming (Rinnan *et al.*, 2009). By contrast, greater warming-induced stimulations of biomass were detected in evergreen shrubs than in deciduous shrubs in our analysis (Fig. 1). The inconsistency could be attributable to the spatial variations in plant functional traits (e.g. plant growth rates) and variable drivers of plant C uptake traits across different regions (De Deyn *et al.*, 2008). In comparison with previous studies (Rustad *et al.*, 2001; Dormann & Woodin, 2002; Walker *et al.*, 2006) in which most data were collected from the Arctic region, more data from other regions were included in this meta-analysis. For example, our meta-analysis included more studies on evergreen shrubs at the mid-latitudes in the northern hemisphere (Table S1) and the positive warming effects on plant growth were greater at the mid-latitudes (Fig. 4a).

Biomass responses to warming varied among plant parts and tissue types

The finding of no difference in the warming-induced responses between above- and below-ground biomass across all terrestrial plants observed in this study (Fig. 2) seems to contradict the assumption that below-ground partitioning of plant biomass increases with MAT (Litton & Giardina, 2008). However, differential responses to warming between above- and below-ground biomass were found in some PFTs (Fig. 2), suggesting that below-ground partitioning of terrestrial plants under climate warming is also functional type-specific. In our analysis, greater warming-induced stimulation of above- than below-ground biomass was found for woody plants, especially for trees (Fig. 2). Our results imply that more resources will be allocated to above-ground growth, and therefore above-ground competition for resources, such as light, will be more important for woody species (Suding *et al.*, 2005) under climate warming. By contrast, greater enhancement of below-ground than above-ground biomass under warming occurred in grasses (Fig. 2). Three possible reasons could help to explain the discrepancy. First, in comparison with trees, grasses have shallow root distributions (Jackson *et al.*, 1996), cannot utilize water in the deep soil, and are thus more sensitive to changes in water availability in the topsoil. Reduced water availability in the surface soil under experimental warming (Harte & Shaw, 1995; Wan *et al.*, 2005; Niu *et al.*, 2008) results in greater resources partitioned to below-ground roots in grasses to seek for more water. Second, stimulation of woody species is significantly greater in above-ground than below-ground biomass under global N enrichment, but no similar pattern is observed in herbaceous species (Xia & Wan, 2008). In addition, climate warming is predicted to increase soil N mineralization rates and availability (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Miller *et al.*, 2007). Therefore, woody plants and grasses show differential responses of below-ground partitioning under experimental warming. Finally, in ecosystems where herbaceous and woody plants coexist, greater biomass stimulation of woody than of herbaceous species may lead to suppressed growth, especially above-ground growth, of herbaceous species via a shading effect (Castro & Freitas, 2009).

Although different plant tissues function differently from each other, no difference in the warming responses among

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tissue types across all the terrestrial plants or within any PFT (i.e. seed plants, herbaceous and woody plants) has been found in this study (Figs 3, S3, Table 3). However, significant differences in the biomass responses to warming among tissue types in some narrow PFTs (e.g. forbs) suggest that responses of plant allocation to warming are dependent upon functional type.

Dependence of warming responses of plant biomass upon latitude, MAT, MAP

It is assumed that high-latitude ecosystems in the northern hemisphere are more affected by climate warming because of greater warming rates (Root *et al.*, 2003; Parmesan, 2007). A previous meta-analysis has demonstrated that the high-latitude tundra is more positively affected by climate warming than the low-latitude grasslands and forests (Rustad *et al.*, 2001). The positive effects of experimental warming on plant above-ground biomass also decline with increasing temperature in European shrublands (Peñuelas *et al.*, 2004). We observed an increasing warming effect on terrestrial plant biomass with latitude from 0 to 60° (Fig. 4a). However, the quadratic relationship between the warming responses of terrestrial plants and latitude revealed in our analysis (Fig. 4a) suggests that plants at the mid-latitudes would benefit most from climate warming. The negative impacts of climate warming on biomass accumulation at low latitudes could be attributed to warming-exacerbated water limitation (Clark, 2004; Peñuelas *et al.*, 2004) and increased plant respiration/photosynthesis ratio (Atkin *et al.*, 2007). Climate change-induced mortality of sub-tropical trees (Adams *et al.*, 2009) and dieback of tropical forests (Malhi *et al.*, 2009) support this argument. The quadratic response of plant biomass to warming along the MAT gradient (Fig. 4b) is consistent with that along the latitude gradient. This response pattern is largely caused by woody plants (Fig. S5b). It has been reported that annual diameter increments of tropical trees negatively depend upon the annual mean of daily minimum temperature (Clark *et al.*, 2003). The quadratic responses of plant biomass to warming along the latitude and MAT gradients support, at least partly, our first hypothesis and will facilitate model simulation of terrestrial vegetation and C cycling under climate warming.

The finding of no clear trend in the warming response of either herbaceous or woody plants along the MAP gradient (Fig. S5c, Table 4) suggests that responses of terrestrial plants to warming are insensitive to variations in water conditions. The finding of no impact of either drought or watering treatment on the warming responses of terrestrial plant biomass (Fig. 6, Table 4) supports this speculation but is contradictory to our second hypothesis. The greater warming-induced stimulation of biomass at MAPs of 750–900 mm (Fig. 4c) could have been caused by the fact that most plants in this MAP range were woody plants (Table S1), which were more favored under warming (Fig. 1). In spite of the independence of the terrestrial plant responses to climate warming upon the current precipitation conditions, the concurrent effects of climate warming and changes in precipitation patterns (Knapp *et al.*, 2008) should be taken into consideration.

Biomass responses change with warming magnitudes but not experimental duration

The finding of no difference in the warming responses of terrestrial plant biomass among different magnitudes of temperature increase (Fig. 5a) is consistent with the results reported by Rustad *et al.* (2001). However, our results showed that warming enhances the biomass of herbaceous plants more at the smallest warming magnitude (≤ 1°C) and that of woody plants more at a relatively large warming magnitude (> 4°C; Fig. 5b). Moreover, the warming response of herbaceous plants did not differ from that of woody plants at the relatively small warming magnitude (i.e. ≤ 4°C), whereas woody plants were more favored than herbaceous plants at the relatively large warming magnitude (i.e. > 4°C) (Fig. 5b). The results suggest that woody plants will be more stimulated than herbaceous plants if global mean temperature continues to increase.

Warming responses of plant growth may vary with time because thermal sensitivity of plants differs among growth stages. Indeed, Arft *et al.* (1999) have reported that plant-growth responses to warming are significantly positive in the first 3 yr, but not in the fourth year. Chapin *et al.* (1995) also found differential warming responses in the short (< 3 yr) and long term (> 3 yr). However, no difference in biomass response to warming was found between any two experimental durations for all the terrestrial plants and herbaceous plants in our study (Fig. 5c,d, Table 4). Our observations are consistent with the results of Rustad *et al.* (2001) and Dormann & Woodin (2002). Significant differences in the biomass responses of woody plants to warming across a range of experimental durations are the result of the lower effects at a duration of 36–48 months. Although plant morphology and characteristics (e.g. determinate vs indeterminate growth) would result in differential biomass responses to warming among plant species over time (Bret-Harte *et al.*, 2001, 2002), no effect of experimental duration was detected in our study (Fig. 5c,d, Table 4). Moreover, greater positive warming effects in woody than herbaceous plants occurred at the shortest duration (≤ 12 months) only, but not at the longer durations (> 12 months; Fig. 5d), suggesting that woody plants are more sensitive to climate warming than herbaceous species in the short term. This speculation still contrasts with the prediction that woody plants with indeterminate growth would take a longer time than herbaceous plants with determinate growth (e.g. grasses with their

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intercalary meristems) to respond to environmental changes, such as climate warming and nutrient addition (Bret-Harte *et al.*, 2001, 2002).

Impacts of other treatments on plant biomass responses to warming

Ecosystem responses to future climate change involve multiple environmental factors, rather than just climate warming or increases in atmospheric CO_2 concentration (Norby & Luo, 2004). In this meta-analysis, the warming effects on terrestrial plant biomass were unaffected when other treatments (CO_2 enrichment, N addition, drought, and water addition) were included. In the groups with and without CO_2 enrichment, we found that warming effects on terrestrial plant biomass were not different from zero or from each other (Fig. 6). The finding of no response of plant biomass to warming in this group was inconsistent with the overall positive warming effects across all the plants, and could be ascribed to the fact that most species in this group were herbaceous plants (Table S1) which showed smaller enhancement than woody plants (Fig. 2). The neutral effects of elevated CO_2 on the warming responses of terrestrial plants could be accounted for by the increasing optimal temperature for light-saturated rates of plant leaf CO_2 uptake with rising atmospheric CO_2 concentrations (Long, 1991). The finding of little effect of atmospheric CO_2 enrichment and N addition (Fig. 6) on the warming responses of terrestrial plant biomass does not support the third hypothesis that both CO_2 enrichment and N addition will enhance the positive response of terrestrial plants to climate warming.

Given that water is also an important factor for terrestrial plant growth and that soil moisture has been observed to decrease under experimental warming (Harte & Shaw, 1995; Wan *et al.*, 2005; Niu *et al.*, 2008), warming responses of terrestrial plant biomass are expected to change with water availability. However, our results have demonstrated that warming effects on biomass are independent of water conditions (Fig. 6), which is consistent with previous studies (Dormann & Woodin, 2002; Shevtsova *et al.*, 2009). In addition, the finding of no change in the warming effect on biomass of herbaceous or woody plants along the MAP gradient (Fig. S5c, Table 4) provides further support for this. The observations are not in agreement with our second hypothesis. Both strengthening and weakening of warming effects at the species level (Shevtsova *et al.*, 2009) might help to explain the lack of dependence of warming effects on water conditions.

Conclusions

Results in this and previous meta-analyses (Arft *et al.*, 1999; Rustad *et al.*, 2001; Dormann & Woodin, 2002; Walker *et al.*, 2006) have revealed that warming generally increases terrestrial plant biomass, indicating enhanced terrestrial C uptake via plant growth and NPP. The dependence of the warming responses of plant biomass on PFTs, plant parts, geographic and climatic factors (e.g. latitude, MAT) and warming magnitudes, but not experimental durations or the other treatments (CO_2 enrichment, N addition, drought, and water addition), suggests complexity and challenges in seeking general patterns of terrestrial plant growth in a future, warmer world. The functional type-specific response patterns of plants are critical for obtaining credible predictions of the changes in plant community structure, vegetation dynamics, biodiversity, and ecosystem functioning of terrestrial biomes under climate warming.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Responses of terrestrial plant biomass to climate warming by using only one comparison from a published study for each plant functional type (PFT).

Fig. S2 Comparisons of terrestrial plant biomass responses to climate warming between field and pot experiments within each plant functional type (PFT).

Fig. S3 Comparisons of terrestrial plant biomass responses to warming among different tissue types within each plant functional type (PFT).

Fig. S4 Impacts of facilities on biomass responses of terrestrial plants to warming.

Fig. S5 Relationships between biomass responses to warming and latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) for herbaceous and woody species.

Notes S1 A list of studies used in the meta-analysis.

Table S1 Raw data in Excel format used in the meta-analysis

Table S2 Species included in the meta-analysis

Table S3 Between-group heterogeneity (Q_b) and probability (P) between field and pot experiments within each plant functional type (PFT)

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