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Leaf respiration/photosynthesis relationship and variation: an investigation of 39 woody and herbaceous species in east subtropical China

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Abstract Thirty-nine plant species including woody and herbaceous species grown in wet and warm subtropical regions were collected and classified into woody and herb functional groups. Net photosynthesis (P_n) and dark respiration (R) were measured at constant 25°C under neither water nor nitrogen limited condition to assess whether the R/P_n ratio was constant across different species and functional groups. Our results suggest that P_n and R were highly skewed among the 39 species, ranging from 5 to 25 and 1 to 5 μmol m^{-2} s^{-1}, respectively, while R/P_n ratio was normally distributed at 0.1–0.3. Mean R/P_n ratio was 0.19 for 39 species, and 0.20 and 0.18 for woody and herbs, respectively, showing no significant difference between the two groups. Leaf P_n, R, and R/P_n ratios exhibited large variations across 39 species while R/P_n ratio in our subtropical species was considerably higher than other studies. Our results also indicated that the difference within each group was even larger than between the two groups. Based on the pooled data set at global scale, and considering R/P_n ratios performance under a combination of wet and warm conditions, the mean R/P_n ratio of 0.19 fell between the R/P_n ratio of 0.23 under dry and warm conditions and the R/P_n ratio of 0.07 under cold regardless of the precipitation conditions. The comparison with published data sets indicated significant effects of long-term precipitation and temperature on leaf R/P_n ratios at global scale, and we found that the plants adapting to warm and wet climates including our thirty-nine species tend to have a lower R/P_n ratio.

Keywords Leaf traits · Carbon use efficiency · Greenhouse · Functional groups · Global

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Introduction

Terrestrial ecosystem carbon (C) sequestration can slow down the increase of greenhouse gases in the atmosphere and therefore plays an important role in global carbon cycle (Fang et al. 2003; Liu et al. 2006). Carbon use efficiency (CUE), at large scale, calculated as the ratio of net primary production (NPP) to gross primary production (GPP) can be used to describe the carbon flux efficiency from atmosphere to terrestrial biomass (DeLucia et al. 2007). On the

leaf scale, the ratio of leaf R to P_n (R/P_n ratio) is also an important indicator of the leaf carbon balance (Dewar et al. 1999; Atkin et al. 2006). Leaf net photosynthesis (P_n) and dark respiration (R) are the two most fundamental plant physiological processes and therefore can affect the carbon cycle at scales ranging from the leaf to the globe (Reich et al. 1998a; Cavaleri et al. 2008).

Ecosystems in the middle and high latitudes of the Northern Hemisphere act as significant carbon sinks (Fang et al. 2005). There have been many studies investigated the carbon flux within tropical, temperate, and boreal regions (Sundquist 1993; Dixon et al. 1994; Chave et al. 2003; Martin et al. 2003; Houghton 2005). However, the carbon budget in China's humid subtropical region has received little attention until recently (Zhang et al. 2007), not to mention leaf CUE, i.e., leaf-level R/P_n ratio that influence carbon budget in terms of sinks or sources at large scale (Wright et al. 2005). Thus, our study site (typically east subtropical China) can make a great contribution to the global climate modification on P_n, R and R/P_n and fill part of the gap.

It has been reported that leaf R correlates with P_n at global scale (Loveys et al. 2003; Wright et al. 2004b; Atkin et al. 2006), but only a limited number of studies have focussed on leaf R/P_n ratio, to determine whether it can be conserved constant in species experiencing different environments. There is ongoing debate as to whether R/P_n ratio is constant among different species. Previously, Wright et al. (2004b) found the P_n–R relationships in an examination of a global data set irrespective of the different functional group, but without wide support from studies of seedlings. Some works contend that instantaneous R/P_n ratio in leaves is usually constant, even in plants experiencing contrasting growth temperatures (Dewar et al. 1999; Loveys et al. 2003; Atkin et al. 2006). However, other results have confirmed that growing under elevated CO_2, while increasing photosynthesis, does not always produce large increases in leaf R that may lead to varied R/P_n ratios (Griffin et al. 2001; Davey et al. 2004). This suggests that both P_n and R are sensitive to ambient environment conditions such as temperature, CO_2 concentration, light, etc., and that species' respective characteristics adapt to various conditions, including light, temperature, nutrition, atmospheric CO_2, etc., which may result in changes in R/P_n ratios at leaf level (Reich et al. 1998a; Hartley et al. 2006; Atkin et al. 2007; Zaragoza-Castells et al. 2007, 2008; Yamori et al. 2009).

This study attempts to assess the R/P_n ratios paradigm across different climatic regions using our greenhouse experiment result of 39 woody and herb species grown in wet and warm climatic conditions, which are prevalent in humid subtropical regions. Our study is unique because 39 species of both broad-leaved woody and herb species were experimentally measured, including some endangered plants (i.e., *Mosla hangchowensis*) and endemic species (i.e., *Chimonanthus zhejiangensis*) in subtropical regions. The objectives of our study are to: (1) determine whether there are significant differences in R/P_n ratios across the different species and plant functional types, and (2) to examine how and to what extent site mean annual precipitation (MAP) and mean annual temperature (MAT) modifies R/P_n ratios across 323 species obtained from the worldwide available literature and data sets.

Methods and materials

Sites and species

This research was conducted at the greenhouse on the campus of Zhejiang University (120°12′E, 30°19′N), Hangzhou, Southeast China (Fig. 1). The region has a continental climate, with MAT of 17.5°C and MAP of 1,350 mm (Hangzhou Statistical Yearbook 1997–2006).

Plants were collected from the eastern subtropical region of China. The 39 species represent a range of growth forms, including woody and herb plants. The woody plants were two-year-old evergreen seedlings that germinated from seeds in the greenhouse and new leaves grew out in spring and were near maturation when measured. Five

Fig. 1 Climate diagram of Hangzhou, Zhejiang. Showing seasonal patterns of temperature and precipitation (drawn as per Walter 1979)
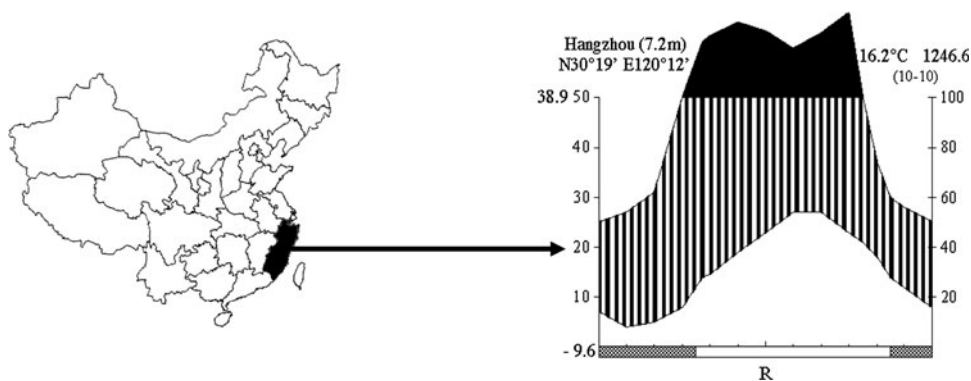
Mosla species are also germinated from seeds; in mid-March 2007 in trays of peat (Sunshine Mix 6, Sun Gro Horticulture Canada Ltd., Canada) and maintained in growth chambers with a 16-h photoperiod, day/night temperatures of 25/15°C and 70–80% relative humidity and irradiance ($\lambda = 400$–700 nm) of ca. 25 μmol photon m^{-2} s^{-1}. When the height of seedlings reached about 5 cm, they were transplanted to pots having 10.8 cm bottom diameter by 21 cm top diameter with 15.8 cm height and 120 g commercial peat, vermiculite and perlite mixture at a volume ratio of 10:7:3 in April 2007 in the greenhouse. Other 18 herbs were collected in the campus of Zhejiang University in Hangzhou which are not planted by people and then transplanted into pots of 10.8 cm bottom diameter by 21 cm top diameter by 15.8 cm height from habitats with the original undisturbed soil. All the species were grown for 10 weeks under well-watered and nitrogen supply (35 kg ha^{-1}) condition and placed at constant 18°C, 12 h d^{-1} under 600 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD), which simulated the natural condition.

Leaf gas exchange measurement

A portable gas exchange system (model LCA-4, ADC, Hoddesdon, UK) was used to measure leaf P_n and R. CO_2 concentration was maintained at 380 μmol mol^{-1}. Leaf gas exchange was measured from 9:30 to 13:00 hours for P_n and from 19:00 to 22:30 hours for R both at 25°C in late April and May. P_n was measured at saturating or near-saturating light conditions (PPFD > 1,000 μmol m^{-2} s^{-1}). Prior to R measurements, plants were kept in an entirely darkened growth chamber for more than 30 min. Two mature leaves were randomly chosen and measured near the top of the whole plant in each of three to four replicate plots for a species. P_n and R were calculated based on leaf area (μmol m^{-2} s^{-1}).

Data compilation

To compare our results with those of other studies conducted in other climatic regions, data were compiled from a number of published sources (Kitajima et al. 1997; Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005) (Supplementary material). Articles were identified that reported leaf R and P_n measured on non-senescent, fully expanded leaves at 25°C. The species were studied in their natural habitats or grew in chambers which simulating the natural environment. Leaf gas exchange measurement was conducted on leaves temporarily elevated to a standard temperature (25°C) before measurement. The studies had to provide P_n measurements made under saturated irradiance. Papers that relied on model estimates and theoretical calculations alone were excluded. All studies selected for

the data compilation were conducted on site, allowing climate data such as MAP and MAT to be associated to each site. Long-term climate data (temperature and precipitation) were also obtained from the published data in the literatures.

Data analysis

In the statistical analyses, individual data points represent average values for a single species at three to four replications. Normality of the data set was tested by the Shapio–Wilks test using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA). We used log_{10} transformation to normalize the distributions, a common practice in large-scale ecological studies (Sterner and Elser 2002; McGroddy et al. 2004; Reich and Oleksyn 2004; Wright et al. 2004b). Analyses were performed to test whether the slopes of the P_n–R relationship varied between woody and herb groups. Average P_n, R, and R/P_n ratios for the 39 species and for two functional groups and two data sets were compared by t test. One-way ANOVA followed by multiple comparison tests (Games–Howell test when variances were deemed heterogeneous with Levene's test; LSD test when variances were deemed homogeneous) was used to test the difference in P_n, R, R/P_n ratios within each group.

The bivariate relationship of P_n and R across different groups was analyzed by fitting standard major axis (SMA) lines (Wright et al. 2004a). Both correlation coefficients (r) and SMA slopes were calculated using a DOS-based computer package, (S)MATR (Falster et al. 2003). In this program, heterogeneity between SMA slopes is tested via a permutation test. Where deemed non-heterogeneous, a common SMA slope is estimated using a like-hood-ratio method (Warton and Weber 2002). Differences in SMA elevation (intercept) can then be tested with the SMA analog of standard analysis of covariance (ANCOVA). All data are presented as mean ± standard error (SE), and statistical significance was determined at $\alpha = 0.05$. Climatic variables, including MAP and MAT, were selected as the major climatic factors for the multiple regression analysis using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA). (Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005).

Results

Differences in P_n, R, and R/P_n ratios across 39 species in humid subtropical areas

Among the 39 species measured, the mean area-based P_n, R, and R/P_n ratios of each species exhibit large variations,

Fig. 2 Net photosynthesis (P_n), dark respiration rate (R) and respiration to photosynthesis ratios (R/P_n ratios) value of 39 species, representing woody plants (**a**, **c**, **e**) and herbs (**b**, **d**, **f**). The x-axis is indicated by the abbreviation of the species name. Species are arranged from left to right on the x-axis by R/P_n ratios ranking (low to high). (Woody: Iin: *Ilex integra*; Cpr: *Chimonanthus praecox*; Esy: *Elaeocarpus sylvestris*; Afa: *Acer fabri*; Dma: *Daphniphyllum macropodum*; Ssu: *Schima superba*; Plo: *Parakmeria lotungensis*; Mfo: *Michelia foveolata*; Cca: *Carya cathayensis*; Sch: *Sinocalycanthus chinensis*; Mpa: *Machilus pauhoi*; Czh: *Chimonanthus zhejiangensis*; Ach: *Altingia chinensis*; Mma: *Michelia maudiae*; Mf: *Manglietia fordiana*; Ppr: *Photinia prunifolia*; Cgl: *Cyclobalanopsis glauca*; Msk: *Michelia skinneriana*; Lme: *Lindera megaphylla*; Csc: *Castanopsis sclerophylla*; Lfo: *Liquidambar formosana*. Herb: Ms: *Mosla scabra*; Rka: *Roegneria kamoji*; Md: *Mosla dianthera*; Rca: *Reineckia carnea*; Mca: *Mosla cavaleriei*; Ite: *Iris tectorum*; Cja: *Cirsium japonicum*; Ila: *Ixeris laevigata*; Sc: *Sambucus chinensis*; Mh: *Mosla hangchowensis*; Pvi: *Plantago virginica*; Mso: *Mosla soochowensis*; Tmo: *Taraxacum mongolicum*; Ean: *Erigeron annuus*; Jef: *Juncus effusus*; Rja: *Rumex japonicus*; Cin: *Canna indica*; Lpe: *Lolium perenne*)
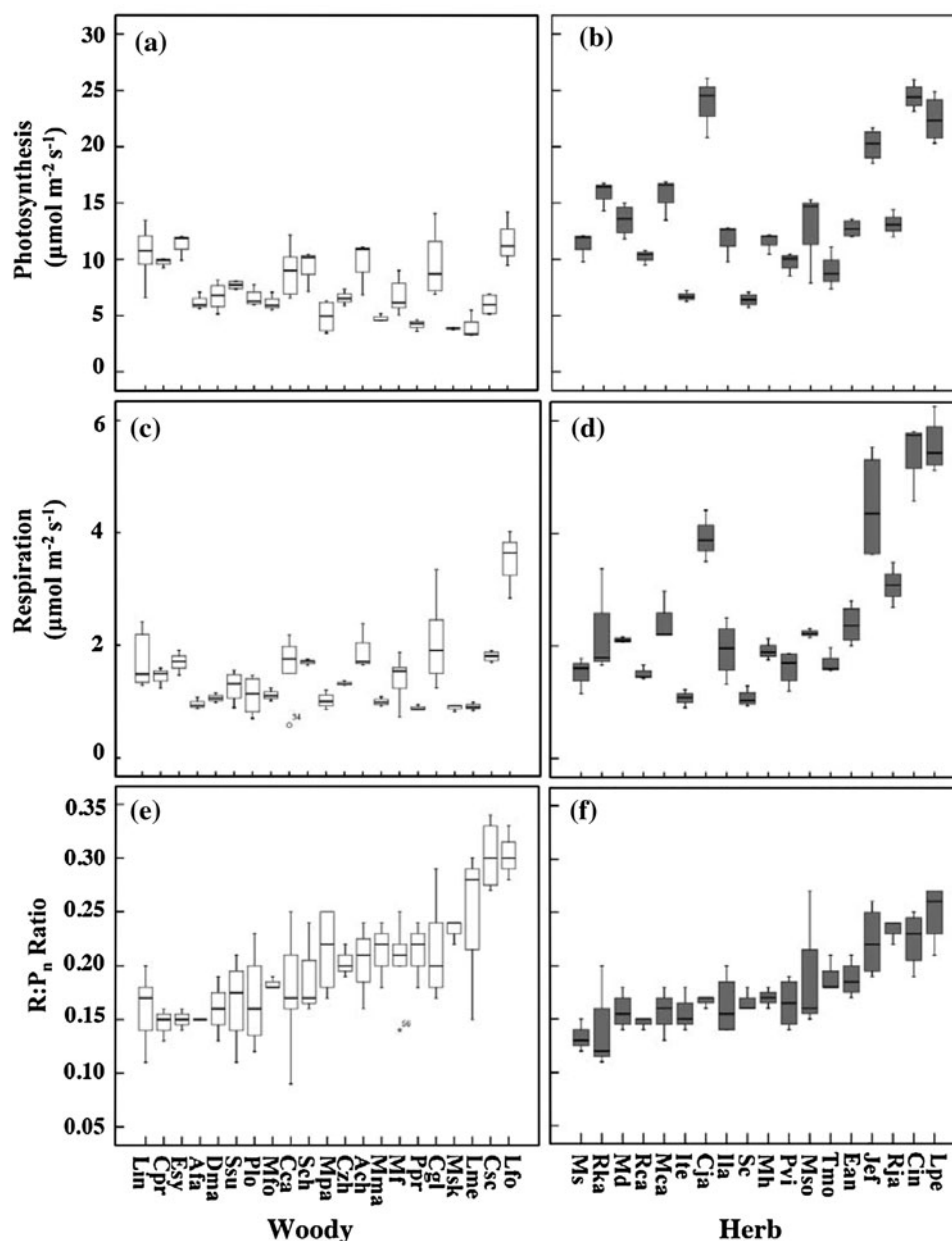
primarily ranging from ca. 4 to 25, 1 to 6, and 0.1 to 0.3, respectively (Fig. 2). The highest P_n is found in *Canna indica* at 24.4 μmol m^{-2} s^{-1}, followed by *Cirsium japonicum* at 23.9 μmol m^{-2} s^{-1}. *C. indica* also has the highest R, and followed by *Lolium perenne* at 5.3 μmol m^{-2} s^{-1}. The broad leaf tree *Michelia skinneriana* has the lowest P_n and the lowest R. The highest R/P_n ratio is found in the tree species *Castanopsis sclerophylla* and *Liquidambar formosana* with a ratio of 0.30. Mean values for P_n, R, and R/P_n ratios among all species are 10.5, 2.0, and 0.19 μmol m^{-2} s^{-1}, respectively (Table 1).

Differences in P_n, R, and R/P_n ratios between woody and herb groups

The 39 species were divided into two major functional groups, woody plants and herbs. Mean value of P_n is 7.5 μmol m^{-2} s^{-1} for the woody group and 14.0 μmol m^{-2} s^{-1} for the herb group (Table 2). However, the woody group has a significantly lower R (1.5 μmol m^{-2} s^{-1}) than the herb group (2.6 μmol m^{-2} s^{-1}, $P < 0.05$). Woody group has an insignificant higher R/P_n ratio of 0.20 compared to 0.18 for the herb group ($P > 0.05$) (Table 1).

Table 1 Mean values of net photosynthesis (P_n), respiration rate (R) and R/P_n ratios for this study and other publications (Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005)

Parameter	Growth form	This study		Publications	
		Mean ± SE	n	Mean ± SE	n
P_n (µmol m^{-2} s^{-1})	Overall	10.50 ± 0.84[B]	39	13.18 ± 0.43[A]	268
	Woody	7.45 ± 0.53[bB]	21	10.59 ± 0.31[bA]	190
	Herb	14.04 ± 1.28[aB]	18	19.47 ± 0.98[aA]	78
R (µmol m^{-2} s^{-1})	Overall	1.99 ± 0.19[A]	39	1.50 ± 0.63[B]	284
	Woody	1.45 ± 0.13[bA]	21	1.39 ± 0.06[bA]	190
	Herb	2.62 ± 0.33[aA]	18	1.78 ± 0.16[aB]	78
R/P_n ratio	Overall	0.19 ± 0.01[A]	39	0.13 ± 0.01[B]	284
	Woody	0.20 ± 0.01[aA]	21	0.14 ± 0.01[aB]	190
	Herb	0.18 ± 0.01[aA]	18	0.10 ± 0.01[bB]	78

Means followed by different lower-case or upper-case letters were statistically different at $P < 0.05$ between functional groups and between our study and other publications by T test, respectively

P_n net photosynthesis, R dark respiration, R/P_n ratio respiration photosynthesis ratio, *SE* standard error

Table 2 Mean values of net photosynthesis (P_n), respiration rate (R), and R/P_n ratios (± SE) for our results and other publications for the two functional groups

Combination	Parameter	Woody	Herb
Dry and warm	P_n (µmol m^{-2} s^{-1})	10.05 ± 0.51	10.90 ± 1.54
	R (µmol m^{-2} s^{-1})	2.06 ± 0.13	3.26 ± 0.46
	R/P_n ratio	0.22 ± 0.01	0.30 ± 0.02
Wet and warm	P_n (µmol m^{-2} s^{-1})	10.60 ± 0.51	12.05 ± 0.85
	R (µmol m^{-2} s^{-1})	1.29 ± 0.07	1.85 ± 0.22*
	R/P_n ratio	0.15 ± 0.01*	0.14 ± 0.01
Cold	P_n (µmol m^{-2} s^{-1})	9.13 ± 0.66	19.61 ± 1.00
	R (µmol m^{-2} s^{-1})	1.00 ± 0.60	1.54 ± 0.09
	R/P_n ratio	0.13 ± 0.01	0.09 ± 0.01
Overall	P_n (µmol m^{-2} s^{-1})	9.78 ± 0.32	15.65 ± 0.70
	R (µmol m^{-2} s^{-1})	1.75 ± 0.08	1.82 ± 0.12
	R/P_n ratio	0.19 ± 0.01*	0.13 ± 0.01

* Significant difference based on the $R–P_n$ regression slope between woody and herb according to SMA

The majority of woody R/P_n ratios are in the range of 0.15–0.22, while relatively lower values are found in the herb group, from 0.1 to 0.18 (Fig. 2). The overlap of R/P_n ratios also revealed a relatively narrow difference between the two functional groups (Fig. 2). However, R/P_n greatly varies within each functional group, from 0.1 to 0.3 in the woody group and from 0.07 to 0.25 in herbs, with significant differences among species within each group (woody: $P < 0.01$, herb: $P < 0.01$) indicating the difference within each group was even larger than between the two groups.

$P_n–R$ relationships of humid subtropical areas compared with global data set

This work presents the survey of leaf P_n and R of the plant species in wet and warm regions. Comparison of our data with the global data set (Table 1), indicates that the present data fall within the global ranges (Fig. 3). Among species, $P_n–R$ relationships were consistent with previous results from the global data set. Overall, the subtropical species in our study had a higher R (2.0 µmol m^{-2} s^{-1}) and lower P_n (10.5 µmol m^{-2} s^{-1}) which lead to a higher R/P_n ratio of 0.19 (Table 1) than global data set ($P < 0.05$). When compared with the global data set for the two functional groups, the SMA slopes between respiration and photosynthesis of woody species were found to be the same between the two data sets (Fig. 3). Furthermore, elevation shifts of the two data set for $R–P_n$ were significant, indicating that subtropical woody species in our study tended to have a higher R at a given P_n. However, the SMA slopes of herbs differed between these two data sets (Fig. 3).

The two climatic variables, MAP and MAT had a direct influence on leaf R/P_n ratios (Wright et al. 2006). To further investigate the influence of MAT and MAP on R/P, the data were divided into wet and dry regions according to a MAP of around 400 mm at global scale, following Lieth (1973, 1975), and divided into warm and cold regions according to a MAT of around 10°C. The pattern of $P_n–R$ relationships was established with regression lines for the 323 species coded into three combinations of temperature and precipitation conditions: combination (1) dry and warm regions (MAP < 412 mm and MAT > 10°C);
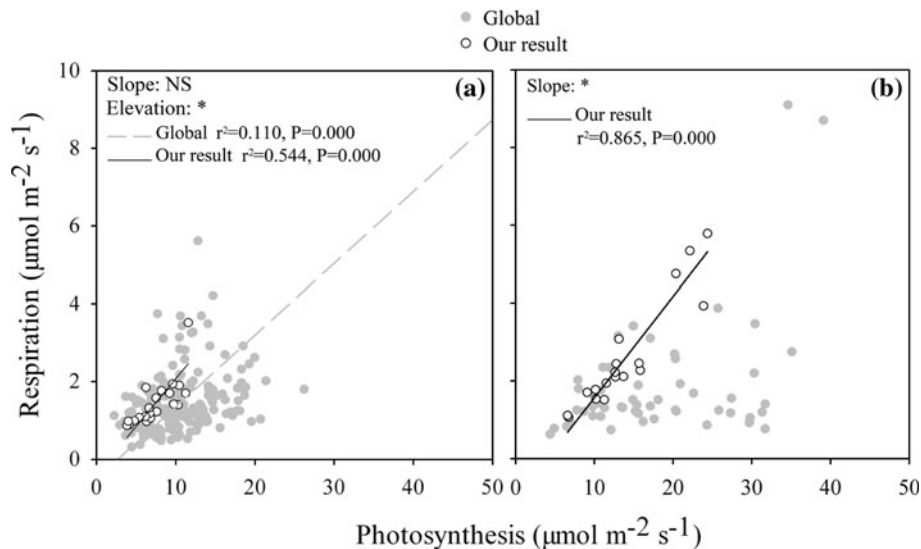
Fig. 3 P_n–R relationships for subtropical species and from global data set (Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005) within **a** woody; **b** herb. Slope, difference in standardized major axis (SMA) slopes; Elevation, difference in SMA elevations; NS, not significantly different; *, significantly different ($P < 0.05$). *Gray circle*: Global data set that collected from published papers and the *dashed line* is trendline indicating standardized major axis (SMA) slope for the global data set when the relationship between respiration and photosynthesis is significant. *Blank circle*: our results of 39 species. And the *solid line* is the trendline standardized major axis (SMA) slope for our results when the relationship between respiration and photosynthesis is significant

combination (2): wet and warm regions (MAP > 680 mm, MAT > 10°C); and combination (3): cold regions (MAT < 10°C) regardless of precipitation.

Of the 323 species, R/P_n ratio increases with increasing drought and warmer temperatures at global scale (Fig. 4; Table 2). The plants grown in dry, warm regions had the highest R/P_n ratio at 0.23, whereas the R/P_n ratio value of 0.19 found in our study fell into the medium humidity and temperature condition at MAP > 680 mm and MAT > 10°C. R/P_n ratio was the lowest in cold regions at around 0.1, with no difference between dry and wet conditions (Fig. 4). We also executed another experiment to investigate the response of photosynthesis and respiration on the same species under drier condition (Unpublished data). As a result, a higher R/P_n ratio was found than for the same species in wet condition (Fig. 4). Values measured in the drier condition well fitted the first combination of dry and warm regions (Fig. 4). We compiled global data set (Kitajima et al. 1997; Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005) with our results and executed the multi regression analysis by SPSS. We found that with increasing drought and warmer temperatures, R/P_n ratio increases at global scale as follows:

$$R = 0.818 + 0.061\,P_n - 0.001\text{MAP}$$
$$+ 0.05\text{MAT} \ \left(r^2 = 0.496,\ n = 323,\ P < 0.005\right) \quad (1)$$

Discussion

Differences in R/P_n ratios between woody and herb species

In our results of 39 species, large variation was observed in leaf P_n and R across functional groups, with woody plants showing significant lower P_n and R than herbs (Fig. 1; Table 1). In common environment, herbs have greater photosynthetic gains and also respiratory costs due to leaf morphology (SLA) and leaf nitrogen (leaf N) on leaf level (Reich et al. 1998a). Galmés et al. (2005) and Delucia et al. (2007) also found a lower R/P_n in herbs, we believe that the difference in R/P_n between functional groups in our study is mainly contributed by the much higher photosynthetic capacity in herbs comparing with the difference in respiration (Table 1). Because of the highly positive correlations between leaf P_n and R, the R/P_n ratios between herbs and woody plants varied less than P_n or R alone (Table 1). However, large differences were found in the global data set in leaf-level R/P_n ratios across functional groups, with woody plants showing obvious higher R/P_n ratios than herbs (Table 1). We believe that different mixes of woody species and herbs occurring at different sites at global scale could contribute to heterogeneity for there was variation in P_n–R relationship and correlation strength with growth form.

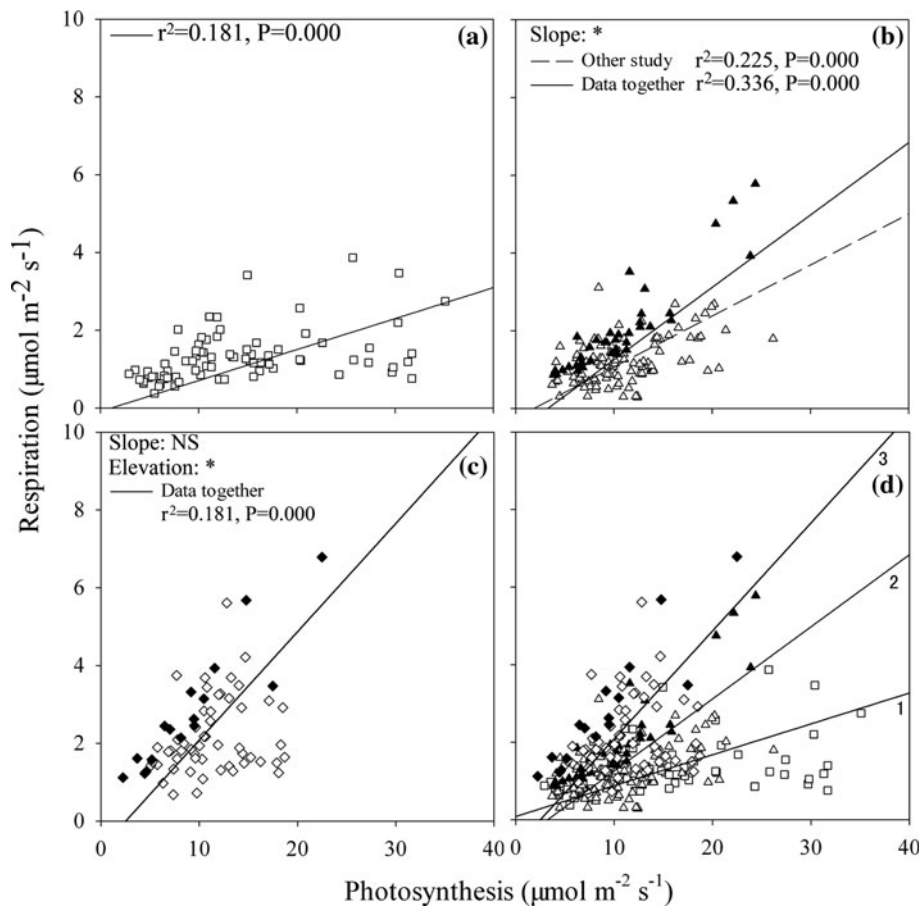**Fig. 4** Scatter plot between leaf R and P_n in three combinations of conditions: **a** cold regions, mean annual temperature (MAT) < 10°C regardless of precipitation; **b** wet warm regions, MAT > 10°C, mean annual precipitation (MAP) > 680 mm; and **c** dry, warm regions, MAT > 10°C and MAP < 412 mm; and **d** for all conditions. Slope, difference in standardized major axis (SMA) slopes; Elevation, difference in SMA elevations; NS, not significantly different; *, significantly different ($P < 0.05$). Line *1*, *2* and *3* represented lines in (**a**), (**b**) and (**c**), respectively. *Blank markers* in (**a**), (**b**), (**c**) and (**d**) represent the compiled data set from published papers. *Dashed line* in (**b**) is the trendline indicating standardized major axis (SMA) slope for the global data set since significant slope difference was found between our study and global data set. *Solid markers* in (**b**), (**c**) and (**d**) represent the results from our study. *Solid lines* represent the trendlines indicating standardized major axis (SMA) slope for all the data (including our results and global data set) in (**a**), (**b**), and (**c**), respectively

Plant functional traits are considered to reflect adaptation to variation in the physical environment and eco-physiological as well as evolutionary trade-offs among different functions within a plant (Cornelissen 1999; Ackerly et al. 2000). The insignificant difference of R/P_n ratios between two functional groups in our study of 39 species may be due to the smaller sample size. In the global scale, woody species holds a significant higher R/P_n ratio (based on the slope of regression between the two) than herb species according to standardized major axis (SMA). Comparing our findings in this study with global data set, the different metabolic characters in potential carbon gains through photosynthesis and losses through respiration plays an important role in the carbon balance of individual plants and lead to uneven carbon distribution in herbs and woody plants.

Furthermore, the range within each group was much larger while no significant difference was observed while comparing the arithmetic means of R/P_n ratios between the two groups (Fig. 2; Table 1). We agreed with He et al. (2006) that the data collection at the genus level with focus only on inter-specific differences may not reflect the actual global patterns among different climatic sites and functional type. Thus, our results also suggest that the comparison of leaf R/P_n ratios should focus on intra- and inter-specific variation. These aspects are to be improved in our future studies.

Differences in R/P_n ratios among all 39 species

As a meaningful indicator of carbon balance at leaf-level, leaf R/P_n ratio is used to examine the feedback between

environmental change and plants productivity (Wythers et al. 2005). In our study, there was a large variation in P_n and R among 39 species. Herbaceous species *C. indica* and *C. japonicum* had a higher P_n for the higher growth capacity (Galmés et al. 2005). R/P_n ratio is normally distributed at around 0.19 among the 39 species, with a linear relationship between P_n and R across 39 species ($r^2 = 0.890$, $P < 0.01$). We found strong correlation between P_n and R that may result from the dependence of respiration on substrate supply that accumulated through photosynthesis processes (Hoefnagel et al. 1998). For the high correlations between P_n and R, R/P_n ratios varied less than P_n or R alone. The relative constancy of R/P_n ratios reflected a fundamental feature in plants with respect to leaf carbon balance.

Our study measured P_n, R, and R/P_n ratios of 39 plants including one-year herbs and seedlings of trees in common garden. The subtropical species reported in this study had a higher R/P_n ratio of 0.19 than global data set (Table 1, $P < 0.05$). In our study of 39 species, the 21 woody seedlings showed lower P_n and higher R, resulting in higher leaf R/P_n ratio (0.20) than mature plants (0.14) of the global data set. There is no evidence to attribute the difference in P_n, R, and R/P_n ratio to the different species age (Campbell et al. 2007). In addition, according to Reich et al. (1998b) studies, the metabolic characters (i.e., P_n, R) were similar for greenhouse grown seedlings with field grown species. So we excluded the possibility that the reason behind the deviation was from natural or artificial environment. Thus, our leaf R/P_n ratios' comparison between common garden and field results is reasonable.

Collectively, the difference in R/P_n ratios between our 39 species and other studies should be attributed to the thermally contrasting sites. The higher R/P_n ratios than other studies, a potential cause for the higher R/P_n ratios in our 39 species may be the subtropical climate with high temperature (Tjoelker et al. 1999). A modified process model also predicted that vegetation in warm regions would have higher leaf R/P_n ratios (Wythers et al. 2005). Although many studies found the evidence of thermal acclimation of P_n and R, a horizontal comparison between plants grown in cold and warm regions demonstrated that cold-developed leaves exhibit a higher P_n rate and lower R rate than warm-developed plants (Wythers et al. 2005; Atkin et al. 2006; Campbell et al. 2007). In addition, there could have different extent of temperature homeostasis among all the species (Yamori et al. 2009). The acclimation of respiration and photosynthesis to the growth environment plays a crucial role in determining the productivity of vegetation (Zaragoza-Castells et al. 2008). Our results demonstrated that the constant R/P_n ratios cannot be warranted across large variance in climate condition at global scale. More details should be investigated on the extent to

which the relationship between P_n and R vary at global scale and which factors behind to drive those variances.

Differences in R/P_n ratios at global scale

In recent years, several studies have documented the relationship between P_n and R at global scale, but details of the R/P_n ratios is still lacking (Wright et al. 2004b; Tjoelker et al. 2005; Turnbull et al. 2005). The data obtained on the 39 species in our study, which were mainly located in subtropical regions, were pooled with a global data set in which measurements had also been made at 25°C to determine leaf R/P_n ratios data for species worldwide.

To pool our data into global scale, our study supported that R/P_n ratio increases at global scale with increasing drought and temperatures. Plants grown in dry, warm regions had the highest R/P_n ratio while in the cold regions had the lowest values. Precipitation ($r^2 = 0.442$, $P < 0.001$) had stronger impact on the relationship between Pn and R than temperature ($r^2 = 0.407$, $P = 0.018$). The weaker influence of MAT in the two climatic variables was consistent with previous study, which suggested that the respiration measured under ambient temperature suffered more from MAT than that measured under standard temperature (25°C here) (Campbell et al. 2007). In drier condition, plants would develop strategies to overcome the arid environment such as closing stomata avoiding water loss. The reduced stomatal conductance resulted by low precipitation and the energy cost during the maintenance of solute gradients under dry habitat could potentially lead to a higher R at a given P_n. In extreme cold regions where MAT < 10°C, regardless of precipitation, plants had a similar R/P_n ratio at around 0.1, which indicated the influence of leaf traits by MAP was weak. Similar result was reported in those studies on the Tibetan Plateau (He et al. 2006). We found that low temperature associated chemical composition and physiological processes increased P_n and resulted in a lower R/P_n ratio, although R measured under 25°C was less impacted in comparison with the ambient temperature (Table 2).

Comparing mean R/P_n ratios between the two functional groups for the three precipitations and temperature combinations, we found that the woody plants had a higher R/P_n ratio than herbs only in warm, wet regions (Table 2). Both the woody plants and herbs show trend discrepancies in their acclimation to long-term temperature changes in the environment, with differences in overall metabolism rates, chemical composition, and leaf structure (Wright and Westoby 2002; Cavender-Bares et al. 2004; Campbell et al. 2007). Therefore, our results supported that R/P_n ratio cannot be conserved among all the species at global scale due to large geographical differences, including precipitation and temperature and also shift in functional group composition.

Our results reported the R/P_n ratios of 39 species in a wet subtropical region, an area where fewer studies have been conducted. By associating R/P_n ratios' variation with precipitation and temperature at the global scale, our results supported the conclusion that R/P_n ratios homeostasis among species and between functional groups cannot be achieved across all climatic conditions. This suggests that large-scale models cannot warrant constant R/P_n ratios across global spatial scales.

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