



# Variations and determinants of carbon content in plants: a global synthesis

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**Abstract.** Plant carbon (C) content is one of the most important plant traits and is critical to the assessment of global C cycle and ecological stoichiometry; however, the global variations in plant C content remain poorly understood. In this study, we conducted a global analysis of the plant C content by synthesizing data from 4318 species to document specific values and their variation of the C content across plant organs and life forms. Plant organ C contents ranged from 45.0 % in reproductive organs to 47.9 % in stems at global scales, which were significantly lower than the widely employed canonical value of 50 %. Plant C content in leaves (global mean of 46.9 %) was higher than that in roots (45.6 %). Across life forms, woody plants exhibited higher C content than herbaceous plants. Conifers, relative to broad-leaved woody species, had higher C content in roots, leaves, and stems. Plant C content tended to show a decrease with increasing latitude. The life form explained more variation of the C content than climate. Our findings suggest that specific C content values of different organs and life forms developed in our study should be incorporated into the estimations of regional and global vegetation biomass C stocks.

## 1 Introduction

Carbon (C) is one of the most abundant elements in all living organisms (Hessen et al., 2004; Dietze et al., 2014). Plant photosynthesis transfers C from CO<sub>2</sub> to the forms of biological compounds to maintain metabolic functions and build basic structures (Dietze et al., 2014; Martínez-Vilalta et al., 2016). This process creates a huge organic C pool in terrestrial vegetation (Schlesinger and Bernhardt, 2013), which is usually estimated by multiplying total plant biomass by a corresponding biomass C conversion factor, i.e., the C content (Bert and Danjon, 2006; Thomas and Martin, 2012). The most widely employed C content in plants is 50 % in the regional and global vegetation C stock estimations (De Vries et al., 2006; Keith et al., 2009; Lewis et al., 2009; Saatchi et al., 2011; Zhu et al., 2015, 2017). Originally, this value was calculated from an average molecular formula CH<sub>1.44</sub>O<sub>0.66</sub>, i.e., elemental composition of about 50 % C, 6 % hydrogen, 44 % oxygen, and trace amounts of several metal ions in living plant wood (Pettersen, 1984; Bert and Danjon, 2006).

However, an increasing number of studies have indicated that C content varied significantly among plant organs (Åriksson and Eriksson, 1998; Bert and Danjon, 2006; Yao et al., 2015), life forms (Tolunay, 2009; Fang et al., 2010; Cao and Chen, 2015), biomes (He et al., 2006; Martin and Thomas, 2011; Martin et al., 2015), and even across individuals (Elias and Potvin, 2003; Uri et al., 2012; Martin et al., 2013). Using the default value of 50 % as biomass C con-

version factor which ignores the variation of C content may lead to biases (Zhang et al., 2009; Martin and Thomas, 2011; Rodrigues et al., 2015). For example, a change of 1 % wood C content from the canonical value of 50 % can bring up to  $\sim 7$  Pg C variation in global vegetation C stocks, which is almost equivalent to half of the vegetation C stocks of the continental United States (Dixon et al., 1994; Jones and O'Hara, 2016). Therefore, accurate knowledge of plant C content is crucial for estimating the potential magnitude of C sequestration in different biomes and understanding the roles of vegetation in the global C cycle (Thomas and Martin, 2012).

To reduce the uncertainty in estimation of vegetation C stocks, several studies have used the species-specific organ C content at regional scales (Jones and O'Hara, 2012; Rodrigues et al., 2015; Wu et al., 2017). Basically, the weighted mean C content (WMCC) of plants, especially woody plants, was useful for precise C stock estimation (Zhang et al., 2009). However, it is hard to obtain available data of C content and biomass allocation for every species and organ in diverse vegetation. Combining the phylogenetic, taxonomic and environment-dependent traits of species, the generalized C contents of specific life forms provide an alternative for realistic estimations (Thomas and Martin, 2012; Wu et al., 2017). For instance, the Intergovernmental Panel on Climate Change (IPCC, 2006) provided the wood C content of trees in tropical/subtropical forests (47 %) and temperate/boreal forests (48 % of broad-leaved trees and 51 % of conifers). Although the values were more accurate than the default value of 50 %, errors were still introduced to C stock estimation in the actual application (Martin and Thomas, 2011), especially when the uncertainty that resulted from estimation using available plant C contents of limited specific life forms could not be eliminated (Thomas and Martin, 2012). Thus, the specific C contents of different life form plants require explicit consideration and application in vegetation C stock evaluations. In addition, exploring the biogeographic pattern and driving factors of plant C content will be of benefit for the elucidation of ecological stoichiometry and the mechanisms of plants' response to global change (Fyllas et al., 2009; Ordoñez et al., 2009; Zhang et al., 2012).

For the above reasons, we compiled a global dataset of plant organ C content to provide referable C contents of plant organs in different life forms. We tried to answer the following two questions: (1) how much C do specific plant organs contain? (2) What are the biogeographical patterns of plant C content and the possible driving factors?

## 2 Material and methods

### 2.1 Data compilation

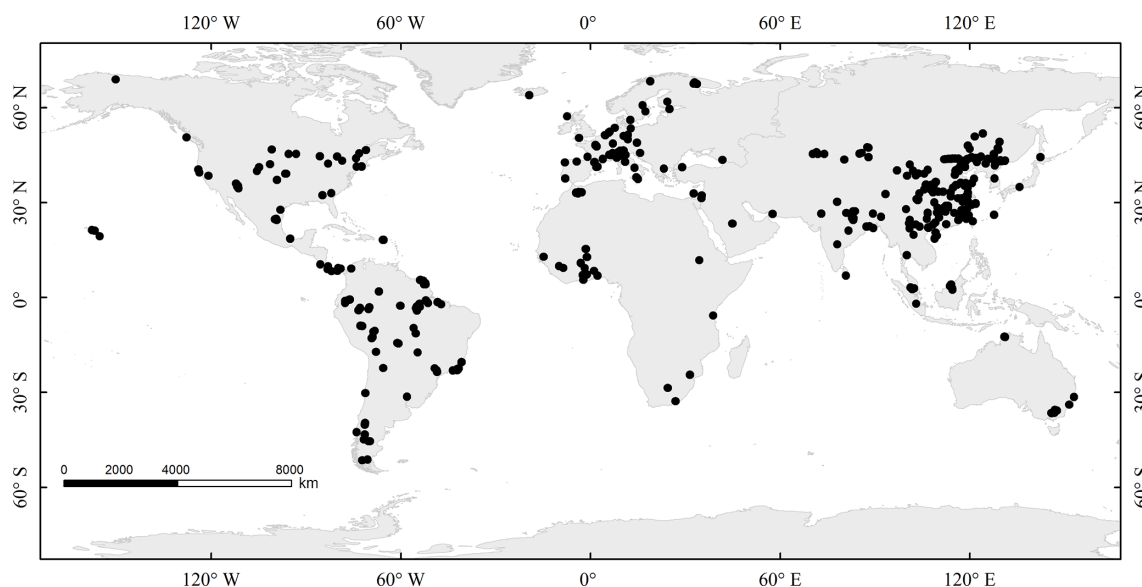
We searched Google Scholar (<https://scholar.google.com/>), Web of Science (<http://isiknowledge.com>), and CNKI (China National Knowledge Infrastructure) (<http://www.cnki.net/>)

for literatures reporting the C content of plants published from 1970 to 2016. We documented 315 publications according to the following two criteria: (1) the data from natural ecosystems (including wetland and mangrove) or plantation ecosystems (including grassland and cropland) were included, while the data from laboratory or field experiments were excluded; and (2) plant C content detected by two commonly used methods (i.e., the  $K_2Cr_2O_7-H_2SO_4$  oxidation and the combustion methods) was included, while studies that used the default value, assumed value, or values calculated from the chemical compositions were excluded from our data compilation. In addition, we also included data of specific plant organs from the TRY database (<https://www.try-db.org>) (Kattge et al., 2011) (Table S1 in the Supplement).

Finally, a total of 24 326 records of 4318 species in 1694 genera and 238 families were included in our global dataset (Fig. 1), in which 36.33 and 63.67 % were from literatures and the TRY database, respectively. For each data record, we documented the geographical information (latitude, longitude, and altitude), Latin binomial, genus and family of species, organ (reproductive organ, root, leaf, and stem), life forms, chemical compounds (lignin and cellulose), and plant C content. Plant life forms were divided into five categories: herbaceous species (herb), woody plants, fern, vine, and bamboo. Data of crops were separately analyzed in the herbaceous category. The woody plants were further categorized into three groups: evergreen broad-leaved woody plants, deciduous broad-leaved woody plants, and conifers. The data with no information on life forms were documented from Flora of China (<http://foc.eflora.cn>), Wikipedia (<https://en.wikipedia.org/wiki/Wiki/>), Useful Tropical Plants (<http://tropical.theferns.info>), or The Plant List (<http://www.theplantlist.org>). In order to explore biogeographic patterns and the driving factors of C content of plant organs, we used the latitude and longitude of each site to extract data of climatic variables (mean annual temperature, MAT, °C; mean annual precipitation, MAP, mm) from WorldClim (<http://www.worldclim.org/>) (Hijmans et al., 2005). Given that plant C content might vary with the growth stages of individuals (Elias and Potvin, 2003; Uri et al., 2012; Martin et al., 2013), we recorded the averaged C content of herbaceous species across different growth stages.

### 2.2 Statistical analyses

We first documented statistics of plant organ C content for different life forms, including arithmetic mean (Mean), median (Median), standard deviation (SD), and coefficient of variation (CV) (Table 1). The C content of each organ showed a normal distribution (Fig. 2), and thus the one-sample Student's *t*-test was used to determine whether the stem C content of woody plants significantly differed from the default value of 50 % and the IPCC values (47, 48, and 51 %), respectively. The two-sample Student's *t*-test was



**Figure 1.** Geographic distribution of sample sites used in this synthesis.

**Table 1.** Plant carbon content (%) in four organs across different life forms. *n* is the sample size, and SD is the abbreviation of standard deviation. Samples for stem include the samples from shoot, stem, twig, and branch. “–” indicates no data.

Life form	Reproductive organ		Root		Leaf		Stem	
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
Herbaceous plants	83	42.56 ± 4.57	749	42.45 ± 5.12	5181	44.73 ± 3.45	162	42.41 ± 3.54
Crop	42	42.40 ± 5.11	56	38.20 ± 5.23	85	41.32 ± 3.38	69	43.26 ± 3.15
Woody plants	57	48.56 ± 4.07	1392	47.43 ± 3.94	12 064	47.83 ± 3.81	3461	48.16 ± 3.27
Deciduous broad-leaved	17	46.81 ± 3.93	513	46.59 ± 3.55	5074	47.25 ± 3.42	1581	47.69 ± 2.68
Evergreen broad-leaved	29	49.64 ± 4.42	520	47.72 ± 4.14	4490	48.48 ± 3.86	1212	47.78 ± 3.58
Conifers	8	48.25 ± 2.56	252	48.43 ± 4.16	560	50.25 ± 3.33	502	50.48 ± 3.07
Fern	–	–	2	43.64 ± 3.83	98	44.47 ± 3.33	–	–
Vine	2	45.83 ± 0.33	38	46.25 ± 4.46	251	45.74 ± 4.77	82	46.73 ± 2.69
Bamboo	–	–	23	45.06 ± 4.28	30	42.98 ± 5.09	39	49.20 ± 3.54
All	142	45.01 ± 5.23	2306	45.64 ± 4.95	18 124	46.85 ± 3.98	3754	47.88 ± 3.49

used to determine whether statistical differences of plant organ C content existed between different life forms. Specifically, we compared the C contents of herbs vs. woody plants, conifers vs. deciduous broad-leaved woody plants, and conifers vs. evergreen broad-leaved woody plants.

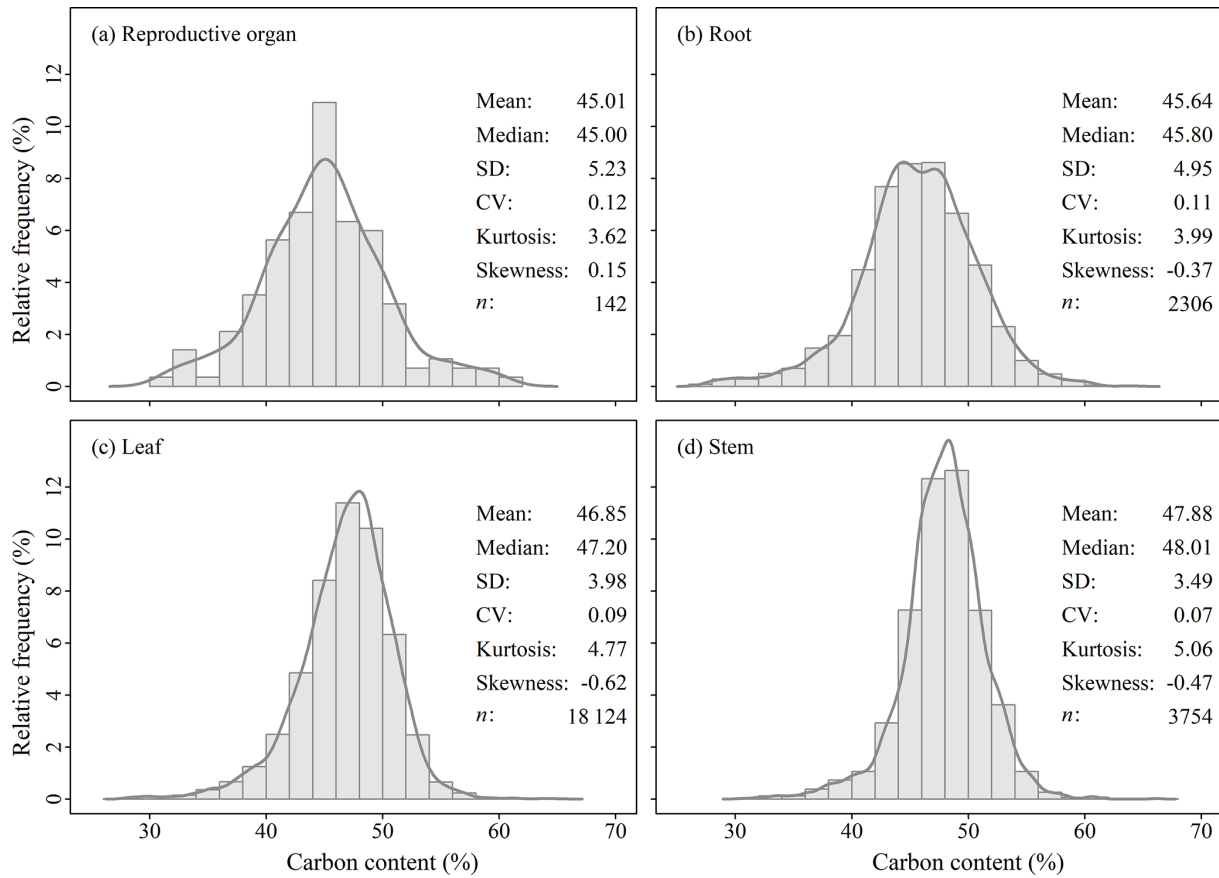
A linear model without accounting for other factors was used to explore biogeographical patterns of plant organ C content along latitudinal gradients, MAT and MAP (Han et al., 2011). To evaluate the effects of life form and climatic factors (i.e., MAT and MAP) on the variations of plant C contents, a partial generalized linear model was used to calculate the total explanation, the independent explanation, and the interactive explanation of climatic factors and life forms for different organs (i.e., reproductive organ, root, leaf, and stem) (Han et al., 2011). Additionally, a linear model and an analysis of variance (type III) were performed to test the vari-

ations of C contents explained by climatic factors and life forms. A linear model was used to explore the relationship of plant C content with the content of lignin and cellulose. All statistical analyses were performed in the R 3.3.1 software (R core Team, 2016).

### 3 Results

#### 3.1 Carbon content of plant organs

Plant C content varied significantly among organs. Arithmetic means of C content for reproductive organ, root, leaf, and stem were 45.01, 45.64, 46.85, and 47.88 %, respectively (Fig. 2, Table 1), all of which were significantly lower than the default value of 50 % ( $p < 0.05$ ). Plant organ C content also varied markedly across life forms (Table 1). Among



**Figure 2.** Histograms of carbon content of (a) reproductive organ, (b) root, (c) leaf and (d) stem. Abbreviations: SD, standard deviation; CV, coefficient of variation;  $n$  indicates sample size.

herbaceous plants, C content ranged from 42.41 % in stems to 44.73 % in leaves, and among woody plants, C content changed from 47.43 % in roots to 48.56 % in reproductive organs (Table 1). C contents in all four organs were significantly higher in the woody species than in the herbaceous species. Across woody species, C contents in roots, leaves, and stems of conifers were significantly higher than those of deciduous broad-leaved and evergreen broad-leaved woody plants. In addition, the C contents of ferns, vines, and bamboo ranged from 42.98 to 49.20 % (Table 1).

### 3.2 Latitudinal trends of carbon content and possible driving factors

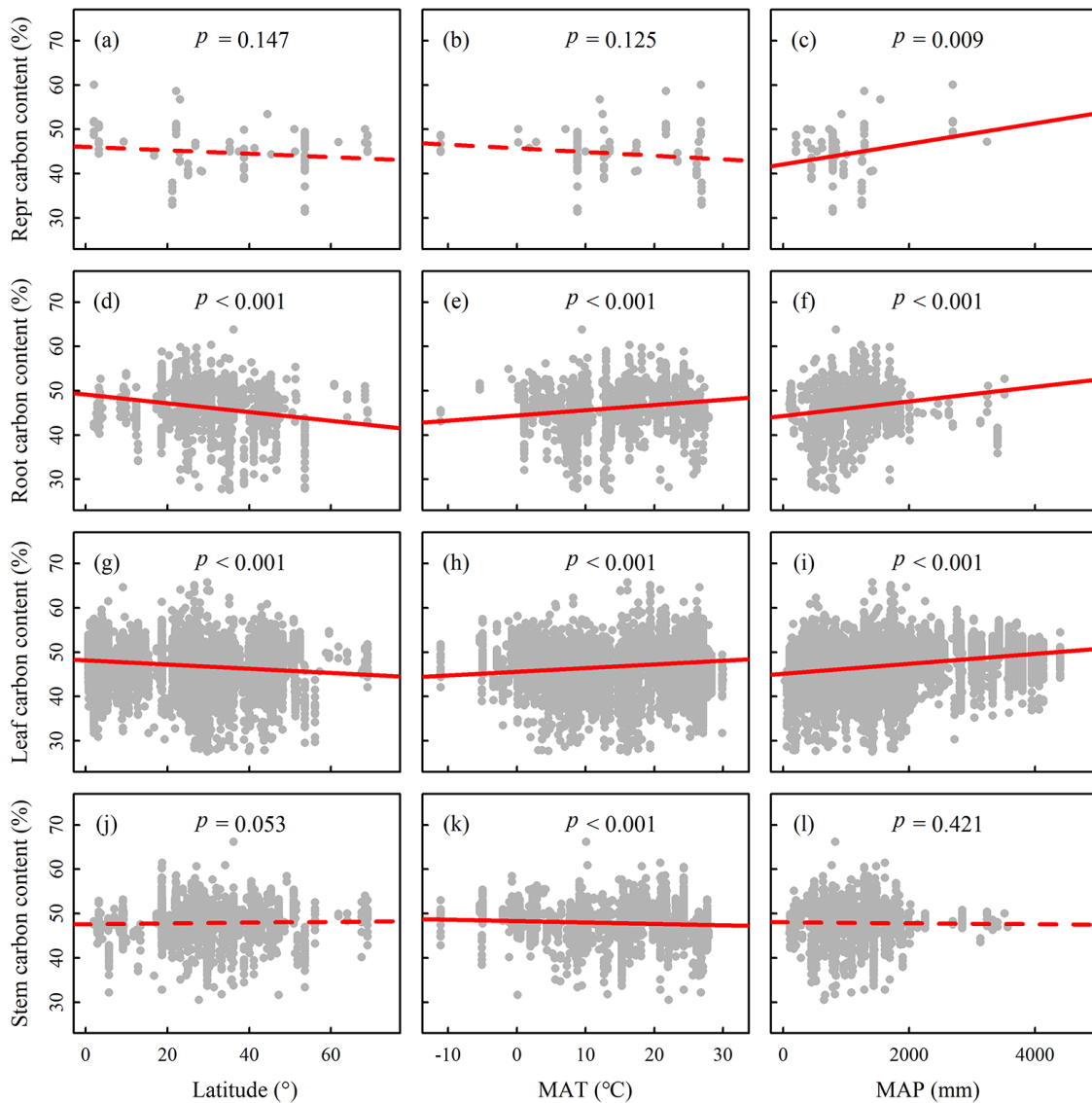
Plant C contents in roots and leaves decreased with increasing latitude and decreasing MAT and MAP ( $r^2 = 0.05$ ,  $p < 0.001$  in all cases), while reproductive and stem C content displayed no significant latitudinal trends ( $r^2 = 0.02$ ,  $p > 0.05$ ;  $r^2 < 0.01$ ,  $p > 0.05$ ; Fig. 3, Table S2).

The C content of plant organs was significantly affected by climatic factors ( $p < 0.05$  in stem), life form, and their interaction ( $p < 0.05$  in all cases, except for reproductive organs) (Tables S3–S6). The effects of climatic factors and life

forms on plant C content varied largely across the plant organs (Fig. 4). The independent explanations of climatic factors on the variation in the C contents of the reproductive organs, roots, leaves, and stems were 8.4, 0.2, 3.8, and 0.5 %, respectively. The variation of C content in the reproductive organs, roots, leaves, and stems explained independently by life forms were 19.8, 21.5, 7.2, and 10.0 %, respectively. The interactive explanations of climatic factors and life form on the variation of C content of the reproductive organs, roots, leaves, and stems were 15.7, 3.6, 5.2, and 0.7 %, respectively. These results demonstrated that the variation of plant C content was explained more by life form than by climatic factors (Fig. 4; Tables S3–S6).

## 4 Discussion

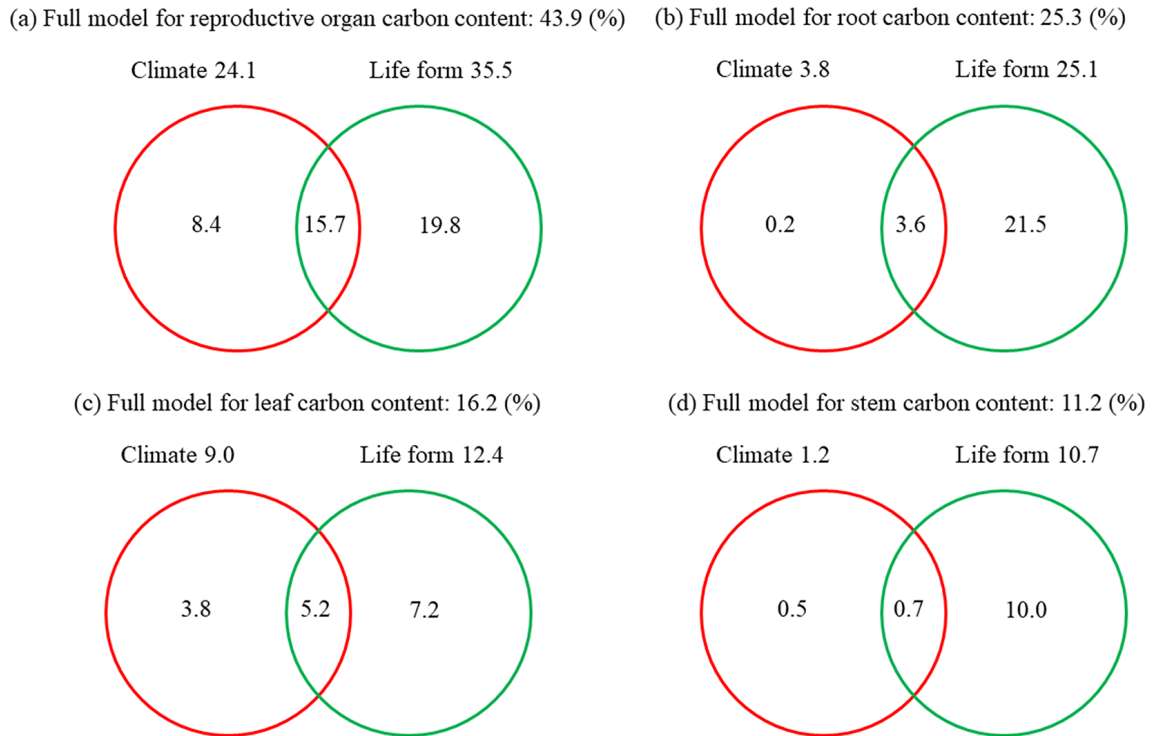
We evaluated plant C content across plant organs and life forms by establishing a global plant C content dataset. Our results showed that plant C content varied remarkably among organs, which was consistent with previous studies (Alriksson and Eriksson, 1998; Northup et al., 2005; Tolunay, 2009). Notably, we found that the global average C contents



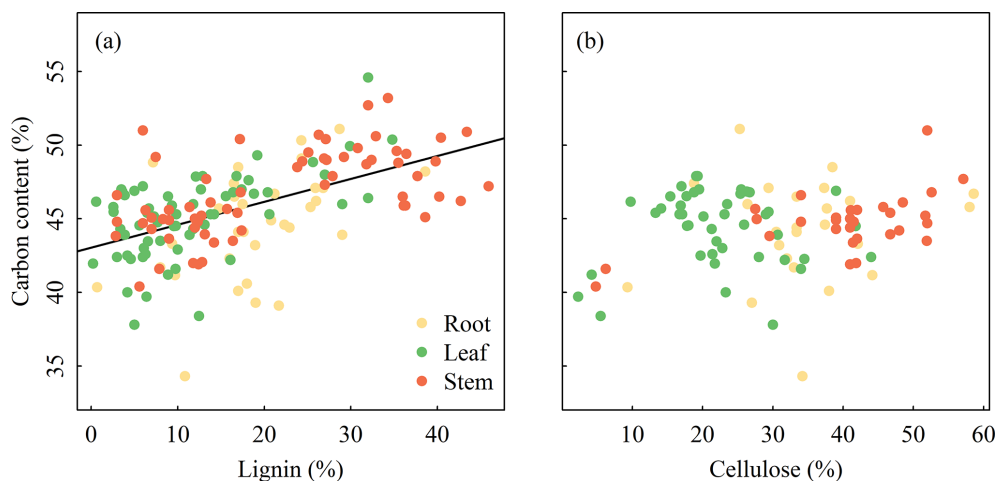
**Figure 3.** Trends in the plant carbon contents along latitude and climate gradients. MAT, mean annual temperature; MAP, mean annual precipitation. Ordinary least squares (OLS) regression lines are fit to the data. Solid lines indicate the significant relationships with  $p < 0.05$ , and dashed lines denote the insignificant relationships with  $p > 0.05$ . Abbreviations: repr carbon content refers to the reproductive organ carbon content. Plant carbon content in roots and leaves showed a significant latitudinal trend.

of four organs were significantly lower than the canonical value of 50 %, which was widely used to convert vegetation biomass to C stock at large scales, such as in temperate forests (De Vries et al., 2006), tropical forests (Lewis et al., 2009; Saatchi et al., 2011), and global forests (Keith et al., 2009). In addition, C contents of stems and leaves were significantly higher than another default value of 45.45 % proposed by Whittaker (1975), although the C contents of roots and reproductive organs showed no significantly statistical difference. Furthermore, our results showed that plant C contents varied significantly among life forms (Table 1). Among woody plants, the stem C contents of broad-leaved woody

species (i.e., 47.69 % in deciduous and 47.78 % in evergreen) and conifers (51.48 %) were comparable with those (47.7 and 50.8 %, respectively) reported by Thomas and Martin (2012). However, these data were significantly lower than the values of temperate broad-leaved woody species (48 %;  $p < 0.001$  and  $p = 0.018$ ) and conifers (51 %;  $p < 0.001$ ), though higher than those of tropical broad-leaved woody species (47 %;  $p < 0.001$  and  $p < 0.001$ ) proposed by IPCC (2006). This suggested that these values from IPCC may underestimate or overestimate the stem C content for broad-leaved trees and conifers at global scales.



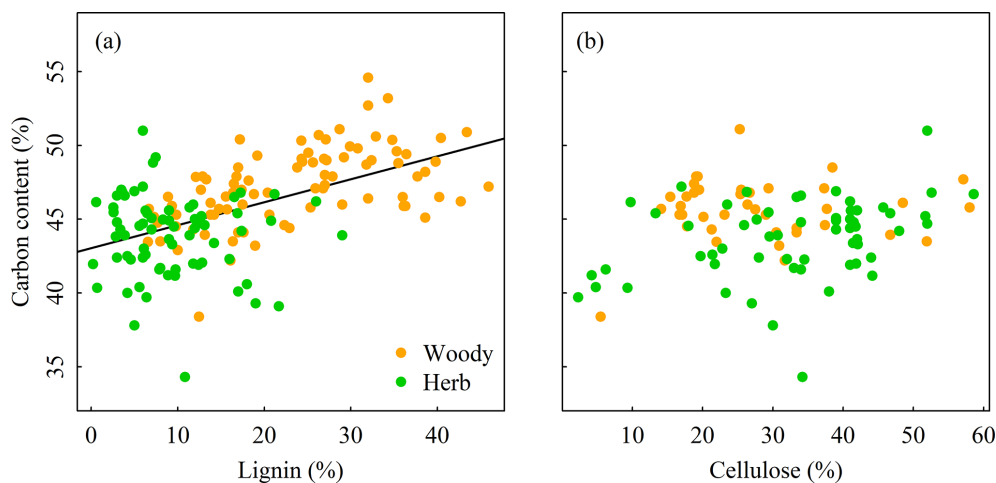
**Figure 4.** Variation partitioning ( $r^2$ ) of climate and life forms to account for the variation in plant carbon contents across different organs. (a) Reproductive organ, (b) root, (c) leaf, and (d) stem. Life form independently explained more variation of carbon content in each organ than climate.



**Figure 5.** Relationships between plant carbon content and lignin and cellulose among three organs. Plant carbon content increases significantly with the increasing lignin in plants ( $r^2 = 0.29$ ,  $p < 0.001$ ), whereas it is not correlated with the cellulose in plants.

The variation of plant C content among organs and life forms was associated with differences in their chemical compositions (Figs. 5–6). Plant organs are composed of several organic compounds with different C content, such as lignin (with C content of 63–66%), cellulose (with C content of about 44%), and nonstructural carbohydrates (NSC) (e.g., sugar or starch with C content of about 44%) (Adler, 1977;

Poorter and Bergkotte, 1992). Our result was consistent with previous findings that plant organs with higher lignin (e.g., stems) tend to have a higher C content than organs with lower lignin content (e.g., leaves, roots, and reproductive organs; Fig. 5a) (Savidge, 2000; Lamloom and Savidge, 2003; Bert and Danjon, 2006; Martin and Thomas, 2011). Despite the high lignin in roots, the C content in roots was lower than that



**Figure 6.** Relationships between plant carbon content and lignin and cellulose in woody plants and herbaceous plants. Plant carbon content increases significantly with increasing lignin in plants ( $r^2 = 0.29$ ,  $p < 0.001$ ), whereas it is not correlated with the cellulose in plants.

in leaves, probably because of the high proportions of protein and other C-rich compounds in leaves (Rouwenhorst et al., 1991; Niinemets et al., 2002) and high content of starch in roots (Bert and Danjon, 2006). The lowest C content in reproductive organs was consistent with its high quantities of NSC and low content of lignin (Barros et al., 1996). Across life forms, woody plants generally require proportionally greater investments of C at the cellular level to synthesize lignin to support structures with relatively low growth rate, which result in high lignin and C content (Fig. 6a). In contrast, the high relative growth rate of herbs is accordant with their low lignin and C content (Armstrong et al., 1950; Johnson et al., 2007). Furthermore, the difference in stem C contents of broad-leaved woody plants (i.e., 47.69 and 47.78 % for deciduous and evergreen species, respectively) and conifers (50.48 %) could also be explained by their corresponding differences in chemical compositions (Lamlom and Savidge, 2003; Thomas and Martin, 2012).

Our results showed that C contents in roots and leaves decreased significantly with increasing latitude (Fig. 3). This was inconsistent with previous studies reporting that C content of global plant fine root showed no latitudinal trend (Yuan et al., 2011) but was consistent with the latitudinal trends of plant C contents of roots and leaves in China's forests (Zhao et al., 2016). Generally, climatic factors (i.e., temperature and precipitation) regulate elemental contents in plant organs by influencing the associated plant metabolism and functioning (Reich and Oleksyn, 2004; Reich, 2005; Zhang et al., 2012). In our study, climatic factors explained independently less variation of plant C contents of four organs (0.2–8.4 %, see Fig. 4) than other factors. The climatic factors and life form together explained higher proportion of the variation in C contents of roots and leaves (25.3 and 16.2 % in Fig. 4), while both the independent effect of climatic factors and the interactive effect of climate and life

form on the C content of stem were lower (0.5 and 0.7 %, respectively) than those of other organs. This may be one reason for the lack of significant latitudinal trend for C content in stems.

Our data showed that the life form independently explained more variation of plant C content of four organs (7.2–21.5 %, Fig. 4), which was consistent with the results of Fyllas et al. (2009) and other studies about plant nutrient stoichiometry at global scales (Han et al., 2011; Zhao et al., 2016; Tian et al., 2017). Further, the interactive effects of climatic factors with life forms were higher than the independent explanations of climate (0.7–15.7 %, Fig. 4). These results conjointly revealed the important role of plant life form in shaping plant C content, which implied that the shift of species composition in regional vegetation along the latitudinal gradients influenced by climate could partly explain the biogeographic pattern of plant C content. Generally, the proportion of woody plants tends to a decrease while that of herbs increases with increasing latitude and decreasing MAT and MAP (Fig. S1 in the Supplement). Hence, the variation in life forms grouping in different biomes further corroborates our results of the biogeographic pattern of plant C content.

## 5 Conclusions

Plant C content varied with organs and life forms at global scales. Specifically, plant C content in leaves was higher than that in roots. Across life forms, woody plants exhibited higher C content than herbaceous plants. Using the canonical values of 50 % may underestimate and overestimate the C content in stems and leaves of conifers and in all organs of other life forms, respectively. Thus, specific plant C contents given in Table 1 provided an alternative to IPCC for their guidelines to update the plant C fractions and could improve the accuracy of vegetation C stock estimations. Furthermore,

plant C content showed significant latitudinal trends induced by climatic factors and life forms. This suggests that these latitudinal trends and driving factors should be incorporated into the research of plant ecological stoichiometry and biogeochemical modeling.

*Data availability.* Data used in this study can be found in the Supplement.

**The Supplement related to this article is available online at <https://doi.org/10.5194/bg-15-693-2018-supplement>.**

*Competing interests.* The authors declare that they have no conflict of interest.

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