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# 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 in the assessment of global C cycle and ecological stoichiometry. However, the global variation in plant C content remains poorly understood. We conducted a global analysis of the plant C content by synthesizing data from 4,318 species to provide specific values of C content and to assess their variation across plant organs and life forms. Our results showed that C content varied markedly across plant organs. Plant organ C content ranged from 45.01% in reproductive organs to 47.88% in stems at global scales, which were significantly lower than a canonical value of 50% that has been widely employed in previous studies. Plant C content in leaves was higher than that in roots. 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 decrease with the increasing latitude. The life form explained more variation of the C content than climate due to plant structural requirements. Our findings suggest that specific C content values from different organs and life forms may be more suitable to evaluate global vegetation C stock and plant ecological stoichiometry.

**Keywords:** plant, carbon content, organ, life form, climate, biogeographical pattern

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## 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 $CO_2$ to the forms of biological compounds to maintain metabolic functions and build basic structures (Dietze et al., 2014; Mart ńez−Vilalta et al., 2016). This process creates a huge organic C pool in terrestrial vegetation (Schlesinger and Bernhardt, 2013). The vegetation C stock is usually estimated by multiplying total plant biomass by a corresponding biomass C conversion factor, i.e., the C content (gram of C per gram of dry biomass) (Bert and Danjon, 2006; Thomas and Martin, 2012). Therefore, C content is one of the key factors determining the assessment accuracy of global terrestrial vegetation C stocks (Lamlom and Savidge, 2003; Thomas and Martin, 2012; Jones and O'Hara, 2016). Additionally, as a major element in plants and contributing roughly half of dry biomass, C is relatively more stable than mineral elements in plants and can be easily measured simultaneously with other key elements (Hessen et al., 2004; Han et al., 2011). Thus the ratio of C, nitrogen (N), phosphorus (P) in plants is widely used in ecological stoichiometry to diagnose nutrition limitation, competition, and biogeochemical cycle (Sardans et al., 2012; Liu and Sun, 2013). Further study on plant C content will improve our understanding of the variation in plant key elements in ecological stoichiometry.

The most widely employed C content in plants is 50% in the forest C stock estimations (De Vries et al., 2006; Keith et al., 2009; Lewis et al., 2009; Saatchi et al., 2011; Borchard et al., 2017). Originally, this value is calculated from an average molecular formula $CH_{1.44}O_{0.66}$ in living plant wood (Pettersen, 1984; Bert and Danjon, 2006). However, using the default value of 50% for different plant organs ignore the variation of C content among plant organs and life forms and may lead to biases in vegetation C stock estimation (Zhang et al., 2009; Martin and Thomas, 2011; Rodrigues et al., 2015). The Intergovernmental Panel on Climate Change (IPCC) (2006) provided the C content of biomass of trees in tropical/subtropical forests (47%), and that of broad-leaved trees and conifers in temperate/boreal forests (48% and 51%) which was based on chemical analysis of pooled samples. The values do enhance the accuracy of vegetation C stock estimation Compared with the default value of 50%. Nevertheless, error was still introduced to C stock estimation in an actual application (Martin and Thomas, 2011). Thomas and Martin (2012) reported the more precise C content of tree tissues among three biomes based on a global database including 31 studies. However, the lack of plant C content in other life forms (such as herb, crop, vine, etc.) in their study limited its applications in the accurate estimation of global vegetation C stocks.

Despite of a smaller variation than the N and P in plants (Han et al., 2011; Zhao et al., 2016), C content in plant organs still varies significantly with different organs (Alriksson and Eriksson, 1998; Northup et al., 2005; 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). This indicates a high risk of inaccurate C storage estimation at large scales. In addition, the geographical pattern of plant C content has been explored by recent studies (Yuan et al., 2011; Yang et al., 2015a; Zhao et al., 2016). C content in plant leaves and roots showed significant latitudinal trends in Chinese forests (Zhao et al., 2016). However, other studies reported no significant latitudinal trends of plant fine root and aboveground tissue (Yuan et al., 2011; Yang et al., 2015a). These controversial results suggest that the geographical pattern of plant C content at global scale is still unclear.

With above consideration, we compiled a global dataset of plant organ C content, and then conducted a synthetic analysis of its global variation in plant organ C content and two possible driving factors, climate and life form, to answer the following two questions: (1) how much C do plant organs contain? And (2) what are the biogeographical pattern of plant C content and the possible driving factors?

## 2 Material and methods

### 2.1 Data compilation

We searched three databases including 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 data in plants which were published during 1970 to 2016. To collect reliable and comparable data, 315 research papers were obtained according to the following two criteria: (1) data must have been obtained in natural ecosystems (including wetland and mangrove) or plantation ecosystems (including grassland and cropland which were disturbed by human activities such as cultivation, fertilization and grazing), excluding data from laboratory-grown or field control experiment-grown plants; and (2) dataset only included plant C content obtained by the two commonly used methods (i.e., the $K_2Cr_2O_7$–$H_2SO_4$ oxidation method and the combustion method), excluding studies used the default value, assumption value, or values calculated from the chemical compositions for plant C content. In addition, we compiled the data on plant C content in specific plant organs from the TRY database (https://www.try-db.org) (Kattge et al., 2011) using the aforementioned criteria (Table S1).

Finally, a total of 24,326 records for plant organ C content from 627 sites in six continents were included in our global dataset (Fig. 1), in which 36.33% were from literatures and 63.67% were from the TRY database. The dataset is consisted of 4,318 species in 1,694 genera and 238 families. For each data, we recorded the geographical location information (latitude, longitude and altitude), Latin binomial species name, genus, family, organ type (reproductive organ, root, leaf and stem), life forms, chemical compounds (lignin and cellulose), and plant C content. To provide detailed C content of plant for future estimation of vegetation C stock, plant life forms were divided into five categories: herbaceous species (herb), woody plants, fern, vine, bamboo in this study. Crop was listed in the herbaceous category. Due to the high proportion of woody plants in the terrestrial vegetation, we divided them into three sub categories: evergreen broadleaved woody plants, deciduous broadleaved woody plants, and conifers. If the compiled literature showed no information of life forms, then it was attained from the 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) to get accurate information of plant life form. In order to explore the biogeographic pattern and the driving factors of C content in plant organs, we used the latitude and longitude of each site to extract data of climatic variables (mean annual temperature, MAT, ºC; mean annual precipitation, MAP, mm) from WorldClim (http://www.worldclim.org/) (Hijmans et al., 2005). Given that plant C content can vary with the size of individual (Elias and Potvin, 2003; Uri et al., 2012; Martin et al., 2013), we recorded the average C content in herbaceous species at different growth stages during the annual growing season.

**2.2 Statistical analyses**

First, we calculated the statistical measures of central tendency and variability, including arithmetic mean (Mean), median, standard deviation (SD), coefficient of variation (CV) and sample sizes (n), for plant organ C content values of different life forms (Table 1). The data of C content of each organ showed a normal distribution (Fig. 2). Thus, the Student's t-test was used to determine whether the plant C content of each organ significantly differed from the default value of 50%, and whether statistical differences of plant organ C content existed between life forms. Specifically, we compared herbs vs. woody plants; conifers vs. deciduous broad-leaved woody plants; and conifers vs. evergreen broad-leaved woody plants. Linear model was used to explore the biogeographical pattern of plant organ C content along the latitude gradient as well as the relationships between plant organ C content and MAT and MAP. To differentiate the effects of life form and climatic factors (i.e. MAT and MAP) on the variations of plant C content among four organs, 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 four organs (i.e. reproductive organ, root, leaf, and stem), respectively (Han et al., 2011). Linear model was used to explore the relationship of plant C content with the lignin and the 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 with 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% ($p < 0.05$ in all case). Plant organ C content also varied markedly across the life forms (Table 1). Among herbaceous plants, C content ranged from 42.41% in stems to 44.73% in leaves and among woody plants, it 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 content in roots, leaves, and stems of conifers was significantly higher than that of deciduous broad-leaved and evergreen broad-leaved woody plants. In addition, the C contents of ferns, vines and bamboo ranged from 42.98% in bamboo leaves to 49.20% in bamboo stems (Table 1).

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

Plant C content in roots and leaves decreased with the increasing latitude and decreasing MAT and MAP, while reproductive organ and stem C content displayed no significant latitudinal trends ($r^2 = 0.02$, $p = 0.15$; $r^2 < 0.01$, $p = 0.05$; Fig. 3, Table S2).

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. These results demonstrated that the variation of plant C content was explained more by life form than by climatic factors.

## 4 Discussion

We evaluated plant C content across plant organs and life forms by using a global plant C content dataset established in this study. Our results showed that plant C content varied remarkably across the four organs, which is supported by previous studies (Alriksson and Eriksson, 1998; Northup et al., 2005; Tolunay, 2009). The global average C contents of all organs were significantly lower than the canonical value of 50%, indicating that this default value could lead to the overestimation of vegetation C stocks at global scales and could induce errors between 3.77 −13.8% in regional C stock estimations (Bert and Danjon, 2006; Tolunay, 2009; Fang et al., 2010; Rodrigues et al., 2015). Similarly, global average C contents in stems and leaves were significantly higher than the other default value of 45.45% (Whittaker, 1975), while C contents of roots and reproductive organs showed no significant differences with 45.45%, respectively. This means that the canonical value of 50% or other values (e.g. 45.45%) may also introduce errors to vegetation C stock estimations due to the ignorance of the variation of plant C content among organs.

Additionally, our results showed that plant C content varied significantly among life forms (Table 1). This implies that using the canonical value of 50% could ignore the variances of C contents across life forms. The stem C contents of broad-leaved woody species (i.e. 47.69% in deciduous and 47.78% in evergreen) and conifers (51.48%) in this study were comparable with that (47.7% and 50.8%) reported by Thomas and Martin (2012). However, our results were lower than the default values of temperate broad-leaved woody species (48%) and conifers (51%), and higher than the default value of tropical broad-leaved woody species (47%) proposed by IPCC (2006). This suggests that these values may overestimate or underestimate the stem C content for broadleaved trees and conifers at global scales due to the uncertainty caused by data scarcity. Furthermore, our study also estimated the C content of herbaceous species, vines, ferns and bamboo, which were seldom studied at large scale (Thomas and Martin, 2012). Our results may improve the accuracy of vegetation C stock model and our understanding of the contribution of terrestrial vegetation to global C budgets (Zhang et al., 2009).

The variation of plant C content among organs and life forms were associated with differences in their chemical compositions (Fig. 5 and Fig. 6). Plant organs consist of several organic compounds with different C content, such as lignin (with 63 − 66% of C content), cellulose (with about 44% of C content), and nonstructural carbohydrates (NSC) (e.g., sugar or starch, with about 44% of C content) (Adler, 1977; Poorter and Bergkotte, 1992). Plant organ with high lignin (e.g., stems) is likely to have higher C content than organs with lower lignin content in this study (e.g., leaves, roots, and reproductive organs. see Fig. 5a). This is consistent with the previous results (Poorter and Bergkotte, 1992; Savidge, 2000; Lamlom and Savidge, 2003; Bert and Danjon, 2006; Martin and Thomas, 2011). Despite of the high lignin in root, the C content in roots was lower than that in leaves, which is likely due to high protein and others 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 in consistent with its high quantities of NSC but little lignin (Barros et al., 1996).

C content of woody plants was higher than that of herbs (Table 1). This is consistent with their different lignification. Woody plants generally have low relative growth rate and need proportionally greater investments of C at the cellular level to synthesize lignin for the supporting structures, which leads to a high lignin and C content (Fig. 6a). This also is supported by previous results (Lambers and Poorter, 1992; Poorter and Bergkotte, 1992; Sariyildiz and Anderson, 2005; Majdi, 2007; Poorter et al., 2012; Mart ńez−Vilalta et al., 2016). In contrast, herbs generally show high relative growth rate and high NSC (Mart ńez−Vilalta et al., 2016). Thus herb has low lignin and C content (Armstrong et al., 1950; Poorter and Bergkotte, 1992; Johnson et al., 2007). Furthermore, our results show that stem C content of broad-leaved woody plants (i.e., 47.69% in deciduous and 47.78% in evergreen) was lower than that of conifers (50.48%), which might be due to higher lignin in coniferous stems than that of broad-leaved woody stems (Lamlom and Savidge, 2003; Thomas and Martin, 2012).

Our results showed that C contents in roots and leaves decreased significantly with the increasing latitude (Fig. 3). This is consistent with the latitudinal trends in plant C content in roots and leaves in China’s forests (Zhao et al., 2016). Climate and life form may be potential causes for the biogeographical pattern of plant C content in roots and leaves (Zhao et al., 2016). The climatic factor and life form can together explain relatively large parts of variation in C contents of roots and leaves (25.3% and 16.2%, see Fig. 4), while it can only explain small amount of changes in C content of stems (11.2%, see Fig. 4). This may be one reason for the lack of significant latitudinal trend for C content in stems. The C content of reproductive organs showed no significant latitudinal trend may be due to scarcity of data (Table S2).

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Climatic factors explained independently less variation of plant C content among four organs (0.2 − 8.4%, see Fig. 4), which suggests a weak effect of climate on the variation of plant C content (Yuan et al., 2011; Yang et al., 2015a; Zhao et al., 2016). Climatic factors may directly affect the plant photosynthesis and respiration rate, and then influence the dynamic of the assimilation and demand of the NSC (Farrar, 1987; Hoch et al., 2003; O'Brien et al., 2014; Yang et al., 2015b). The global average of NSC in plants only account for ~10% of dry biomass (NSC with about 44% of C content) and plays only a minor role in regulating plant C content (Mart ńez−Vilalta et al., 2016).

In addition, life form explained independently more variation of plant C content (7.2 − 21.5%, see Fig. 4), which suggests that life form mainly shape the biogeographic patterns of plant C content. The shift in the species composition along the latitudinal gradient resonates with this biogeographical pattern. The proportion of woody plants (i.e. species with high C content) tends to decrease with the increasing latitude, while that of herbs (i.e. species with low C content) increases with the increasing latitude (Fig. S1), which possibly result in the decreasing latitudinal trend of plant C content. Furthermore, we found that life form explained more variation in the plant C content across organs than climate (Fig. 4). This suggests that ontogenetic differences between plants had a stronger effect on the variation of plant C content than climate due to structural requirements.

## 5 Conclusion

Plant C content varied with organs and life forms, suggesting that the canonical values of 50% may underestimate the C content of conifers and overestimate of C content of other life forms. Thus, specific plant C content should be used in the estimations of the regional and global C stocks. Besides, global C content of plants may give an alternative reference to IPCC for their guidelines. Furthermore, plant C content showed significant latitudinal trends induced by ontogenetic differences among life forms. This suggests that the research in plant ecological stoichiometry and biogeochemical model should take these latitudinal trends and driving factors into consideration.

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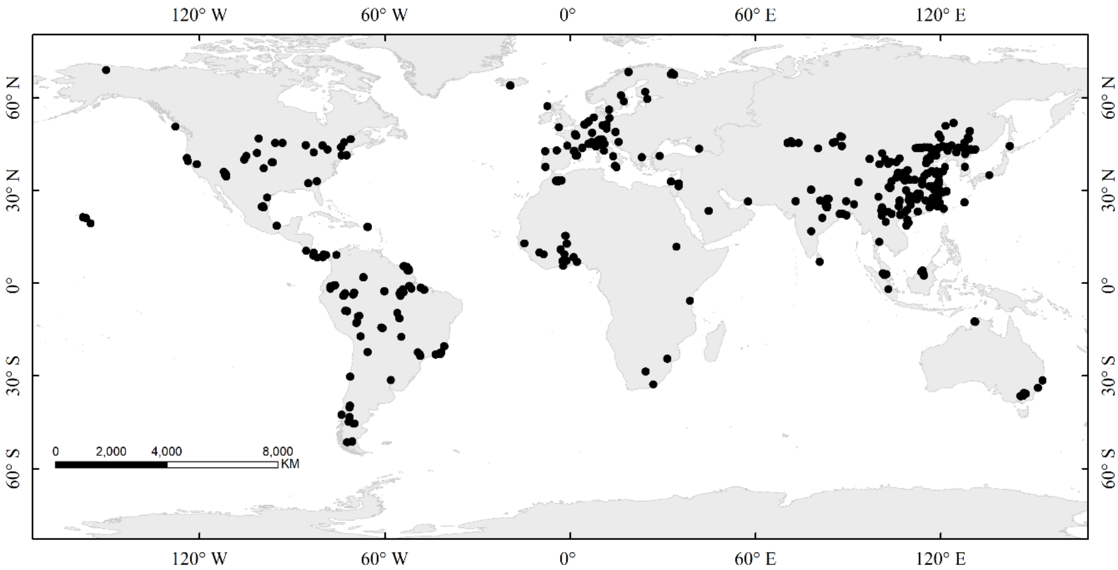
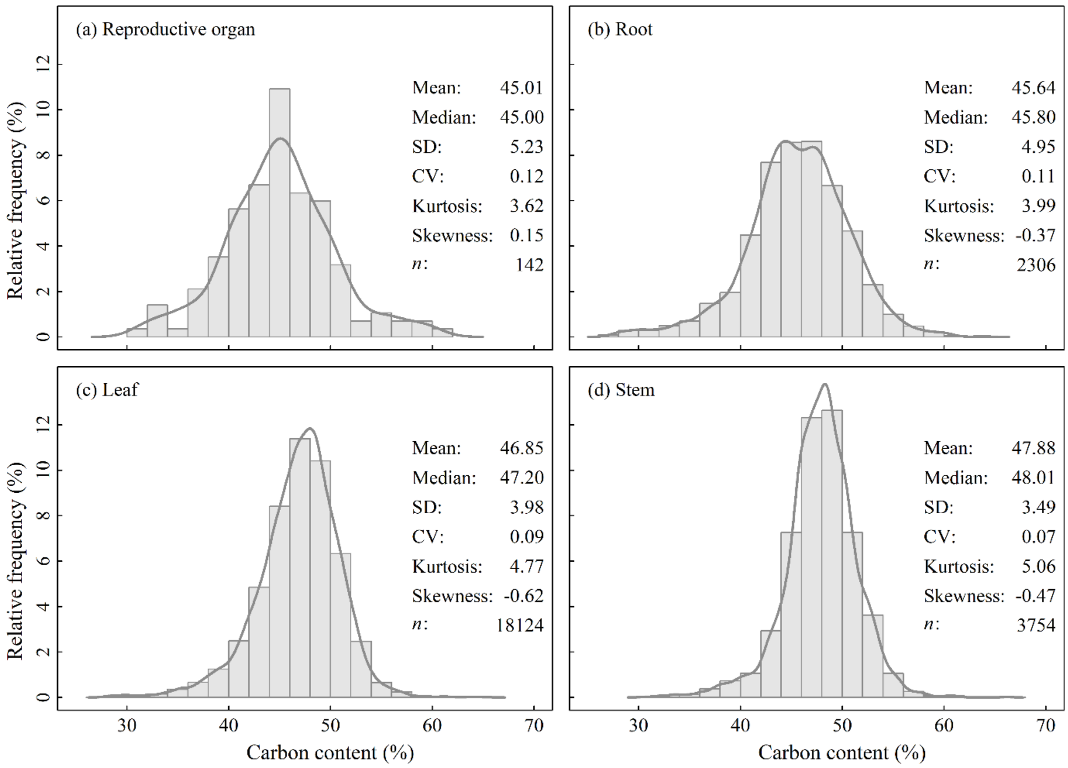
**Table 1.** Plant carbon content (%) in four organs across different life forms. *n* is the sample size, and SD is the abbreviation of standard deviation. Samples for stem include the samples from shoot, stem, twig and branch. "-" indicates no data.

| Life form | Reproductive organ | | Root | | Leaf | | Stem | |
|---|---|---|---|---|---|---|---|---|
| | *n* | Mean ± SD | *n* | Mean ± SD | *n* | Mean ± SD | *n* | 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 | 12064 | 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 | 18124 | 46.85 ± 3.98 | 3754 | 47.88 ± 3.49 |

**Figure 1.** Geographic distribution of sample points used in this synthesis. The samples are from 627 sites.



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

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352 **Figure 3.** Trends in the plant carbon contents along latitude and climate gradients. MAT, mean annual temperature;
353 MAP, mean annual precipitation. Ordinary least squares (OLS) regression lines are fit to the data. Solid lines indicate
354 the significant relationships with $p < 0.05$, and dashed lines denotes the insignificant relationships with $p > 0.05$.
355 Abbreviations: Repr carbon content, Reproductive organ carbon content. Plant carbon content in roots and leaves showed
356 a significantly latitudinal trends.

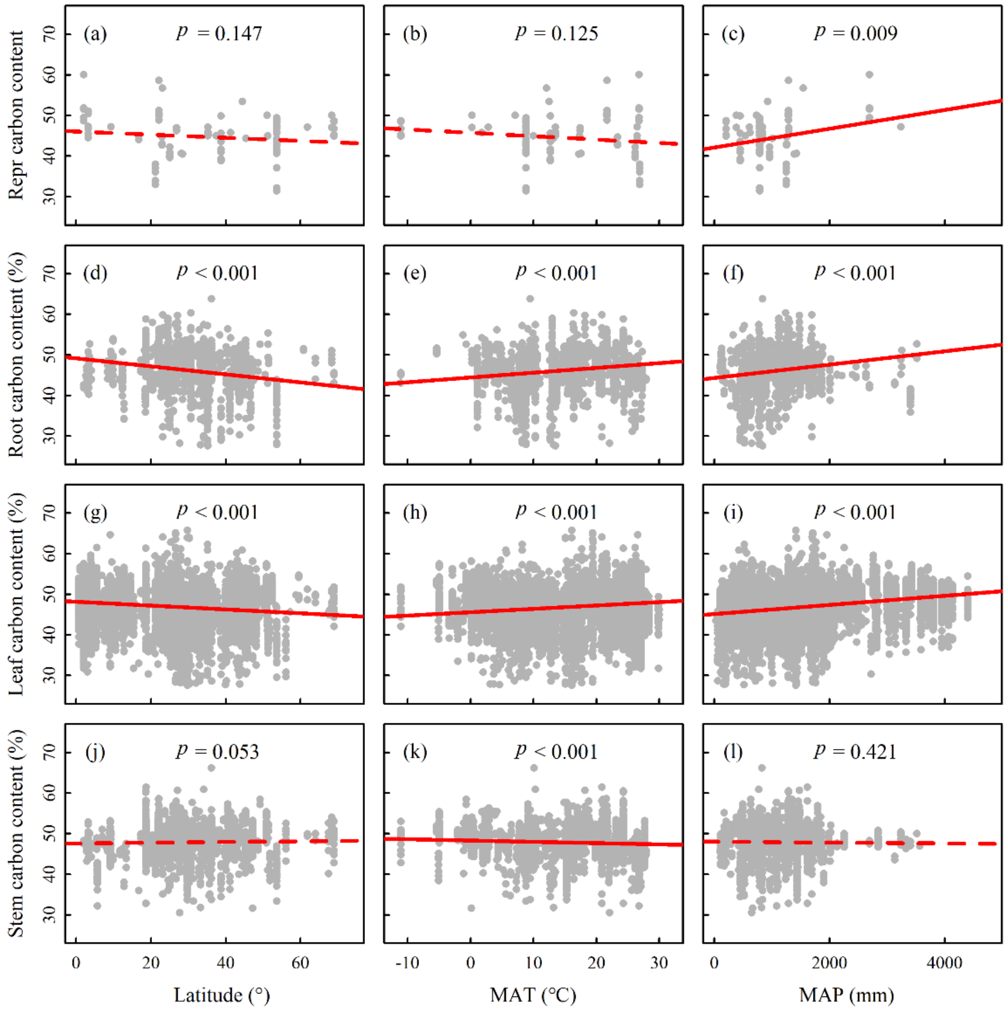


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**Figure 4.** Variation partitioning ($r^2$) of climate and life forms in accounting for the variances in plant carbon contents across different organs. (a) reproductive organ, (b) root, (b) leaf, and (d) stem. Life form independently explained more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

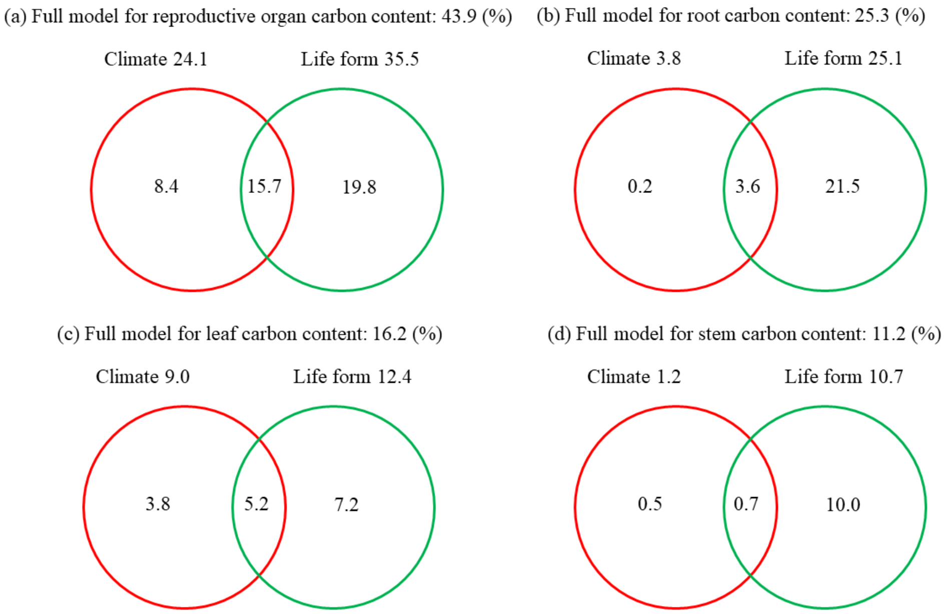

**Figure 5.** The relationship between plant carbon content and lignin and cellulose among three organs. Plant carbon content increases significantly with the increasing lignin in plant ($r^2 = 0.29$, $p < 0.001$), whereas is no correlated with the cellulose in plant.

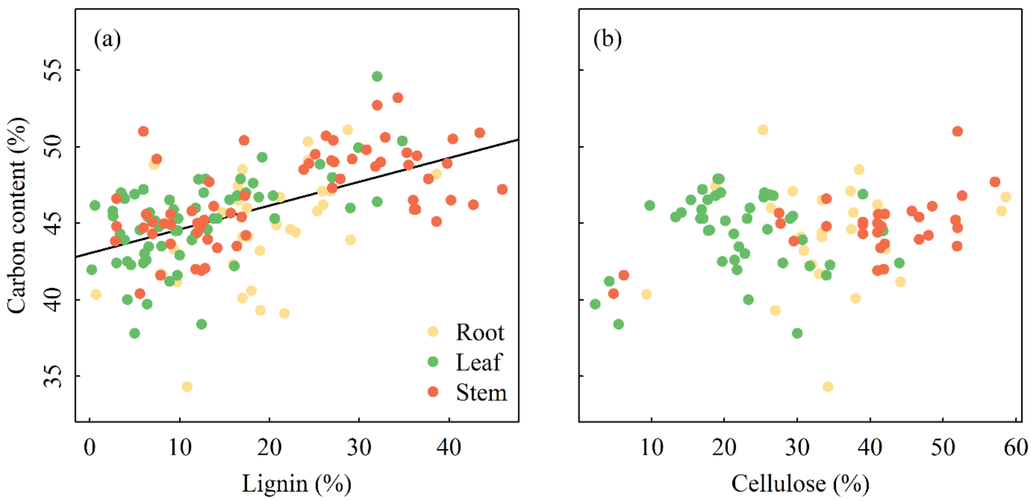

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**Figure 6.** The relationship between plant carbon content and lignin and cellulose in woody plants and herbaceous plants. Plant carbon content increases significantly with the increasing lignin in plant ($r^2$ = 0.29, $p$ < 0.001), whereas is no correlated with the cellulose in plant.