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 4,318 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 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.

Keywords: plant, carbon content, organ, life form, climate, biogeographical pattern
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; 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$_{1.44}$O$_{0.66}$ 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 (Alriksson 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 conversion 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, change of 1% wood C content from the canonical value of 50% can bring up to ~7 petagrams variation in global vegetation C stocks, which is almost equivalent to half of the vegetation C stocks of continental USA (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 in 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 phylogenic, 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%), temperate/boreal forests (48% of broad-leaved trees and 51% of conifers), respectively. 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 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 benefit for elucidating 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? and (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 accepted, 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$_2$Cr$_2$O$_7$–H$_2$SO$_4$ 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).

Finally, a total of 24,326 records of 4,318 species in 1,694 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 broadleaved woody plants, deciduous broadleaved woody plants, and conifers. For those data with no information on life forms, we documented it 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 pattern 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, ºC; 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 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 pattern 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 total explanation, independent explanation and interactive explanation of climatic factors and life forms for different organs (i.e. reproductive organ, root, leaf, and stem), respectively (Han et al., 2011). Additionally, a linear model and an analysis of variance with the type III were performed to test the variations 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 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, respectively. 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 organ), respectively (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 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), but higher than that 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 overestimate or underestimate the stem C content for broadleaved trees and conifers at global scales.

The variation of plant C content among organs and life forms were 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 a higher C content than organs with lower lignin content (e.g. leaves, roots, and reproductive organs, Fig. 5a) (Savidge, 2000; Lamlom and Savidge, 2003; Bert and Danjon, 2006; Martin and Thomas, 2011). Despite of the high lignin in roots, the C content in roots was lower than that in leaves, probably because of the high proportions of 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 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, respectively. 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). 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 contents 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.
Supporting information

Figure S1. Changes in the species composition along the gradients of latitude, mean annual temperature (MAT) and mean annual precipitation (MAP). The percentage of woody plants decreased with increasing latitude and with decreasing MAT and MAP. Herbs showed the opposite trends with woody plants. Other life forms showed no significant change along latitudinal and climatic gradient.

Table S1. Data sets in TRY that contributed to our global dataset of plant carbon (C) content. References cited in this table are attached below.

Table S2. Model summary for the ordinary least squares (OLS) regression of plant carbon content on three factors (Latitude, MAT and MAP). Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation.

Table S3. The summary of anova (Type III tests) for plant C content in reproductive organs. Climatic factor includes mean annul temperature (MAT) and mean annual precipitation (MAP).

Table S4. The summary of anova (Type III tests) for plant C content in roots. Climate factor contains mean annul temperature (MAT) and mean annual precipitation (MAP).

Table S5. The summary of anova (Type III tests) for plant C content in leaves. Climate factor contains mean annul temperature (MAT) and mean annual precipitation (MAP).

Table S6. The summary of anova (Type III tests) for plant C content in stems. Climate factor contains mean annul temperature (MAT) and mean annual precipitation (MAP).

Competing interests

The authors declare that they have no conflict of interest.

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References


**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.

<table>
<thead>
<tr>
<th>Life form</th>
<th>Reproductive organ</th>
<th>Root</th>
<th>Leaf</th>
<th>Stem</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( n )</td>
<td>Mean ± SD</td>
<td>( n )</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>Herbaceous plants</td>
<td>83</td>
<td>42.56 ± 4.57</td>
<td>749</td>
<td>42.45 ± 5.12</td>
</tr>
<tr>
<td>Crop</td>
<td>42</td>
<td>42.40 ± 5.11</td>
<td>56</td>
<td>38.20 ± 5.23</td>
</tr>
<tr>
<td>Woody plants</td>
<td>57</td>
<td>48.56 ± 4.07</td>
<td>1392</td>
<td>47.43 ± 3.94</td>
</tr>
<tr>
<td>Deciduous broad-leaved</td>
<td>17</td>
<td>46.81 ± 3.93</td>
<td>513</td>
<td>46.59 ± 3.55</td>
</tr>
<tr>
<td>Evergreen broad-leaved</td>
<td>29</td>
<td>49.64 ± 4.42</td>
<td>520</td>
<td>47.72 ± 4.14</td>
</tr>
<tr>
<td>Conifers</td>
<td>8</td>
<td>48.25 ± 2.56</td>
<td>252</td>
<td>48.43 ± 4.16</td>
</tr>
<tr>
<td>Fern</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>43.64 ± 3.83</td>
</tr>
<tr>
<td>Vine</td>
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<td>45.83 ± 0.33</td>
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<td>46.25 ± 4.46</td>
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<tr>
<td>Bamboo</td>
<td>-</td>
<td>-</td>
<td>23</td>
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</tr>
<tr>
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<td>142</td>
<td>45.01 ± 5.23</td>
<td>2306</td>
<td>45.64 ± 4.95</td>
</tr>
</tbody>
</table>
Figure 1. Geographic distribution of sample sites used in this synthesis.
**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.
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, Reproductive organ carbon content. Plant carbon content in roots and leaves showed a significant latitudinal trend.
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.

(a) Full model for reproductive organ carbon content: 43.9 (%)  
Climate 24.1  Life form 35.5  
8.4  15.7  19.8

(b) Full model for root carbon content: 25.3 (%)  
Climate 3.8  Life form 25.1  
0.2  3.6  21.5

(c) Full model for leaf carbon content: 16.2 (%)  
Climate 9.0  Life form 12.4  
3.8  5.2  7.2

(d) Full model for stem carbon content: 11.2 (%)  
Climate 1.2  Life form 10.7  
0.5  0.7  10.0
Figure 5. Relationships 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 it is not correlated with the cellulose in plants.
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 plant ($r^2 = 0.29$, $p < 0.001$), whereas it is not correlated with the cellulose in plants.