Key Points:
- In China, high leaf $\delta^{13}C$ mostly appear in central and western regions
- Leaf $\delta^{13}C$ varies significantly among different life forms and environmental conditions
- Environmental factors primarily affect the spatial distribution of leaf $\delta^{13}C$ in China

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Spatial patterns of leaf $\delta^{13}C$ and its relationship with plant functional groups and environmental factors in China

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Abstract The leaf carbon isotope ratio ($\delta^{13}C$) is a useful parameter for predicting a plant's water use efficiency, as an indicator for plant classification, and even in the reconstruction of paleoclimatic environments. In this study, we investigated the spatial pattern of leaf $\delta^{13}C$ values and its relationship with plant functional groups and environmental factors throughout China. The high leaf $\delta^{13}C$ in the database appeared in central and western China, and the averaged leaf $\delta^{13}C$ was −27.15‰, with a range from −21.05‰ to −31.5‰. The order of the averaged $\delta^{13}C$ for plant life forms from most positive to most negative was subshrubs > herbs = shrubs > trees > subtrees. Leaf $\delta^{13}C$ is also influenced by some environmental factors, such as mean annual precipitation, relative humidity, mean annual temperature, solar hours, and altitude, although the overall influences are still relatively weak, in particular the influence of MAT and altitude. And we further found that plant functional types are dominant factors that regulate the magnitude of leaf $\delta^{13}C$ for an individual site, whereas environmental conditions are key to understanding spatial patterns of leaf $\delta^{13}C$ when we consider China as a whole. Ultimately, we conducted a multiple regression model of leaf $\delta^{13}C$ with environmental factors and mapped the spatial distribution of leaf $\delta^{13}C$ in China by using this model. However, this partial least squares model overestimated leaf $\delta^{13}C$ for most life forms, especially for deciduous trees, evergreen shrubs, and subtrees, and thus need more improvement in the future.

1. Introduction

Carbon isotope discrimination extensively exists in the process of global carbon cycling in terrestrial ecosystems [*Farquhar et al.*, 1989; *Enting et al.*, 1995; *Flanagan and Ehleringer*, 1998]. Plants discriminate against the heavier isotope (^{13}C) during photosynthesis [*Farquhar et al.*, 1989], resulting in a lower carbon isotope ratio in leaf organic carbon ($^{13}C/^{12}C$) compared with atmospheric CO_2. In earlier studies, leaf $\delta^{13}C$ usually served as a criterion with which to distinguish C_3 and C_4 photosynthetic pathways [*Craig*, 1953; *Tieszen et al.*, 1979]. Since the 1980s, many experiments have demonstrated that leaf $\delta^{13}C$ is linearly related to the ratio of internal to ambient CO_2 concentration (c_i/c_a) [*Farquhar et al.*, 1982], and leaf $\delta^{13}C$ is primarily restricted by leaf conductance, RuBP carboxylation efficiency, and other environmental factors that affect the plant physiology and biochemistry [*Condon et al.*, 1987; *Ehleringer et al.*, 1991; *Virgona and Farquhar*, 1996]. Therefore, variations in leaf $\delta^{13}C$ patterns can potentially record a feedback of climate-driven changes in modern plant physiology and biogeochemistry [*Hultine and Marshall*, 2000; *Evans and Von Caemmerer*, 2013]. In addition, due to the positive correlation between leaf $\delta^{13}C$ and leaf water use efficiency (WUE), where WUE refers to amount of water loss accompanies the assimilation of CO_2 during photosynthesis, leaf $\delta^{13}C$ usually serves as a proxy for leaf water use efficiency (WUE) [*Farquhar and Richards*, 1984; *Wright et al.*, 1994; *Condon et al.*, 2002]. More recently, leaf $\delta^{13}C$ has also been frequently applied to the grouping of plants in ecosystems [*Brooks et al.*, 1997] and the reconstruction of paleoclimate [*Kohn*, 2010].

The results from numerous field surveys and laboratory experiments have shown that leaf $\delta^{13}C$ is largely affected by plant functional groups (e.g., plant life form and phylogeny type) and environmental factors (e.g., precipitation, air temperature, and altitude) [*Sun et al.*, 2003; *Wang et al.*, 2008]. In C_4 plants, for example, the extra C_4 carbon fixation enables them to gather more ^{13}C and to have higher $\delta^{13}C$ values compared with C_3 plants [*Farquhar et al.*, 1989; *O'Leary*, 1988]. *Brooks et al.* [1997] found that life forms (e.g., deciduous/evergreen trees, deciduous/evergreen shrubs, deciduous/evergreen forbs, and mosses) could

explain 50% of the variation in leaf δ^{13}C values in three boreal forest ecosystems in Northern America. And they further pointed that similar functional traits (e.g., δ^{13}C) could be used to group life forms [*Brooks et al.*, 1997]. Moreover, other genetic differences also more or less affect the leaf δ^{13}C values, such as leaf longevity, anatomical characters (e.g., stomata density) [*Sun et al.*, 2003], plant phylogeny type [*Leavitt and Newberry*, 1992], and leaf nutritional status (e.g., SLA, specific leaf area; N_{area}, nitrogen per unit leaf area) [*Sparks and Ehleringer*, 1997; *Li et al.*, 2006].

Additionally, climate change not only determines the survival and distribution of vegetation regionally and globally but also profoundly affects terrestrial plant morphology and functional traits (e.g., δ^{13}C) [*Condon et al.*, 1987]. *Diefendorf et al.* [2010] presented a strong positive correlation between leaf carbon isotope fractionation (Δleaf, which is negatively related to leaf δ^{13}C) and mean annual precipitation ($R^2 = 0.55$) using a database that covered 3310 published leaf δ^{13}C values from 105 sampling locations around the world. Other authors further indicated that precipitation was the dominant factor controlling leaf δ^{13}C at large spatial scales, a finding that was almost unanimously supported by related research from different regions [*Van de Water et al.*, 2002; *Zhang et al.*, 2003; *Schulze et al.*, 1998]. Previous studies have reported conflicted conclusions over the potential for changes in mean annual temperature to influence δ^{13}C. Most studies suggested that low temperatures could weaken the photosynthetic enzymatic reactions, resulting in increased c_i/c_a and decreased leaf δ^{13}C values [*Tieszen*, 1991; *Körner et al.*, 1991; *Arens et al.*, 2000]; however, there are also some studies insisted that low temperatures could reduce the conductance of stoma and concentration of intercellular CO_2 [*Panek and Waring*, 1995], resulting in higher leaf δ^{13}C values [*Ning et al.*, 2002]. Altitude usually serves as a unique environmental factor that integrates CO_2 concentration, air temperature, and VPD (vapor pressure deficit), compared with other climate variables, deeply influencing the leaf δ^{13}C values. In general, leaf δ^{13}C increases with higher elevations, both regionally and globally [*Hultine and Marshall*, 2000; *Körner et al.*, 1988; *Li et al.*, 2009]. And extensive studies have also shown the correlation between foliar δ^{13}C and other abiotic factors (e.g., irradiance and atmospheric CO_2 concentration) [*Farquhar et al.*, 1989; *Feng and Epstein*, 1995] and edaphic factors (e.g., soil salinity) [*Flanagan and Jefferies*, 1988]. Recently, the importance of biochemical and physiological mechanisms in controlling the leaf δ^{13}C values of plant tissue has got growing concern. The biochemical and physiological mechanisms include different carbohydrate storage strategies, coordination between stomatal conductance and photosynthetic capacity, and adjustment of leaf area to water-conducting tissue [*Epron et al.*, 2012; *Dubbert et al.*, 2012; *Tcherkez et al.*, 2011; *Cernusak et al.*, 2013].

Most studies have focused on the dissimilarity of leaf δ^{13}C among different species or vegetation types, or on the varied leaf δ^{13}C patterns along distinct environmental gradients under natural or artificially controlled conditions [*Song et al.*, 2008; *Wang et al.*, 2008]. However, these studies, especially those from China, have primarily concentrated on a few sites or in partial areas for which there are abundant published data. Thus far, no consistent conclusions have emerged regarding how environmental conditions affect plant leaf δ^{13}C and how living plants adapt to dynamic changes in habitat by adjusting their leaf δ^{13}C values. Additionally, few studies have simultaneously analyzed interbiome and intrabiome variations in leaf δ^{13}C along environmental gradients at lager scales.

Hence, we have built a national data set of leaf δ^{13}C for China's C$_3$ terrestrial plants using published literature as well as unpublished data from the Northeast China Transect [*Prentice et al.*, 2011] and the Tibetan Plateau [*Song et al.*, 2008]. The objectives of this study are as follows: (1) to explore the spatial distribution pattern of leaf δ^{13}C throughout China, (2) to examine the variation in leaf δ^{13}C values among plant functional groups (e.g., life forms and plant phylogeny types) and analyze the correlations between leaf δ^{13}C and environmental factors, and (3) to develop a multivariate linear model for leaf δ^{13}C and environmental factors for further study.

2. Materials and Methods

2.1. Leaf δ^{13}C Database Construction

The database of leaf δ^{13}C in China was constructed from published literature (in Chinese or English) between 1992 and 2016. We only included data on the leaf δ^{13}C of terrestrial C$_3$ plants under natural conditions. Samplings from campuses or parks were rejected to avoid the influence of human activities or industrial pollution. Leaf δ^{13}C values below $-31.5‰$ were also rejected, as this level is considered to reflect

sampling from the understory, where the $\delta^{13}C$ of ambient CO_2 is seriously affected by soil respiration [*Kohn*, 2010]. Then, we recorded the geographic location (latitude and longitude) for each sampling site, and the averaged or estimated location was computationally inferred based on related articles if the locations were lacking. Ultimately, our database consisted of 2538 observations from 480 sampling sites, including 649 species representing 137 families and 349 genera throughout China.

2.2. Environmental Data and Species Taxonomy

Annual values of precipitation, relative humidity, air temperature, and sunshine hours were derived from 756 meteorological stations between 1992 and 2013. Climate data were interpolated at 10 km resolution using a smoothing spline interpolation software (ANUSPLIN version 4.36) [*Hancock and Hutchinson*, 2006]. Then, the mean annual precipitation (MAP, mm), relative humidity (RH, %), mean annual temperature (MAT, °C), and solar hours (SH, hours) were calculated for each site.

To compare the differences in plant functional groups, the species in our database were classified into different life forms (i.e., herbs, subshrubs, shrubs, subtrees, and trees) and phylogeny types (i.e., dicots, monocots, gymnosperms, and ferns). Where subshrub is a kind of plant between grass and shrub. Usually, the stems of subshrub which are close to the ground are semilignified, while the rest part of stems are herbaceous. The semilignified stem of subshrubs can bear hibernating buds which can help subshrubs to regenerate after winter or suffering some disasters (e.g., frost, drought, or overgrazing). Subshrubs are found to grow under stressful environments with poor-nutrient soil, high temperatures, and drought in previous study [*Mencuccini*, 2003] and in our database. Examples of subshrubs include *Reaumuria soongorica* and *Artemisia desertorum*. "Subtree" is a kind of low wood plant between shrub and tree. In fact, there is no clear classification between trees and shrubs for some large shrubs and low trees. These large shrubs and low trees are called "subtree" in this study, because they have main branches compared with shrubs but are lower than common trees (higher than 6 m). Examples of subtrees include *Olea europaea* and *Sapium discolor*, whereas different researchers often treat them as shrubs or trees based on morphological characteristics in different sites. For example, *Olea europaea* is treated as shrub in Jaén province, southern Spain [*Rey and Alcantara*, 2000], but treated as tree in Pisa, Italy, and Córdoba, Spain [*Marchi et al.*, 2008; *Rallo et al.*, 2000]. In our database, subtrees are found in environments with abundant precipitation and long-time sunshine. We determined whether the plant was a subshrub or subtree based on the original description in related papers or from other papers sampling at adjacent areas [*Chu*, 2007; *Sun*, 2007]. According to leaf longevity, herbs were further subdivided into annual or perennial and shrubs, and trees were further subdivided into evergreen or deciduous.

2.3. Data Analysis

To compare the differences in leaf $\delta^{13}C$ among plant functional groups, we calculated the means of leaf $\delta^{13}C$ for each life form and plant phylogeny type. The $\delta^{13}C$ variation in different plant functional groups was examined by one-way analysis of variance and a least significant difference multiple comparison or *Tamhane's T2* method. All statistical analyses were conducted using SPSS software (2012, ver. 22.0; SPSS Inc., USA).

Then, we attempted to use the factors that were closely correlated with leaf $\delta^{13}C$ to build a partial least squares (PLS) regression model. In comparison to traditional multiple regression modes, PLS model type is more effective for constructing a multiple linear relationship between dependent and independent variables if these independent variables are severely autocorrelative [*Haenlein and Kaplan*, 2004; *Rosipal and Krämer*, 2006; *Wold et al.*, 1984]. Moreover, the outliers were removed via residual analysis for correcting the PLS model. Finally, we predicted the spatial distribution of leaf $\delta^{13}C$ for C_3 plants in China based on the interpolation of the PLS model.

3. Results
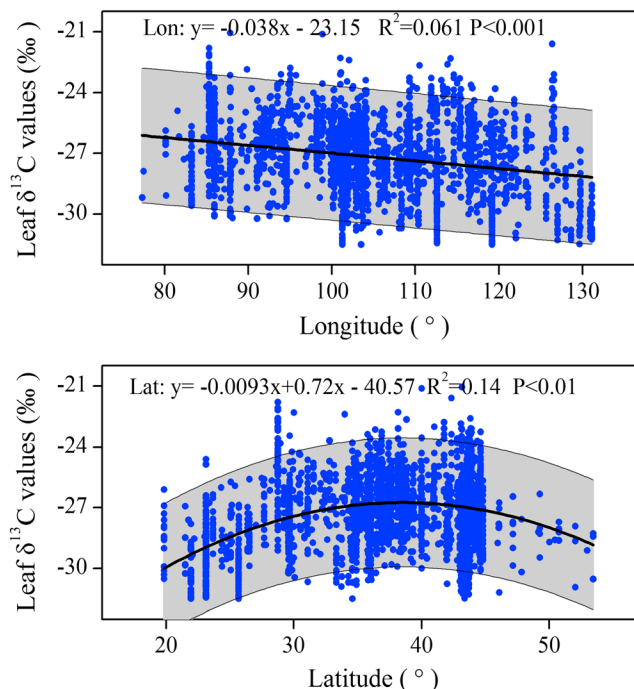
3.1. The Spatial Distribution and Overview of Leaf $\delta^{13}C$ in China

The frequency histogram of leaf $\delta^{13}C$ showed a sequential variation, primarily ranging from $-21.05‰$ to $-31.51‰$, with a mean value of $-27.15‰$. The sampled data of leaf $\delta^{13}C$ were collected from almost all of China, although most data were concentrated in central and western China (Figure 1). More intensive leaf $\delta^{13}C$ sampling was conducted on the Loess Plateau, on the Qinghai-Tibet Plateau, and in eastern Inner Mongolia. Leaf $\delta^{13}C$ sampling from southeastern China was relatively sparser. For the spatial patterns of leaf
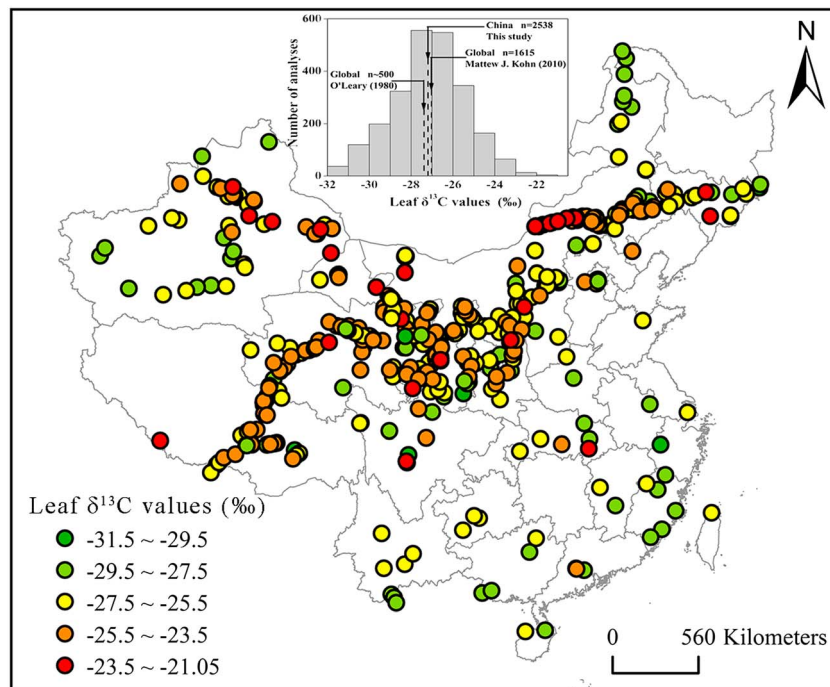
Figure 1. Spatial distribution and frequency histogram of leaf δ^{13}C (‰) sampled from China.

δ^{13}C, we further analyzed the linear relationship between leaf δ^{13}C and longitude, latitude, respectively (Figure 2). Leaf δ^{13}C slightly decreased as longitude increased ($P < 0.01$, slope $= -0.038$‰ per degree) but first increased and then decreased as the latitude increased ($P < 0.01$, $R^2 = 0.14$). Combined with Figure 1, we found that high leaf δ^{13}C mostly collected from central and western China, such as Loess Plateau and Qinghai-Tibet Plateau, southern Xinjiang province, and most areas of Inner Mongolia.

3.2. Patterns of Leaf δ^{13}C Across Life Forms and Phylogeny Types

Leaf δ^{13}C was varied with different plant species. Among all observations, the maximum leaf δ^{13}C (-21.05‰) was found in *Alhagi sparsifolia*, a sub-shrub sampled from Bihu Lake, where the annual rainfall is only 164 mm. The minimum leaf δ^{13}C (-31.5‰) was found in *Castanopsis sp.*, an evergreen tree in Lingshishan National Forest Park (in Fujian Province), where the annual rainfall is 1780 mm. The inner-class average of leaf δ^{13}C varied markedly across the life forms, ranging from -26.52‰ for subshrubs to -28.99‰ for subtrees (Table 1). The order of averaged leaf δ^{13}C from different life forms was as follows: subshrubs (-26.52‰) > herbs (-26.94‰) = shrubs (-27.17‰) > trees (-27.69‰) > subtrees

Figure 2. Variation of leaf δ^{13}C (‰) along longitude and latitude. The gray bands represent 95% prediction intervals.

Table 1. Overall Patterns of Leaf $\delta^{13}C$ Values for Plant Life Forms and Phylogeny Types

	N	Min	Max	Average	SD
Life Forms					
Herbs	1303	−31.50	−21.60	−26.94	1.61
Annual herbs	166	−30.85	−22.20	−27.23	1.74
Perennial herbs	1023	−31.50	−21.60	−26.84	1.60
Subshrubs	148	−30.53	−21.05	−26.52	1.69
Shrubs	411	−31.41	−22.30	−27.17	1.85
Deciduous shrubs	359	−31.27	−22.30	−26.98	1.77
Evergreen shrubs	44	−31.41	−23.88	−28.57	1.88
Subtrees	75	−31.42	−26.10	−28.99	1.47
Trees	437	−31.50	−23.46	−27.69	1.75
Deciduous trees	188	−31.47	−23.46	−27.88	1.65
Evergreen trees	230	−31.50	−23.88	−27.54	1.84
Phylogeny Types					
Dicots	1766	−31.5	−21.05	−27.31	1.76
Monocots	354	−31.167	−21.6	−26.36	1.57
Gymnosperms	137	−30.392	−23.88	−26.74	1.52
Ferns	22	−31.04	−23.4	−28.97	1.78

(−28.99‰) (Figure 3). Moreover, no remarkable difference was found between annual (−27.23‰) and perennial herbs (−26.84‰), and no notable distinction was found between evergreens (−27.54‰) and deciduous trees (−27.88‰). Conversely, the leaf $\delta^{13}C$ values of evergreen shrubs (−28.57‰) were ~2‰ lower than deciduous shrubs (−26.98‰).

In addition, the order of averaged leaf $\delta^{13}C$ for all phylogeny types was monocots (−26.36‰) > gymnosperms (−26.74‰) = dicots (−27.31‰) > ferns (−28.97‰) (Figure 3 and Table 1). This finding indicated that monocots sampled at the sites in our study have higher leaf $\delta^{13}C$ than other phylogeny types.
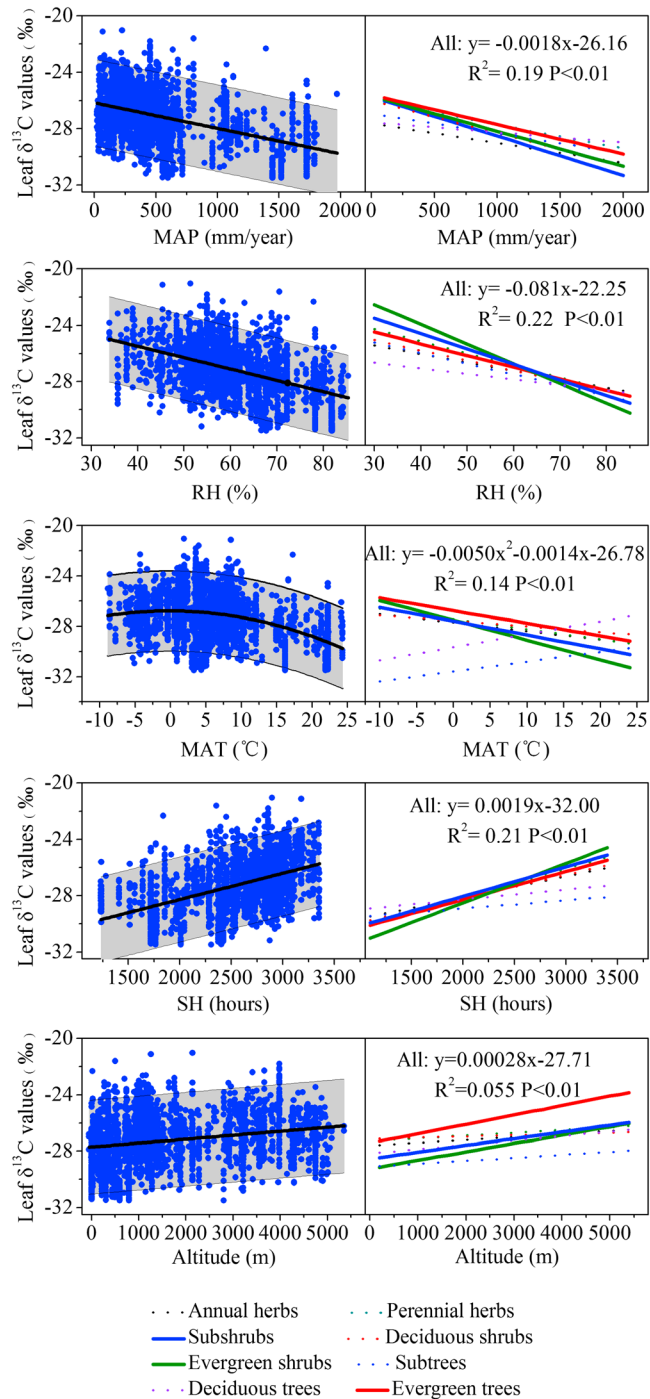
3.3. Relationships Between Leaf $\delta^{13}C$ and Environmental Factors

Figure 4 shows the relationship between leaf $\delta^{13}C$ (‰) and environmental factors for all life forms (Figure 4, left column) and for each different life form (Figure 4, right column) in the sampling data. For all the observations (n = 2538) in our database, leaf $\delta^{13}C$ had negative correlations with mean annual precipitation (MAP, slope = −0.18‰/100 mm, R^2 = 0.19) and relative humidity (RH, slope = −0.081/percent humidity, R^2 = 0.22), implying higher leaf $\delta^{13}C$ values in drought environments compared with rainy and wet areas. This correlation is also suited to each life forms (Figure 4, right column, and Table 2). Leaf $\delta^{13}C$ was positively related to solar hours (SH, slope = 0.0019‰/hour, R^2 = 0.21), showing that leaf $\delta^{13}C$ values could increase with longer solar hours. By contrast, leaf $\delta^{13}C$ had slighter correlation with altitude (slope = 0.28‰/1000 m, R^2 = 0.055). Leaf $\delta^{13}C$ of most life forms were positively related to SH and altitude, except for subtrees, deciduous shrubs, and deciduous trees (e.g., deciduous shrubs and deciduous trees are uncorrelated with altitude). The relationship between leaf $\delta^{13}C$ values and mean annual temperature (MAT) was relatively weak and showed a second-order quadratic curve

Figure 3. Mean comparison of leaf $\delta^{13}C$ (‰) for the dominant plant (a) life forms and (b) phylogeny types. The length of the column and error bars represent mean values of leaf $\delta^{13}C$ and its standard error. The signs with lowercase letters (a, b, c, and d) indicate significant differences at $P < 0.05$.

Figure 4. The relationship between leaf $\delta^{13}C$ (‰) and five environmental factors: mean annual precipitation (MAP, mm/year), relative humidity (RH, %), mean annual temperature (MAT, °C), sunshine hours (SH, hours), and altitude (m) for all samples (All) and different life forms. The solid lines represent a strong relationship (the higher slope on the premise of linear significantly) between leaf $\delta^{13}C$ values and environmental factors among the life forms. Conversely, the dashed lines represent a weaker linearity for the remaining life forms. The gray bands represent 95% prediction intervals.

($R^2 = 0.14$, $P < 0.01$). The leaf $\delta^{13}C$ of subtrees and deciduous trees increased as MAT increased, but the leaf $\delta^{13}C$ decreased for other life forms under the same conditions (or has no significant change for deciduous shrubs). This phenomenon suggests that the response of leaf $\delta^{13}C$ to rising air temperatures is complex and varies for different life forms. In summary, leaf $\delta^{13}C$ is affected by kinds of environmental factors, such

Table 2. Linear Regression of Leaf δ^{13}C (‰) With Environmental Variables (MAP, RH, MAT, SH, and Altitude) in China

	MAP			RH			MAT			SH			Altitude		
	Slope	R^2	Sig.	Slope	R^2	Sig.	Slope	R^2	Sig.	Slope	R^2	Sig.	Slope	R^2	Sig.
Annual herbs	−0.0014	0.11	**	−0.060	0.076	**	−0.063	0.050	**	0.0015	0.098	**	0.00021	0.025	**
Perennial herbs	−0.0017	0.12	**	−0.086	0.15	**	−0.072	0.064	**	0.0020	0.18	**	0.00019	0.033	**
Subshrubs	−0.0028	0.071	**	−0.083	0.14	**	−0.087	0.031	*	0.0020	0.12	**	0.00067	0.14	**
Deciduous shrubs	−0.0023	0.17	**	−0.072	0.18	**	−0.036	0.0064	-	0.0017	0.20	**	0.00087	0.00019	-
Evergreen shrubs	−0.0025	0.45	**	−0.14	0.41	**	−0.14	0.39	**	0.0028	0.38	**	0.00060	0.14	**
Subtrees	−0.0013	0.046	*	−0.070	0.026	*	0.10	0.074	*	0.00058	-	-	0.00021	-	-
Deciduous trees	−0.00073	0.018	*	−0.040	0.058	**	0.092	0.062	*	0.00070	0.028	*	0.00031	0.0099	-
Evergreen trees	−0.0021	0.36	**	−0.11	0.43	**	−0.098	0.25	**	0.0021	0.27	**	0.00048	0.16	**

*$P < 0.05$;
**$P < 0.01$; - no significance.

as MAP, RH, SH, altitude, and MAT, but the overall effects are still relatively weak, in particular the effect of MAT and altitude. Besides, the slopes of leaf δ^{13}C across environmental factors were significantly different when the species were divided into life forms. We found that leaf δ^{13}C from subshrubs, evergreen shrubs, and evergreen trees show a slightly higher correlation with environmental factors than from other life forms (Figure 4, right column, and Table 2).

According to the above results, we established a PLS regression of leaf δ^{13}C with environmental factors as follows:

$$Leaf\ \delta^{13}C = -26.59 + 0.0063^*MAT + 0.068^*SH + 0.00020^*altitude$$
$$- 0.00081^*MAP - 0.0043^*RH$$
$$R^2 = 0.33, n = 2415$$

And then we attempted to apply this model into the entire study region (Figure 5). Figure 5 shows that leaf δ^{13}C is higher in western China, such as Qinghai-Tibet Plateau, Loess plateau, southern Xinjiang province, and most areas of Inner Mongolia. Conversely, lower leaf δ^{13}C appeared in northeastern and southeastern China.

4. Discussion

4.1. Overall Patterns of Leaf δ^{13}C in China

This work presented an analysis of the leaf δ^{13}C of a large number of terrestrial C$_3$ plant species throughout China. Our analysis indicated that the arithmetic mean of leaf δ^{13}C from 2538 observations in China is −27.15‰, which was nearly identical to the global average of leaf δ^{13}C, −27.0‰. The latter was reported by *Kohn* [2010], who collected leaf δ^{13}C values from approximately 570 sites on a global scale. Moreover, our result was slightly higher than the global average (−27.25‰) reported by *O'Leary* [1988]. The histogram of δ^{13}C values showed the range from −21.05‰ to −31.50‰, with the maximum δ^{13}C in relatively arid ecosystems and the minimum in the tropical rain forest. This range also demonstrated the vast niche breadth and extensive adaptability of C$_3$ plants in China.

On further analysis, we found that high leaf δ^{13}C mostly appeared in central and western China, such as Loess Plateau and Qinghai-Tibet Plateau, southern Xinjiang province, and most areas of Inner Mongolia.

4.2. Variations in Leaf δ^{13}C Across Life Forms and Phylogeny Types

Various genetic and environmental factors generate the abundant diversity in the structure and function of terrestrial plants [*Díaz and Cabido*, 2001; *Swenson*, 2012; *Tilman et al.*, 1997]. In recent studies, one hot spot has been determining which and how structural and functional traits can be used to identify plant species and to infer the environmental conditions during the life of studied plants [*Flynn et al.*, 2011; *Norberg et al.*, 2001; *Suding et al.*, 2008]. In this study, we found obvious leaf δ^{13}C distinction between life forms: subshrubs > herbs = shrubs > trees > subtrees. Previous studies have also indicated a robust link between leaf δ^{13}C and life forms. *Brooks et al.* [1997] demonstrated that life forms could explain 50% of the variation in leaf δ^{13}C based on the sampling of the dominant species in three boreal forest ecosystems. They ascribed the
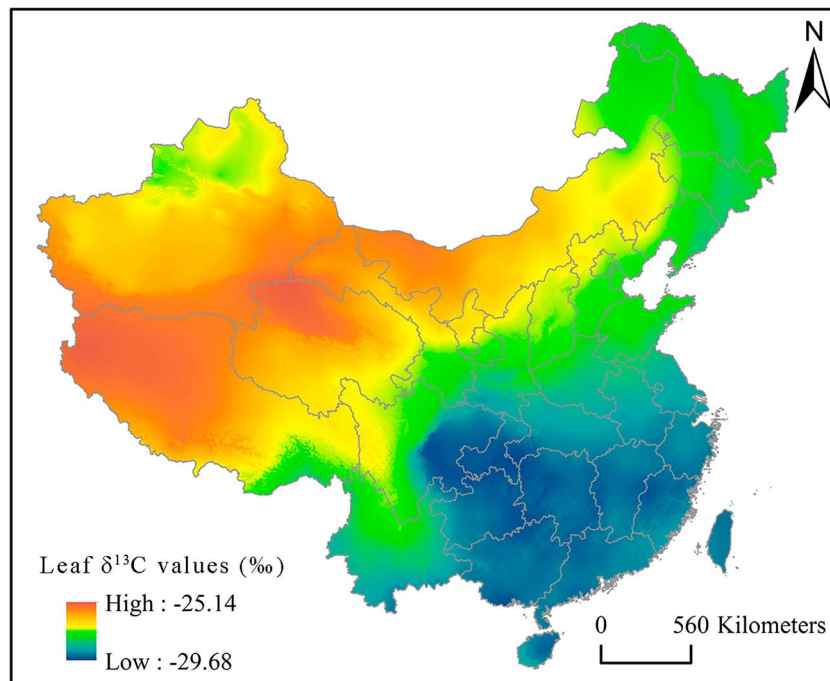
Figure 5. The spatial pattern of potential distributions of leaf $\delta^{13}C$ values, which is simulated based on a partial least squares model (R^2 = 0.33, n = 2415).

variation in leaf $\delta^{13}C$ among different life forms to light intensity and leaf longevity, suggesting that undergrowth leaves have lower leaf $\delta^{13}C$ values compared with canopy leaves, because the light intensity is reduced from canopy to undergrowth, and evergreen leaves also have lower $\delta^{13}C$ values compared with deciduous leaves due to the lower c_i/c_a ratios of intercellular than ambient CO_2 for evergreen plants. *Medina and Minchin* [1980] pointed the vertical stratification of leaf $\delta^{13}C$ could also be caused by lower $\delta^{13}C_{air}$ values of soil emission (lower proportion of δ^{13} values of CO_2 closer to ground). Based on the results from *Brooks et al.* [1997] and *Medina and Minchin* [1980], the rank of leaf $\delta^{13}C$ averaged across life forms should be tree > shrub > herb (i.e., the vertical gradients of leaf $\delta^{13}C$ in a forest), deciduous > evergreen leaves at a single sampling site. However, *Song et al.* [2008] found that the leaf $\delta^{13}C$ of dominant species on the Tibetan Plateau follows the order xeromorphs > graminoid ~ sedges > alpine shrub > evergreen broadleaved tree > evergreen coniferous, an order that was explained by the difference in species' adaptation to water stress. These studies showed that the link between leaf $\delta^{13}C$ and life forms varies among different areas. In our study, we found that averaged leaf $\delta^{13}C$ of herbs was higher than trees and slightly higher than shrubs (Figure 3), which could be related to different nitrogen allocation strategies in leaves. Trees and shrubs prefer to store more nitrogen and biomass in cell walls to increase the structural toughness of leaves, and consequently less nitrogen in the photosynthetic apparatus, which results reduced photosynthetic capacity [*Hikosaka et al.*, 1998; *Onoda et al.*, 2004; *Warren and Adams*, 2004]. Conversely, herbs prefer to allocate more nitrogen into RuBPCase and thylakoid resulting in increased photosynthetic capacity [*Takashima et al.*, 2004; *Wright et al.*, 2004]. Finally, the higher photosynthetic capacity will reduce more CO_2 concentration in leaf (c_i), resulting in lower c_i/c_a and higher leaf $\delta^{13}C$.

Therefore, plant functional grouping (e.g., life form and phylogeny type) is an important factor that regulates the magnitude of leaf $\delta^{13}C$ in the same or similar environments according to environmental adaptability and reflects the adaptability of plants to that habitat. And these factors could partly determine the spatial distribution of appropriate conditions for different species.

4.3. Response of Leaf $\delta^{13}C$ to Different Climate Variables

Climate change has a lasting impact on spatial variation and its characteristics of vegetation, potentially altering certain functional traits of plants, such as leaf $\delta^{13}C$ [*Diefendorf et al.*, 2010]. Previous studies

have proposed that variation in leaf $\delta^{13}C$ is affected by water availability, temperature and altitude, and so on [*Diefendorf et al.*, 2010; *Ning et al.*, 2002; *Lin*, 2008]. However, no consistent conclusion has been reached about the type (positive or negative) and intensity of these effects.

In this study, we analyzed and quantified the relationship between water availability (including MAP and RH) and leaf $\delta^{13}C$ values based on our database. We found that leaf $\delta^{13}C$ dropped by 0.18‰ for every 100 mm increase in MAP and decreased by 0.81‰ for every 10% increase in RH in China, findings that align with related studies at regional or global scales. *Diefendorf et al.* [2010] suggested that MAP is the strongest predictor of Δleaf (i.e., leaf $\delta^{13}C$) among the climate variables in a global database because of the markedly positive correlation of MAP with Δleaf. Water deficit might reduce either stomata conductance or stomata density, leading to a lower c_i/c_a and a positive leaf $\delta^{13}C$ [*Sun et al.*, 2003; *Warren et al.*, 2001]. However, in the wet environment, the slope of leaf $\delta^{13}C$ with MAP will likely be "flattened" as high MAP, indicating that carbon isotope discrimination remains relatively constant as MAP further increase [*Kohn*, 2010]. Subshrubs, leaf $\delta^{13}C$ of evergreen shrubs, and evergreen trees showed a steeper slope as MAP and RH increased, indicating that their leaf $\delta^{13}C$ is more sensitive to water availability than other life forms.

The response of leaf $\delta^{13}C$ to MAT is important but relatively complex. *Farquhar et al.* [1984] noted that the photosynthetic enzyme activities strengthened as temperature increased, resulting in a lower ratio of c_i/c_a and higher $\delta^{13}C$ within a certain range. Conversely, low temperature was believed to reduce the transmission rate of c_i and lead to a low ratio of c_i/c_a and high $\delta^{13}C$. In this study, we found a second-order quadratic curve for the relationship of leaf $\delta^{13}C$ with MAT, where leaf $\delta^{13}C$ reached its peak value when MAT = −0.14°C. The leaf $\delta^{13}C$ of subtrees and deciduous trees slightly increased as MAT increased, but the leaf $\delta^{13}C$ slightly decreased for other life forms under the same conditions (or has no significant change for deciduous shrubs), resulting in a quadratic function of leaf $\delta^{13}C$ with MAT when all the data were pooled. We also found a weakly positive correlation of leaf $\delta^{13}C$ with elevation (slope = 0.28‰ per 1000 m). Many studies treated altitude as a special environmental factor that integrated several climate factors such as temperature, relative humidity, partial pressure of CO_2, and vapor pressure deficit (VPD) [*Körner et al.*, 1991; *Morecroft and Woodward*, 1990]. Variation of leaf $\delta^{13}C$ values along altitude gradients has been reported to be consistently positive in different locations around the world [*Hultine and Marshall*, 2000; *Marshall and Zhang*, 1994; *Körner et al.*, 1988]. For instance, *Körner and Farquhar* [1988] analyzed the 150 leaf $\delta^{13}C$ samplings from mountains around the world, including Australia, China, New Zealand, and Venezuela, and discovered a 1.2 ± 0.9‰ increase for every 1000 m increase in elevation. At upper elevations, cold temperature, reduced CO_2 partial pressure and low VPD could individually or synergistically decrease leaf $\delta^{13}C$ through controlling the stomatal conductance, CO_2 transmission velocity, or photosynthetic efficiency [*Craig*, 1957; *Körner et al.*, 1991; *Morecroft and Woodward*, 1990].

Hence, high leaf $\delta^{13}C$ mostly appeared in central and western China, such as Loess Plateau and Qinghai-Tibet Plateau, southern Xinjiang province, and most areas of Inner Mongolia, which might be related to the less rainfall, high altitude, and long-time sunshine in these regions. Conversely, low leaf $\delta^{13}C$ in northeastern and southeastern China could be explained by the moist and cloudy weather as well as the low altitude in those regions.

The leaf $\delta^{13}C$ of life forms has different responses to each climate variable change (Figure 4 and supporting information). For example, leaf $\delta^{13}C$ of evergreen species has higher change rate (steeper slope under the precondition of $P < 0.05$) than deciduous species under changing environment conditions in this study, except for evergreen trees versus deciduous shrubs with changing MAP. Combining with the results of previous studies, we explored some possible explanations for this tendency. On the one hand, the deciduous species is more vulnerable to water stress-induced embolism than the evergreen species under arid and hot environment. Hence, deciduous species tend to shed their leaves to reduce the risk of water stress-induced embolism [*Sobrado*, 1993], while evergreen species are more inclined to enhance WUE (i.e., higher leaf $\delta^{13}C$) to maintain physiological capacity [*Chen et al.*, 2009; *Wang et al.*, 2013]. So compared with deciduous species, evergreen species have higher leaf $\delta^{13}C$ changing rate for tackling the environment change. On the other hand, different carbohydrate storage strategies of deciduous and evergreen species are maybe another key point. Evergreen species prefer to use new carbon (i.e., recently assimilated carbohydrate) for
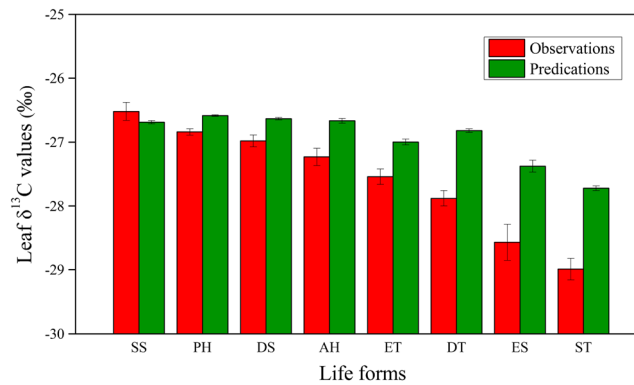
Figure 6. The comparison of observed and predicated averaged leaf $\delta^{13}C$ with PLS model across life forms, where SS, PH, DS, AH, ET, DT, ES, and ST represent subshrubs, perennial herbs, deciduous shrubs, annual herbs, evergreen trees, deciduous trees, evergreen shrubs, and subtrees, respectively.

sprouting in spring, while deciduous spices rely more on remobilization old carbon (assimilated during the previous year and stored overwinter) [*Epron et al.*, 2012; *Kagawa et al.*, 2006; *von Felten et al.*, 2007]. The new foliar carbon is produced by recent photosynthesis, theoretically, which can better record the recent environment change than the remobilization old foliar carbon. In other words, leaf $\delta^{13}C$ of evergreen species could be more sensitive to recently environmental changes than that of deciduous species. In addition, some factors, such as coordination between stomatal conductance and photosynthetic capacity, rate of leaf area to water-conducting tissue, can also adjust the response of leaf $\delta^{13}C$ to environmental changes for different life forms [*Cernusak et al.*, 2013].

Overall, although plant functional groups and environmental conditions are inherently variable, variation of plant leaf $\delta^{13}C$ along environmental gradients offers one way to evaluate potential plant responses to climate change. And the different response of leaf $\delta^{13}C$ of life forms to climate change might also provide a reference for future studies simulating the response of vegetation distribution to climate change.

4.4. Model Uncertainty

We adopted "leave-one-out cross-validation" method [*Arlot and Celisse*, 2010] to evaluate performance of the PLS model and also analyzed the relative error of predicated leaf $\delta^{13}C$ compared with observed leaf $\delta^{13}C$ (Figure S6). The most of relative error is ranged from −10% to 10%. The underestimated leaf $\delta^{13}C$ sites were mainly located in the north and west of China, whereas the overestimated leaf $\delta^{13}C$ sites were found in most of China. And the PLS model build in our study overestimated leaf $\delta^{13}C$ for most life forms, especially for deciduous trees, evergreen shrubs, and subtrees (i.e., difference between the predicated and observed averaged leaf $\delta^{13}C$ is more than 1‰) (Figure 6), which means that there may be a certain risk in applying the PLS model for deciduous trees, evergreen shrubs, and subtrees. On the other hand, due to the limitation of data, the PLS model could only explain 33% variation in leaf $\delta^{13}C$, which would led to a high-model uncertainties when we applied this model into continental scale. The further work would be focused on collecting more data, including variety of physiological and biochemical features (e.g., SLA, specific leaf area; N_{area}, nitrogen per unit leaf area; and RuBPCase content) [*Prentice et al.*, 2011; *Takashima et al.*, 2004], to improve this model.

Besides, this leaf $\delta^{13}C$ database lacks abundant sampling data from the western Qinghai-Tibet Plateau as well as northeastern and southeastern China. These data may even lead to slightly higher average values of leaf $\delta^{13}C$ in China. Therefore, we suggest that more research efforts are needed in these regions for a clearer understanding of the spatial distribution of leaf $\delta^{13}C$.

5. Summary

The collected leaf $\delta^{13}C$ data in this study cover almost all of China, with an averaged value of −27.15‰. High leaf $\delta^{13}C$ mostly appeared in central and western China, such as Loess Plateau and Qinghai-Tibet Plateau, southern Xinjiang province, and most areas of Inner Mongolia. Further analysis showed that leaf $\delta^{13}C$ was not only closely correlated with plant life forms but also varied along with environmental change. We concluded that environmental factors (such as precipitation, air temperature, sunshine hours, and altitude) are the important factors influencing the spatial distribution of leaf $\delta^{13}C$ in China. In other words, response of leaf $\delta^{13}C$ to climate change could be a powerful tool in reconstruction of paleoclimatic environments and predication of vegetation succession under future climate change.

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