Regional constraints on leaf physiognomy and precipitation regression models: a case study from China

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The relationship between leaf physiognomy and precipitation has been explored worldwide in regions under different climate conditions. Unlike the linear relationship established between the percentage of woody dicot species with entire margins and mean annual temperature, precipitation has been reported to correlate to different leaf physiognomic characters depending on the region where the correlation is studied. To investigate if precipitation can be calculated from leaf physiognomic characters on the basis of regional sample sites, data from 50 mesic to humid forests in China were analyzed in this study. With data from Chinese forests, the leaf-area analysis based on linear regression between natural logarithms of leaf size and mean annual precipitation (MAP) shows no significant correlation. Both single and multiple linear regression analyses fail to confirm the correlation between leaf physiognomy and precipitation, which may result from the similarity of modern spatial distribution of temperature and precipitation in China. Our results show that, due to variations in climatic conditions among sampling regions, leaf physiognomic characters that correlate to precipitation are not consistent worldwide, and applications of models without considering regional constraints could mislead our understanding of palaeoclimate. Therefore, when choosing a leaf physiognomic model for palaeoclimate reconstructions, it is important to determine if the leaf physiognomy of the palaeoflora lies within the leaf physiognomic spectrum of the model used. • Keywords: palaeoflora, palaeoclimate reconstruction, leaf size, precipitation, CLAMP.

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Proxies play an important role in understanding the climate in the past (National Research Council 2008). The physiognomy of fossil leaf assemblages has been used as a proxy for Cenozoic terrestrial palaeoclimate reconstructions for nearly a century (Bailey & Sinnott 1915, Wolfe 1979, Chaloner & Creber 1990, Wing & Greenwood 1993, Wilf *et al.* 1998, Greenwood 2005, Traiser *et al.* 2007). Studies of modern forests from different regions have demonstrated that leaf/climate relationships often show regional constraints, particularly in the context of univariate analyses (*e.g.*, Wing & Greenwood 1993, Jacobs 1999, Gregory-Wodzicki 2000, Spicer *et al*. 2004, Traiser *et al*. 2005, Miller *et al*. 2006, Steart *et al*. 2010, Su *et al*. 2010, Jacques *et al*. 2011, Jordan 2011). Unlike the correlation between leaf

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physiognomy and mean annual temperature (MAT), relationships between leaf physiognomy and precipitation variables are far from fully investigated (Peppe *et al*. 2011). A further complication is that leaf samples from different regions often yield transfer functions with different leaf physiognomic characters included as independents (Wing & Greenwood 1993, Wilf *et al*. 1998, Jacobs 1999; Table 1).

The main data source to explore leaf and precipitation relationships is from the classical Climate Leaf Analysis Multivariate Program (CLAMP) dataset, maintained at Open University in the UK and the Institute of Botany, Chinese Academy of Sciences (CLAMP 2011). Scores of 31 leaf physiognomic characters and records of 11 climatic parameters were included in each sample. By using the Canonical Correspondence Analysis (CCA), CLAMP can effectively estimate 11 climate parameters such as mean annual temperature (MAT) and growing season precipitation (GSP) if the leaf physiognomic characters of a given palaeoflora are available (Wolfe 1993). Wing & Greenwood (1993) used data from the CLAMP with multiple linear regression analysis (MLR) to quantify the relationships between leaf physiognomy and mean annual precipitation (MAP), precipitation during the 3 consecutive wettest months (3-WET), and precipitation during the 3 consecutive driest months (3-DRY), respectively. Wing & Greenwood (1993) found that, leaf physiognomic character of attenuate apex correlates to MAP, 3-WET and 3-DRY, whereas leaf size correlates to MAP and 3-WET. Wilf *et al*. (1998) used natural logarithm regression analysis (namely leaf-area analysis) to investigate the relationship between leaf size and MAP. They studied 50 forests in North and South America and Africa, and derived a transfer function linking leaf size and precipitation (Wilf *et al*. 1998). Because of the wide range of sampling regions and the high correlation ($r^2 = 0.760$), this function has been widely applied in palaeoprecipitation reconstructions (*e.g*., Gregory-Wodzicki 2002, Gayó *et al*. 2005, Martinetto *et al*. 2007, Greenwood *et al*. 2010, Sunderlin *et al*. 2011). Moreover, in equatorial Africa, the proportion of untoothed margin species is positively correlated with wet months precipitation provided that precipitation is not less than 5 cm per month, while leaf size, particularly in mesophyll size, most strongly correlate with wet months and annual precipitation (Jacobs 1999). However, not all correlations between leaf physiognomy and precipitation are statistically significant, an observation that has been supported by a research from Europe: Traiser *et al*. (2005) noticed that based on European vegetation data, none of these transfer functions can produce reliable precipitation prediction. Peppe *et al*. (2011) studies data from 92 samples on a global scale, they found a low correlation between leaf size and MAP; even when the method of digital leaf physiognomy is used, this correlation increased only slightly.

It is clear that the relationship between leaf physiognomy and precipitation appears more complicated than that between leaf physiognomy and temperature parameters, such as MAT, which usually (but not universally) exhibits a strong linear correlation to the proportion of woody dicot species with untoothed leaves (Wing & Greenwood 1993, Wilf 1997, Gregory-Wodzicki 2000, Greenwood *et al*. 2004, Miller *et al*. 2006, Steart *et al*. 2010, Su *et al.* 2010). The complicated relationship between leaf physiognomy and precipitation may partly be caused by significantly different global precipitation patterns. For example, in southern Europe the precipitation in winter is much higher than that in summer, whereas the precipitation in the Amazon basin is abundant and equally distributes throughout the year (Hijmans *et al*. 2005a). It is reasonable to suppose that distinctive foliar physiognomic adaptations might be required for optimal photosynthetic capacity and competitive survival, and leaf physiognomy should be shaped to maintain the balance of water loss and maintenance. Consequently, precipitation parameters may regionally correlate to several leaf characters (Wing & Greenwood 1993, Jacobs 1999). Phylogeny and leaf habits might be the other factors which influence leaf physiognomy (Little *et al*. 2010, Peppe *et al*. 2011, Royer *et al*. 2012); however, such results are still controversial.

As far as China is concerned, this part of East Asia experiences a strong monsoonal climate characterized by a wet summer and dry winter (Zhang 1991). Based on leaf samples collected from 50 humid to mesic forests across China, Su *et al*. (2010) studied the relationship between the percentage of untoothed leaf margin in woody dicot species and mean annual temperature, and proposed a new regression model relating leaf margin form to MAT, which is statistically different from equations in the slope equality test conducted by sites in other regions worldwide. Subsequently, Jacques *et al.* (2011) plotted these Chinese sites in physiognomic space and found that the Chinese sites are all grouped together and separated away from the group made up of Physg3br sites (fig. 2 in Jacques *et al*. 2011). As Jacques *et al*. (2011) suggested, this phenomenon is most likely affected by the monsoonal climate throughout China. A new calibration for CLAMP has therefore been generated by adding the Chinese sites to the existing Physg3br dataset to form the PhysgAsia1 calibration (PhysgAsia1 calibration files in CLAMP (2011)).

The aims of this study are: 1) to further understand the pattern of leaf physiognomy correlating to precipitation in China; 2) to explore whether models derived from regional data could be reliable for palaeoclimate reconstructions.

Material and methods

Material

In a recent study of the relationship between leaf physiognomy in woody dicots and climate, 50 sites throughout China's humid to mesic forests were sampled following the

CLAMP protocols (Su *et al.* 2010). These 50 Chinese sample sites were chosen from a wide region spreading from southern tropical to northern temperate regions with mean annual precipitation (MAP) > 45 cm, and representing forests experiencing low to minimum direct human impact. The area of every collection site was 1–3 hectares. In each sample site, leaves within the variation of leaf form were collected from every woody dicot species. The number of woody dicot species was no less than 15 in each sample site (Su *et al.* 2010). All field work was carried out in summer and autumn during 2006 to 2008 when all leaves were fully expanded. Based on data derived from these collections, a new leaf margin analysis (LMA) equation was derived to quantitatively reconstruct mean annual temperature (MAT) (Su *et al.* 2010). This equation is statistically different in slope equality test from the traditional East Asian LMA equation and equations derived from other regions (Su *et al.* 2010).

In order to be consistent with the updated definition criterion of each leaf character in CLAMP, Jacques *et al.* (2011) rescored all the leaf characters of each species in 45 sample sites with no less than 20 woody dicot species (available in the file of PhysgAsia1 physiognomic data in CLAMP 2011). Thirty one leaf physiognomic characters and 11 corresponding climatic parameters relating to the 45 sample sites are available on the CLAMP website. Steart *et al.* (2010) argued that a sample site with no less than 15 species are required for single variable linear regression analysis to be statistically valid, so data of the additional five Chinese sample sites with 15~19 species were added in this study (Appendix I). In all, the new calibrated leaf physiognomic data are only slightly different from data used in the original study, such as the percentage of the attenuate apex of leaves (Su *et al.* 2010). Information on the localities of the 50 Chinese sites is available in Su *et al.* (2010). All specimens are deposited in Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences.

Abbreviations. – 3-DRY – precipitation during the 3 consecutive driest months; 3-WET – precipitation during the 3 consecutive wettest months; CCA – Canonical Correspondence Analysis; CLAMP – Climate Leaf Analysis Multivariate Program; CMDSSS – China Meteorological Data Sharing Service System; ESM – Earth Systems Modeling; GSP – growing season precipitation (which is defined by total precipitation with months no less than 10 °C); LMA – leaf margin analysis; MAP – mean annual precipitation; MAT – mean annual temperature; MLR – multiple linear regression; SLR – single linear regression.

Climatic data

This study focuses on the relationship between leaf physiognomic characters and precipitation parameters. There are two ways to get climatic data relating to sample sites: (1) acquiring data directly from the records of the nearest meteorological stations; (2) using climate models or numerical expressions to interpolate data between climate stations. Samples collected for CLAMP should be taken from well preserved natural forests with low human disturbance. Because most of these sample sites are far from climate stations and many Chinese areas are mountainous, neither the direct climatic record nor simple univariate models based on lapse rates could be used to provide precipitation data. The development of gridded climate datasets allows us to estimate local climate conditions (*e.g.*, New *et al.* 1999, 2002; Hijmans *et al.* 2005b). Recently, a global gridded climate resource with 0.166° × 0.166° resolution (New *et al.* 2002) is available on the BRIDGE website (Valdes 2008). In this dataset the climatic information on any sample site can be obtained if data on the latitude, longitude and elevation of the site are all known. We tested the reliability of the gridded data by comparing continuous climate station records from 1961–1990 with calculated data from 401 climate stations in China, and many of these records are available to public recently in China Meteorological Data Sharing Service System (CMDSSS 2012). The results demonstrate that the gridded data can confidently calculate climatic parameters with low estimated errors. For example, the mean absolute error of MAT is 0.632 °C, $p < 10^{-14}$; whereas that of MAP is 9.484 cm, $p = 0.003$. Therefore, we used gridded data to obtain four rainfall-related parameters for all the 50 Chinese sample sites, *i.e.*, mean annual precipitation (MAP), growing season precipitation (GSP), precipitation during the 3 consecutive wettest months (3-WET), and precipitation during the 3 consecutive driest months (3-DRY) (Appendix II). Data for precipitation in all 50 sample sites were extracted from the latest updated data source in 0.166° × 0.166° resolution from the BRIDGE website (Valdes 2008; Appendix II). Data from CLAMP Physg3br, extracted following the same criteria, containing 39 sample sites from Japan and 105 from temperate and tropical America and the Pacific islands of Fiji and New Caledonia were included in this study.

Data analyses

Firstly, leaf-area analysis was used here. In this method, areas of leaf sizes divide into several categories (after Wilf *et al.* 1998). For each category, the mean value of the upper and lower boundary was natural logarithm transformed (Wilf *et al.* 1998). The mean of natural logarithms of leaf areas (MlnA) was calculated using the following formula.

$$M \ln A = \sum a_i p_i \qquad \text{(Wilf } et\ al. \text{ 1998)}$$

Here, a_i is the mean of the natural logarithm area in each of nine leaf size categories in CLAMP (0.41, 2.41, 3.80, 5.19, 6.62, 7.72, 8.48, 9.01 and 10.50). Leaf size categories were derived from Gregory-Wodzicki (2000); p_i is percentage of number of species in each categories.

Secondly, both univariate and multivariate analyses without parameter-transformation were adopted. In the single linear regression analysis, correlation between each of 31 leaf characters and each of four precipitation variables was calculated. In the multiple linear regression analysis, the normality of each leaf physiognomic variables were tested to ensure the confidence of a linear regression. If a variable did not conform to a normal distribution, it was excluded from the analysis. Additionally, the variance inflation factor (VIF) test was adopted to check the independence of each leaf character in the equation.

Additionally, four leaf/precipitation equations (with $r^2 > 0.45$) derived from different regions worldwide were used to calculate precipitation parameters of the 50 Chinese sites (Table 1). The newly updated CLAMP dataset, namely PhysgAsia1 (Jacques *et al.* 2011), was used. Results from these models were compared with observed data by paired samples t-test. The mean absolute error of each model was calculated by the mean absolute difference between calculated and observed values. All analyses above were performed by SPSS 17.0 (SPSS Science, Chicago, IL, USA).

Results

Leaf-area analysis

Leaf-area analysis indicates a low correlation between leaf size and precipitation parameters in Chinese forests, for MAP, GSP, 3-WET and 3-DRY, r^2= 0.068, 0.105, 0.154, and 0.027, respectively. This result is different from previous studies focusing on regions in America and Africa, where leaf size has been reported to reflect precipitation (Wilf *et al.* 1998, Jacobs 1999), but is congruent with a recent study based on 92 globally distributed sites (Peppe *et al.* 2011).

Single Linear Regression Analysis (SLR)

Several leaf characters, such as leaf margin and ratio of leaf length to width, appear to be highly correlated with precipitation (Table 2). Across all 31 leaf characters, those Chinese sample sites with high proportions of woody dicot leaves with entire leaf margins show the strongest correlation with precipitation parameters (Table 2), *e.g.*, for GSP, $r^2 = 0.555$. Among these four precipitation parameters, GSP, MAP and 3-WET show higher correlations to some leaf characters (Table 2), *e.g.*, with the proportion of untoothed leaf species, $r^2 = 0.457$, 0.555 and 0.434, respectively; and 3-DRY presents the lowest correlation; *e.g.*, for the proportion of untoothed leaf species, $r^2 = 0.283$ (Table 2).

When the 50 Chinese sites are added to sites from other regions in the Physg3br dataset, the correlation between precipitation and leaf margin character decreases dramatically. In other words, no significant correlation between leaf physiognomy and precipitation is confirmed. For example, for the percentage of untoothed leaf margin species vs GSP, $r^2 = 0.140$. If data from East Asia, including 38 Japanese sample sites from PhysgAsia1, are combined with 50 Chinese sample sites, the correlation is also not quite high; *e.g.*, for the percentage of untoothed leaf margin species vs GSP, $r^2 = 0.340$. In contrast, when the 38 Japanese sample sites were analyzed separately, the correlation is even higher than from the Chinese sites alone; *e.g.*, for the percentage of untoothed leaf margin *vs* GSP, $r^2 = 0.713$.

Multiple Linear Regression Analysis (MLR)

Eight leaf variables and one precipitation variable can be shown to have a non-normal distribution by using the Kolmogorov-Smirnov Test ($p < 0.05$). These are nanophyll, leptophyll 1, emarginate apex, L : W < 1 : 1, compound teeth, close teeth, obovate, ovate and 3-DRY, therefore, they are not included in the analysis (Table 3). The MLR results show that, only leaf margin and L : W 3–4 : 1 are included as independents in all three transfer functions, and correlations between these two leaf physiognomic characters and precipitation parameters increase slightly, *i.e*, for MAP, GSP, 3-WET, $r^2 = 0.530$, 0.642 and 0.512 respectively. According to the variance inflation factor (VIF) test, leaf margin and L : W 3–4 : 1 are independent features in all transfer functions (with VIF < 5). Since leaf margin and L : W 3–4 : 1 correlate to all the precipitation parameters mentioned above, MAP, GSP and 3-WET should be interrelated to one another (Fig. 1), and these new MLR equations could not be available.

Applying previous models to estimate precipitations of Chinese modern samples

We applied four linear equations used previously for other regions (Wing & Greenwood 1993, Wiemann *et al.* 1998, Wilf *et al.* 1998, Jacobs 2002) and the latest updated CLAMP dataset (namely PhysgAsia1) to estimate precipitation for the Chinese modern sample sites. None of the linear equations could accurately estimate the precipitation for the Chinese modern sample sites. For example, for MAP, the mean absolute error of equations used for North America and Japan (Wing & Greenwood 1993), and North, Central and South America, and Africa (Wilf *et al.* 1998), and Africa and Bolivia (Jacobs 2002) are as large as

Table 1. Selected previous leaf physiognomy-precipitation regressions deduced from different regions worldwide ($r^2 > 0.4$).

No.	Transfer function	Data type	Data source	n	r^2	Standard error	Authors
1 *	MAP (cm) = 11.489 + 167.948 (apex attenuate) + 377.735 (mesophyll 2)	arcsine of the square root	CLAMP1	74	0.497	57.96 cm	Wing & Greenwood (1993)
2	MAP (cm) = 47.5 + 6.18 (mesophyll 1 + + mesophyll 2)	%	CLAMP1	74	0.439	–	Wilf *et al.* (1998)
3 *	ln MAP (cm) = 0.786 + 0.548 (MlnA)	MlnA	North, Central and South America, and Africa	50	0.760	0.36 cm (ln)	Wilf *et al.* (1998)
4	ln MAP (cm) = 4.9415 + 0.6903 (mesophyll) + 0.7059 (apex acuminate) + + 0.884 (apex acute) + 0.7542 (no teeth)	arcsine	Africa	30	0.794	0.19 cm (ln)	Jacobs (1999)
5	ln MAP (cm) = 1.78 + 0.484 (MlnA)	MlnA	CLAMP 3B	144	0.612	0.47 cm (ln)	Gregory-Wodzicki (2000)
6	ln MAP (cm) = 2.640 + 0.298 (MlnA)	MlnA	Bolivia	12	0.520	0.22 cm (ln)	Gregory-Wodzicki (2000)
7 *	ln MAP (cm) = 5.198 + 1.274 (mesophyll 1 + mesophyll 2) – 1.013 (shape elliptic)	arcsine	Africa (modified)	30	0.806	0.18 cm (ln)	Jacobs (2002)
8	ln MAP (cm) = 4.018 + 1.321 (mesophyll 1 + mesophyll 2)	arcsine	Africa (modified)	30	0.764	0.20 cm (ln)	Jacobs (2002)
9	ln MAP (cm) = 3.982 + 1.369 (mesophyll 1 + mesophyll 2)	arcsine	Africa (modified) and Bolivia	42	0.826	0.18 cm (ln)	Jacobs (2002)
10	ln MAP (cm) = 2.476 + 0.321 (MlnA)	MlnA	Africa	30	0.661	0.24 cm (ln)	Jacobs (2002)
11	ln MAP (cm) = 1.705 + 0.429 (MlnA)	MlnA	West Hemisphere, Bolivia and Africa	92	0.713	0.34 cm (ln)	Jacobs (2002)
12	ln MAP (< 260 cm) = 2.167 + 0.354 (MlnA)	arcsine	West Hemisphere, Bolivia and Africa	79	0.709	0.27 cm (ln)	Jacobs (2002)
13	ln MAP (cm) = 2.566 + 0.309 (MlnA)	MlnA	Tropical Africa and Bolivia	42	0.734	–	Jacobs & Herendeen (2004)
14	GSP (< 222 cm) = 48.050 + 141.368 (mesophyll 2) – 136.340 (L : W < 1) + 130.616 (apex attenuate) + 93.936 (shape elliptic) – 79.774 (base round) – 52.386 (teeth acute)	arcsine	CLAMP1	74	0.804	16.00 cm	Gregory & McIntosh (1996)
15 *	GSP (cm) = 31.6 – 3.393 (leptophyll 2) + + 2.40(apex attenuate) – 2.671 (base cordate) +2.360 (L : W 2–3) + 3.122 (L : W 3–4 : 1)	%	CLAMP 3B	144	0.796	–	Wiemann *et al.* (1998)
16	GSP (< 222 cm) = –45.2 + 1.60 (apex attenuate) + 2.80 (L : W 2–3)	%	CLAMP 3B	144	0.63	27.00 cm	Gregory-Wodzicki (2000)
17	ln Wet Ppn (mm) = 4.4993 + 0.8368 (mesophyll) + 0.819 (apex acuminate) + + 1.1718 (apex acute) + 0.8246 (no teeth)	arcsine	Africa	30	0.795	0.22 cm (ln)	Jacobs (1999)
18	ln Wet Ppn (cm) = 6.112 + 1.546 (mesophyll 1 + mesophyll 2)	arcsine	Africa (modified)	30	0.779	0.22 cm (ln)	Jacobs (2002)
19	ln Wet Ppn (cm) = 3.777+ 1.601 (mesophyll 1 + mesophyll 2)	arcsine	Africa (modified) and Bolivia	42	0.833	0.21 cm (ln)	Jacobs (2002)
20	ln Wet Ppn (cm) = 2.07 + 0.367 (MlnA)	MlnA	Tropical Africa and Bolivia	42	0.748	–	Jacobs & Herendeen (2004)
21 *	3-WET (cm) = –172.859 + 110.841 (apex attenuate) + 320.457 (L : W 2–3 : 1) + + 179.775 (mesophyll 2)	arcsine of the square root	CLAMP1	74	0.583	47.226 cm	Wing & Greenwood (1993)
22	3-DRY (cm) = -24.489 +45.54 (apex attenuate) + 38.186 (L : W 2–3 : 1)	arcsine of the square root	CLAMP1	74	0.55	8.91 cm	Wing & Greenwood (1993)

* Equations being used for precipitation estimations of 50 Chinese sample sites.

186.945 cm, 51.829 cm and 46.076 cm, respectively. Among all models used here, PhysgAsia1 gave the closest values, *i.e.*, mean absolute errors for GSP, 3-WET and 3-DRY are 30.10 cm, 11.69 cm and 5.04 cm, respectively.

According to the paired-sample *t* test, all linear equations from other regions except for one 3-WET-related equation deduced from CLAMP1 by MLR (Wing & Greenwood 1993) show significant differences from the

Table 2. Single linear correlations among 31 leaf physiognomic variables and four precipitation variables.

Leaf character	MAP		GSP		3-WET		3-DRY	
	r^2	P	r^2	P	r^2	P	r^2	P
Lobed	0.157	0.004 *	0.209	0.001 *	0.170	0.003 *	0.014	0.416
No teeth	0.457	0.000 *	0.555	0.000 *	0.434	0.000 *	0.219	0.001 *
Regular teeth	0.237	0.000 *	0.327	0.000 *	0.255	0.000 *	0.041	0.156
Close teeth	0.440	0.000 *	0.510	0.000 *	0.385	0.000 *	0.159	0.004 *
Round teeth	0.213	0.001 *	0.234	0.000 *	0.157	0.004 *	0.148	0.006 *
Acute teeth	0.245	0.000 *	0.317	0.000 *	0.271	0.000 *	0.088	0.036 *
Compound teeth	0.410	0.000 *	0.478	0.000 *	0.347	0.000 *	0.233	0.000 *
Nanophyll	0.011	0.470	0.001	0.833	0.001	0.797	0.026	0.260
Leptophyll 1	0.020	0.323	0.029	0.234	0.070	0.064	0.001	0.797
Leptophyll 2	0.010	0.495	0.024	0.288	0.026	0.267	0.002	0.761
Microphyll 1	0.076	0.053	0.124	0.012 *	0.137	0.008 *	0.016	0.387
Microphyll 2	0.043	0.146	0.091	0.033 *	0.116	0.015 *	0.000	0.937
Microphyll 3	0.000	0.974	0.008	0.543	0.017	0.363	0.035	0.193
Mesophyll 1	0.001	0.856	0.001	0.827	0.001	0.823	0.002	0.736
Mesophyll 2	0.063	0.079	0.139	0.008 *	0.155	0.005 *	0.001	0.870
Mesophyll 3	0.033	0.209	0.080	0.046 *	0.122	0.013 *	0.004	0.680
Emarginate apex	0.001	0.842	0.000	0.886	0.000	0.971	0.010	0.498
Round apex	0.068	0.068	0.090	0.034 *	0.088	0.036 *	0.012	0.444
Acute apex	0.158	0.004 *	0.196	0.001 *	0.165	0.003 *	0.054	0.105
Attenuate apex	0.120	0.014 *	0.158	0.004 *	0.140	0.007 *	0.029	0.236
Cordate base	0.231	0.000 *	0.299	0.000 *	0.236	0.000 *	0.039	0.168
Round base	0.013	0.431	0.023	0.289	0.015	0.402	0.008	0.534
Acute base	0.171	0.003 *	0.233	0.000 *	0.177	0.002 *	0.038	0.175
L : W < 1 : 1	0.072	0.060	0.107	0.020 *	0.065	0.073	0.004	0.657
L : W 1–2 : 1	0.389	0.000 *	0.482	0.000 *	0.378	0.000 *	0.116	0.016 *
L : W 2–3 : 1	0.084	0.041 *	0.119	0.014 *	0.084	0.041 *	0.020	0.332
L : W 3–4 : 1	0.401	0.000 *	0.484	0.000 *	0.396	0.000 *	0.128	0.011 *
L : W > 4 : 1	0.095	0.029 *	0.122	0.013 *	0.081	0.046 *	0.012	0.445
Obovate	0.149	0.006 *	0.183	0.002 *	0.117	0.015 *	0.058	0.092
Elliptic	0.225	0.000 *	0.270	0.000 *	0.204	0.001 *	0.056	0.098
Ovate	0.158	0.004 *	0.186	0.002 *	0.156	0.005 *	0.028	0.247

* significant at the 0.05 level.

gridded values ($p < 0.001$). For 3-WET and 3-DRY, PhysgAisa1 gave precipitation values that were not statistically different ($p > 0.05$; Appendix III).

Discussion

Leaf margin correlates to both temperature and precipitation in China

In the living forests of China, the percentage of untoothed leaf margins in woody dicot species not only shows a positive linear correlation with MAT, but also statistically relates to precipitation parameters such as MAP, GSP and 3-WET (Table 2). The result is quite different from most previous studies from other regions where leaf physiognomic characters other than leaf margin type, are related to precipitation parameters (Wing & Greenwood 1993, Wiemann *et al*. 1998, Wilf *et al*. 1998). One of the most widely applied linear functions is based on 50 sites from North, Central and South America, and Africa (Wilf *et al.* 1998). In this function, natural logarithm leaf size data show a strong correlation with MAP (Wilf *et al.* 1998). However, using the same method the Chinese sites show no relationship to MAP.

When combining the Chinese sites with the global data (Physg3br dataset in CLAMP) in the analysis, the correla-

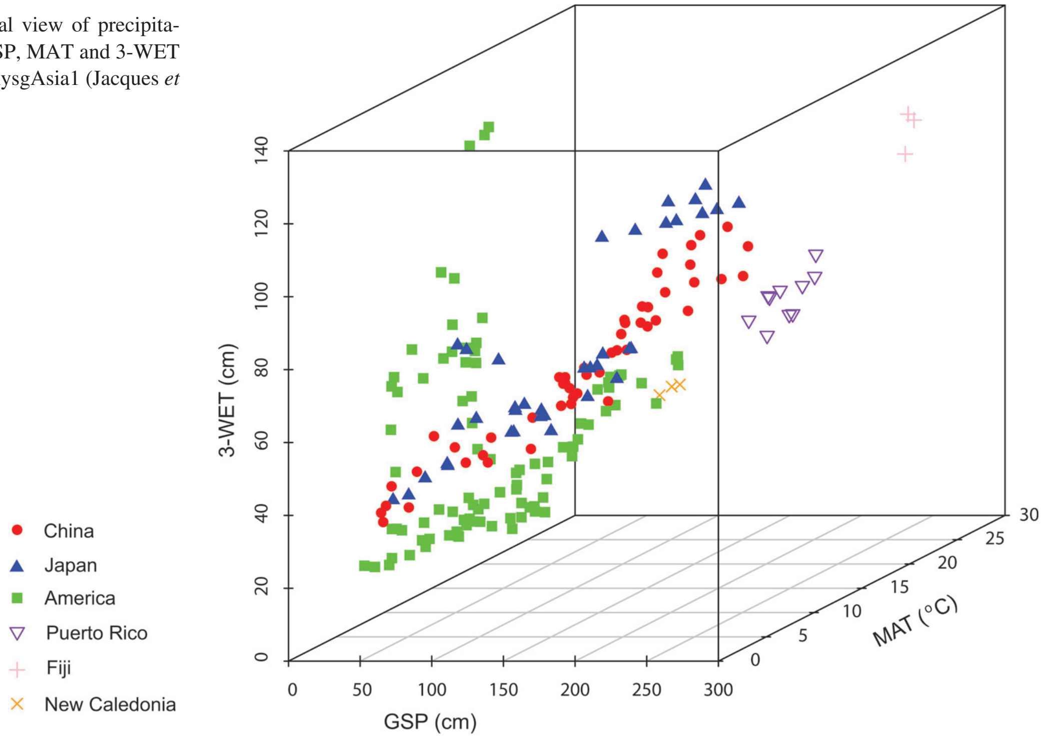

Figure 1. Three dimensional view of precipitation parameters including GSP, MAT and 3-WET worldwide. Data are from PhysgAsia1 (Jacques *et al.* 2011) and this study.

tion decreases sharply, which supports the previous studies that, leaf physiognomy-climate correlation in China shows regional constraint (Su *et al*. 2010, Jacques *et al.* 2011). As far as the relationship between leaf margin type and the mean annual temperature (MAT) is concerned, the transfer function produced by the Chinese data shows a significantly different slope to that from other regions (Su *et al.* 2010). Additionally, the Chinese sites always plot together and separate from the sites representing other geographic regions in physiognomic space (Jacques *et al*. 2011).

In China, both MAT and MAP decrease from lower latitude to higher latitude, (Zhang 1991). According to our analysis based on a 30 year record of 401 Chinese climate stations from 1961 to 1990, the MAT shows a statistically significant correlation with MAP ($r^2 = 0.511$; Fig. 2). It is therefore not surprising that the percentage of entire margined woody dicot leaves correlate to both MAT and MAP. In some other regions with similar climate conditions in the Northern Hemisphere, such as the eastern United States and Japan (Fig. 1), there should be a similar result (Peppe *et al*. 2011). Because MAT and precipitation parameters such as MAP are correlated in these areas, the MAP of a site could be calculated if the MAT of that site is known. While this may hold for the present day, it might not be the case in deep time. For example China, especially the eastern part of the country, was influenced by the palaeo-East Asian monsoon as early as the middle Eocene (Quan *et al*. 2011, 2012), but the monsoon system has been further gradually strengthened since the Neogene (Sun & Wang 2005), and the present day correlation between MAT and MAP is largely a function of monsoon characteristics. Since the origin and phase of the linear correlation between precipitation and temperature in deep time are largely unknown, univariate or multivariate leaf/precipitation association models which include leaf margin as independence could not be reliable for the palaeoprecipitation reconstructions in China.

Why does leaf physiognomy in China show a regional constraint?

As discussed above, it appears that modern leaf physiognomy data from China fails to confirm the validity of any linear regressions generated from non-Chinese data. This obviously indicates a largely unique regional constraint of leaf/precipitation correlation in China. There are several environmental factors contributing to the special leaf physiognomy in China.

Firstly, most parts of China experience a monsoon climate, which is characterized by a rainy season in summer and a dry season in winter, precipitation in the North is much lower than in the South (Zhang 1991). Evergreen plants being particularly prevalent in southern China, such as in Yunnan Province and Sichuan Province, have not only to grow in the summer with abundant water, but also survive the relatively dry winter; whereas most plants in the north are deciduous, with limited growing seasons. Plants especially these in the North might benefit from teeth on the leaf margin with higher photosynthesis ability

Table 3. Normality of 31 leaf physiognomy and four precipitation variables with Kolmogorov-Smirnov Test (K-S Test).

Leaf character	K-S Test
Lobed	0.058 *
No teeth	0.200 *
Regular teeth	0.200 *
Close teeth	0.003
Round teeth	0.200 *
Acute teeth	0.200 *
Compound teeth	0.000
Nanophyll	0.000
Leptophyll 1	0.000
Leptophyll 2	0.200 *
Microphyll 1	0.106 *
Microphyll 2	0.200 *
Microphyll 3	0.200 *
Mesophyll 1	0.200 *
Mesophyll 2	0.200 *
Mesophyll 3	0.200 *
Emarginate apex	0.000
Round apex	0.200 *
Acute apex	0.200 *
Attenuate apex	0.200 *
Cordate base	0.200 *
Round base	0.200 *
Acute base	0.069 *
L : W < 1 : 1	0.000
L : W 1–2 : 1	0.200 *
L : W 2–3 : 1	0.200 *
L : W 3–4 : 1	0.200 *
L : W > 4 : 1	0.067 *
Obovate	0.004
Elliptic	0.169*
Ovate	0.012
MAP	0.086 *
GSP	0.200 *
3-WET	0.200 *
3-DRY	0.004

* Significant at the 0.05 level in normal distribution.

in the spring (Baker-Brosh & Peet 1997), when the rainy season comes. Secondly, arid regions in China such as most of northwestern part have a very low diversity of woody dicot species (Wu 1980), and are not represented in the current Chinese dataset. Amongst the Chinese sites the GSP of only one sample site from Beijing is below 40 cm (Appendix II). However, precipitations from many sites in some other regions are much lower than precipitations of sample sites in China. For example, in the Physg3br dataset, the GSPs of about 30% of the sample sites are below 40 cm. Thirdly, the annual variation of precipitation appears far more greater than temperature. This could partly explain why the correlation of leaf physiognomy and precipitation is not as high as the correlation between leaf physiognomy and temperature worldwide.

Until now, not all precipitation parameters could be calculated by leaf/precipitation models, such as 3-WET, which is useful to explore the evolution of the monsoon system (Jacques *et al.* 2011). Only one study by Wing & Greenwood (1993) proposed an equation for 3-DRY, with apex attenuate and the ratio of leaf length to width (2–3 to 1) as independents. We found the similar statistically low correlation between leaf physiognomy and 3-DRY to results concluded by previous studies. Based on the present study, GSP, MAP and 3-WET show a high correlation with the percentage of entire-margined woody dicot leaves, but 3-DRY shows a weak relationship using linear regression analyses ($r^2 = 0.219$). This low correlation between 3-DRY and leaf physiognomy in China may be caused by the dry season coinciding with low temperatures, and thus low growth rates or dormancy of leaves during winter or early spring (Zhang 1991).

Implications for palaeoclimate reconstructions

The present study indicates that, even with statistically high correlations, none of the univariate linear regressions derived from data from Chinese forests could be used reliably for palaeoprecipitation calculations because of the spatial similarity of temperature and precipitation in China, that is, both temperature and precipitation decrease roughly from south to north in China (Zhang 1991). The forests of China are largely under the influence of the monsoon amplified by the Tibetan Plateau uplift, and leaf physiognomy in forests of China is most likely shaped by the monsoonal climate. Because no precise leaf physiognomic data of Chinese Palaeogene floras are available, we do not yet know if the relationship between leaf physiognomy and precipitation in Chinese Palaeogene floras was different, even the palaeo-East Asian monsoon may exist in the Palaeogene (Quan *et al.* 2011, 2012). In the same way as the previous regressions, all the previous univariate linear regressions for palaeoprecipitation estimations are derived from regional data, and the climate in deep time may affect these correlations. Consequently, these models would give reliable values for floras in the late Neogene and Quaternary for regional palaeoclimate reconstructions, but might not be appropriate to apply to floras of older geological ages under significantly different climate conditions (Peppe *et al.* 2011).

Global models would capture more information on the association between leaf physiognomy and climate (Spicer *et al.* 2009, Peppe *et al.* 2011). According to this study, the new CLAMP dataset (PhysgAsia1, Jacques *et al.* 2011) provided the closest values to those observed among all extant leaf physiognomy based models. To date, using the PhysgAsia1 dataset is a proper approach for estimating palaeoprecipitations of Chinese palaeofloras based on its more global data and a direct ordination method, namely Canonical Correspondence Analysis, the results of which are less affected by regional constraints on leaf physiognomy-climate correlations. In particular CLAMP would be appropriately used for palaeoclimate reconstruction of floras earlier than the Neogene, when the floras and climates were significantly different from nowadays.

In future, more calibrated data from regions such as southeast Asia and Oceania need to be collected to cover a wider range of vegetation types and climate conditions. On the other hand, factors that might influence leaf physiognomy-climate relationship, like edaphic condition and phylogeny, should be quantified based on more global datasets. Because the temporal and spatial constraints on extant

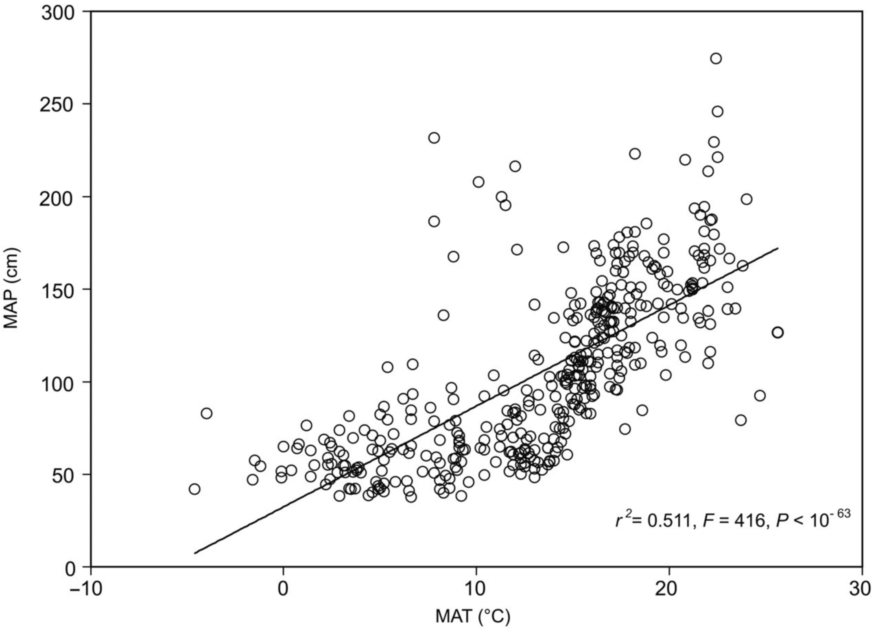

Figure 2. Correlation of mean annual temperature (MAT) and mean annual precipitation (MAP) in China.

regional models are still imperfectly known, we suggests that models with data sources in global spatial scale such as CLAMP (Spicer *et al.* 2009), could be applied for a rapid calculation, but a regional model with data of the aimed palaeoflora lying within the model's leaf physiognomy spectrum should be used as a conservative calculation.

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Appendix 1

Leaf physiognomic data from five sample sites in China. Data from the remaining 45 sample sites are available on CLAMP website (the file of PhysgAsia1 is deposited in CLAMP 2011).

Leaf character	Sample site				
	Antu, Jilin	Beijing	Qitaihe, Heilongjiang	Meihekou, Jilin	Ningan, Heilongjiang
Lobed	13.3	6.3	13.9	16.7	21.1
No teeth	20.0	12.5	5.6	16.7	15.8
Regular teeth	40.0	43.8	66.7	66.7	47.4
Close teeth	30.0	43.8	44.4	61.1	13.2
Round teeth	40.0	25.0	50.0	27.8	52.6
Acute teeth	40.0	62.5	44.4	55.6	31.6
Compound teeth	40.0	37.5	52.8	41.7	50.0
Nanophyll	0.0	0.0	0.0	0.0	0.0
Leptophyll 1	3.3	0.0	0.0	0.0	0.0
Leptophyll 2	5.5	0.0	1.8	0.0	4.4
Microphyll 1	11.1	11.9	5.1	4.6	5.7
Microphyll 2	16.6	28.3	20.7	19.4	22.7
Microphyll 3	32.1	34.5	25.8	22.2	21.4
Mesophyll 1	13.3	17.9	23.0	33.3	22.3
Mesophyll 2	7.7	5.9	8.7	18.5	10.5
Mesophyll 3	10.0	1.3	14.3	1.8	12.7
Emarginate apex	0.0	0.0	11.1	0.0	0.0
Round apex	13.3	4.1	14.8	5.6	2.6
Acute apex	23.3	22.9	34.2	13.9	2.6
Attenuate apex	63.3	72.9	50.9	80.6	94.7
Cordate base	26.7	16.6	18.5	38.9	14.9
Round base	36.7	19.8	18.5	13.9	20.2
Acute base	36.7	63.5	62.9	47.2	64.9
L : W < 1 : 1	13.3	9.4	2.8	8.3	2.6
L : W 1–2 : 1	40.0	35.9	61.1	63.9	65.8
L : W 2–3 : 1	40.0	34.9	30.6	25.0	28.1
L : W 3–4 : 1	3.3	9.9	5.6	2.8	1.7
L : W > 4 : 1	3.3	9.9	0.0	0.0	1.7
Obovate	13.3	6.3	2.8	2.8	5.3
Elliptic	66.7	81.3	86.1	88.9	86.8
Ovate	20.0	12.5	11.1	8.3	7.9
Nanophyll	0.0	0.0	0.0	0.0	0.0
Leptophyll	8.8	0.0	1.8	0.0	4.4
Microphyll	59.8	74.7	51.6	46.2	49.8
Mesophyll	31.0	25.1	46.0	53.6	45.5

Appendix 2

Climatic information on 50 sample sites in China. Data are derived from the BRIDGE website (Valdes 2008). Taxa – the number of woody dicot species in a sample; MAP – mean annual precipitation; GSP – growing season precipitation; 3-WET – precipitation during three consecutive wettest months; 3-DRY – precipitation during three consecutive driest months.

Sample sites	Taxa	MAP (cm)	GSP(cm)	3-WET(cm)	3-DRY(cm)
Antu, Jilin	15	78.19	60.68	49.59	1.54
Beijing	16	46.52	38.75	31.46	1.18
Qitaihe, Heilongjiang	17	53.91	42.84	32.35	1.96
Meihekou, Jilin	18	66.99	55.04	43.17	2.01
Ningan, Heilongjiang	19	56.50	46.55	35.84	1.07
Taibai, Shanxi	21	69.51	58.35	35.14	1.76
Huanren, Liaoning	22	87.04	70.84	54.36	3.00
Anshan, Liaoning	23	71.44	60.60	45.08	2.26
Guiyang, Hunan	23	152.31	129.66	65.62	19.38
Yantai, Shandong	23	74.63	61.89	44.31	3.92
Lingchuan, Guangxi	25	163.38	150.81	76.64	17.33
Jingdong, Yunnan	26	108.40	108.40	61.70	4.56
Jiangkou, Guizhou	27	122.75	100.17	53.78	9.09
Jiaohe, Jilin	27	62.65	50.43	40.69	1.27
Weishan, Yunnan	27	106.17	101.91	59.97	4.77
Chuzhou, Anhui	28	101.10	84.50	46.10	9.47
Baisha, Hainan	29	196.87	196.87	89.10	11.63
Lichuan, Hubei	29	118.07	102.08	49.48	6.55
Xichou, Yunnan	29	129.72	128.22	66.27	6.20
Lüchun, Yunnan	30	126.02	122.49	67.67	5.85
Pingbian, Yunnan	30	140.42	140.28	73.29	7.58
Chengkou, Chongqing	31	100.07	94.60	44.75	3.39
Xinyang, Henan	31	104.74	88.93	44.33	9.81
Lushan, Jiangxi	31	143.08	102.07	63.40	15.52
Zhenyuan, Yunnan	32	113.56	113.56	64.79	4.56
Zaoqing, Guangdong	33	175.33	175.33	79.62	11.18
Shiyan, Hubei	33	87.37	78.08	39.11	4.12
Pingwu, Sichuan	34	74.34	72.64	41.15	1.18
Pu’er, Yunnan	35	138.47	138.47	77.20	5.48
Kunming, Yunnan	35	102.40	96.39	58.54	3.87
Longsheng, Guangxi	35	149.02	134.02	68.58	16.11
Baoxing, Sichuan	36	90.88	86.24	48.93	2.64
Napo, Guangxi	38	121.99	121.94	62.90	5.58
Liuyang, Hunan	39	143.42	95.27	62.93	18.05
Dong’an, Hunan	39	142.25	118.46	63.36	18.27
Wuyishan, Fujian	39	165.66	134.36	78.14	17.33
Yongxiu, Jiangxi	39	144.95	110.95	65.99	15.55
Shimen, Hunan	40	119.82	103.77	48.97	9.67
Jinyunshan, Chongqing	41	109.41	101.75	48.55	6.06
Gongshan, Yunnan	43	92.19	89.39	52.12	3.66
Wuming, Guangxi	43	130.17	130.17	59.87	10.26
Wuzhishan, Hainan	43	197.82	197.82	91.78	11.47
Xinhua, Hunan	44	132.70	108.88	57.97	15.75
Mengla, Yunnan	44	136.54	136.54	72.48	5.61
Liupanshui, Guizhou	44	109.10	99.91	56.79	4.87
Tongshan, Hubei	45	137.27	109.51	59.88	15.75
Chongyi, Jiangxi	45	151.78	134.26	66.94	15.59
Yushan, Jiangxi	47	161.20	121.68	72.70	17.46
Jinfoshan, Chongqing	55	113.53	95.68	49.86	6.36
Weng’an, Guizhou	58	114.20	104.63	52.97	7.26

Appendix 3

Mean absolute errors of precipitation estimations of 50 Chinese sample sites by models derived from different regions.

Equation	MAP (cm)			GSP (cm)		3-WET (cm)		3-DRY (cm)	
Sample site	Wing & Greenwood (1993)	Wilf *et al.* (1998)	Jacobs (2002)	Wiemann *et al.* (1998)	PhysgAsia1	Wing & Greenwood (1993)	PhysgAsia1	Wing & Greenwood (1993)	PhysgAsia1
Antu, Jilin	209.921	58.360	68.801	149.935	1.709	160.512	7.757	41.361	5.850
Beijing	225.573	71.495	85.830	231.720	40.531	153.190	23.916	45.226	11.007
Qitaihe, Heilongjiang	204.362	115.859	106.548	144.269	6.865	123.184	10.715	32.412	4.386
Meihekou, Jilin	294.605	96.000	156.765	130.074	9.234	152.544	3.529	44.074	6.003
Ningan, Heilongjiang	301.079	96.386	105.153	229.580	14.262	176.682	4.940	55.986	1.420
Taibai, Shanxi	127.666	23.085	44.944	190.964	71.379	107.617	28.095	35.002	14.408
Huanren, Liaoning	115.175	80.867	39.987	89.160	42.048	52.897	15.446	27.334	0.693
Anshan, Liaoning	214.172	89.921	68.933	172.499	19.992	131.919	2.421	42.985	3.234
Guiyang, Hunan	91.5360	52.146	33.374	155.429	16.050	123.349	6.004	25.119	3.457
Yantai, Shandong	231.874	102.539	103.046	115.351	15.087	130.644	1.532	34.233	2.954
Lingchuan, Guangxi	195.746	34.047	0.864	236.364	48.894	196.884	18.99	42.620	9.006
Jingdong, Yunnan	264.569	93.001	108.684	301.604	19.221	234.601	9.526	49.554	5.631
Jiangkou, Guizhou	237.647	58.339	57.398	283.277	8.982	233.868	4.219	52.764	1.688
Jiaohe, Jilin	189.954	25.053	55.649	179.626	13.801	157.445	8.397	43.406	8.088
Weishan, Yunnan	212.506	34.325	81.747	196.923	2.048	157.915	0.296	40.063	3.826
Chuzhou, Anhui	162.790	37.885	32.267	121.864	26.761	100.997	0.456	26.094	3.395
Baisha, Hainan	166.991	20.983	54.715	280.946	5.850	127.222	3.253	42.074	4.091
Lichuan, Hubei	64.8430	45.303	36.942	160.012	17.659	120.197	1.301	35.218	3.585
Xichou, Yunnan	172.416	3.978	32.424	209.661	63.866	202.673	20.670	52.123	12.254
Lüchun, Yunnan	230.389	85.687	30.271	254.752	95.331	164.911	39.941	47.950	5.068
Pingbian, Yunnan	238.488	58.024	59.668	242.174	63.276	165.487	20.725	47.219	1.612
Chengkou, Chongqing	77.0640	18.913	22.016	187.930	45.278	125.711	14.678	40.601	12.373
Xinyang, Henan	112.897	20.584	2.504	167.147	24.001	137.514	1.3020	34.109	1.723
Lushan, Jiangxi	51.5780	50.766	25.775	72.538	55.610	94.888	16.033	15.755	8.618
Zhenyuan, Yunnan	237.235	112.324	99.386	316.381	7.124	195.083	0.454	49.005	1.442
Zaoqing, Guangdong	183.588	10.280	9.564	198.863	74.997	142.886	18.378	41.528	4.143
Shiyan, Hubei	188.784	50.876	45.960	139.746	9.101	128.732	9.769	36.612	2.249
Pingwu, Sichuan	215.394	28.958	58.391	193.808	54.890	182.802	25.827	46.443	11.838
Pu’er, Yunnan	185.489	78.820	2.250	189.473	96.764	170.463	41.986	46.555	2.689
Kunming, Yunnan	170.233	23.498	51.217	186.663	25.496	141.831	5.901	37.369	8.055
Longsheng, Guangxi	153.882	40.105	20.113	307.404	6.142	167.504	4.455	43.720	7.533
Baoxing, Sichuan	219.788	18.206	47.737	249.166	38.692	187.625	15.980	50.390	10.31
Napo, Guangxi	243.245	107.166	39.844	262.922	86.060	167.418	29.049	51.620	3.781
Liuyang, Hunan	142.990	14.128	12.906	150.653	12.145	143.934	5.629	27.041	6.170
Dong’an, Hunan	185.837	20.031	9.282	211.175	27.574	154.011	8.337	32.601	11.637
Wuyishan, Fujian	107.180	67.339	45.711	169.800	73.165	99.133	35.010	28.810	11.036
Yongxiu, Jiangxi	136.151	22.556	8.443	164.819	12.075	121.022	6.491	29.751	3.876
Shimen, Hunan	261.236	39.919	45.535	338.248	24.471	202.768	4.555	53.277	4.375
Jinyunshan, Chongqing	199.298	49.350	67.415	287.501	36.189	206.278	26.198	49.035	8.616
Gongshan, Yunnan	225.696	128.996	79.853	251.963	5.105	154.549	8.639	41.535	1.042
Wuming, Guangxi	172.670	1.120	18.240	150.943	25.470	159.564	3.397	36.831	0.243
Wuzhishan, Hainan	213.186	11.856	15.647	241.656	54.211	202.953	18.297	49.101	0.724

Equation	MAP (cm)			GSP (cm)		3-WET (cm)		3-DRY (cm)	
Sample site	Wing & Greenwood (1993)	Wilf *et al.* (1998)	Jacobs (2002)	Wiemann *et al*. (1998)	PhysgAsia1	Wing & Greenwood (1993)	PhysgAsia1	Wing & Greenwood (1993)	PhysgAsia1
Xinhua, Hunan	153.039	9.170	5.391	152.679	5.309	131.286	1.458	27.915	4.886
Mengla, Yunnan	207.102	147.812	6.589	250.744	110.870	183.300	45.132	50.418	8.077
Liupanshui, Guizhou	247.268	67.375	57.273	262.876	17.924	188.091	2.965	56.535	2.334
Tongshan, Hubei	147.030	9.9920	1.648	221.915	13.728	178.579	7.054	35.600	6.902
Chongyi, Jiangxi	158.909	31.266	10.130	228.612	41.820	161.693	12.549	33.546	10.479
Yushan, Jiangxi	138.743	47.144	33.841	240.522	16.219	172.513	5.395	39.711	1.957
Jinfoshan, Chongqing	217.320	21.464	29.225	248.543	1.482	160.822	9.963	46.924	2.373
Weng'an, Guizhou	242.108	58.135	67.899	249.355	23.473	160.765	1.649	47.160	0.783
Mean absolute error (cm)	186.945	51.829	46.076	207.405	32.565	155.969	12.373	40.846	5.438
Paired-samples t-test	0.000	0.000	0.000	0.000	0.018	0.000	0.320 *	0.000	0.602 *

* No statistical difference between estimated and observed values at the 0.05 level.