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 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.

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; Mart ńez−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

60 will benefit for elucidating ecological stoichiometry and the mechanisms of plants' response to global change (Fyllas et

61 al., 2009; Ordoñez et al., 2009; Zhang et al., 2012).

62 For the above reasons, we compiled a global dataset of plant organ C content to provide referable C contents of plant

63 organs in different life forms. We tried to answer the following two questions: (1) how much C do specific plant organs

64 contain? and (2) what are the biogeographical patterns of plant C content and the possible driving factors?

65 **2 Material and methods**

66 **2.1 Data compilation**

67 We searched Google Scholar (https://scholar.google.com/), Web of Science (http://isiknowledge.com) and CNKI (China

68 National Knowledge Infrastructure) (http://www.cnki.net/) for literatures reporting the C content of plants published

69 from 1970 to 2016. We documented 315 publications according to the following two criteria: (1) the data from natural

70 ecosystems (including wetland and mangrove) or plantation ecosystems (including grassland and cropland) were

71 accepted, while the data from laboratory or field experiments were excluded; and (2) plant C content detected by two

72 commonly used methods (i.e. the $K_2Cr_2O_7$–H_2SO_4 oxidation and the combustion methods) was included, while studies

73 that used the default value, assumed value, or values calculated from the chemical compositions were excluded from our

74 data compilation. In addition, we also included data of specific plant organs from the TRY database (https://www.try-

75 db.org) (Kattge et al., 2011) (Table S1).

76 Finally, a total of 24,326 records of 4,318 species in 1,694 genera and 238 families were included in our global dataset

77 (Fig. 1), in which 36.33% and 63.67% were from literatures and the TRY database, respectively. For each data record,

78 we documented the geographical information (latitude, longitude and altitude), Latin binomial, genus and family of

79 species, organ (reproductive organ, root, leaf and stem), life forms, chemical compounds (lignin and cellulose), and plant

80 C content. Plant life forms were divided into five categories: herbaceous species (herb), woody plants, fern, vine, and

81 bamboo. Data of crops were separately analyzed in the herbaceous category. The woody plants were further categorized

82 into three groups: evergreen broadleaved woody plants, deciduous broadleaved woody plants, and conifers. For those

83 data with no information on life forms, we documented it from Flora of China (http://foc.eflora.cn), Wikipedia

84 (https://en.wikipedia.org/wiki/Wiki/), Useful Tropical Plants (http://tropical.theferns.info) or The Plant List

85 (http://www.theplantlist.org). In order to explore biogeographic pattern and the driving factors of C content of plant

86 organs, we used the latitude and longitude of each site to extract data of climatic variables (mean annual temperature,

87 MAT, ℃; mean annual precipitation, MAP, mm) from WorldClim (http://www.worldclim.org/) (Hijmans et al., 2005).

88 Given that plant C content might vary with the growth stages of individuals (Elias and Potvin, 2003; Uri et al., 2012;

89 Martin et al., 2013), we recorded the averaged C content of herbaceous species across different growth stages.

90 **2.2 Statistical analyses**

91 We first documented statistics of plant organ C content for different life forms, including arithmetic mean (Mean),

92 median (Median), standard deviation (SD), and coefficient of variation (CV) (Table 1). The C content of each organ

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93   showed a normal distribution (Fig. 2), and thus the one sample Student's t-test was used to determine whether the stem

94   C content of woody plants significantly differed from the default value of 50% and the IPCC values (47%, 48% and

95   51%), respectively. The two sample Student's t-test was used to determine whether statistical differences of plant organ

96   C content existed between different life forms. Specifically, we compared the C contents of herbs vs. woody plants,

97   conifers vs. deciduous broad-leaved woody plants, and conifers vs. evergreen broad-leaved woody plants.

98   A linear model without accounting for other factors was used to explore biogeographical pattern of plant organ C content

99   along latitudinal gradients, MAT and MAP (Han et al., 2011). To evaluate the effects of life form and climatic factors

100   (i.e. MAT and MAP) on the variations of plant C contents, a partial generalized linear model was used to calculate total

101   explanation, independent explanation and interactive explanation of climatic factors and life forms for different organs

102   (i.e. reproductive organ, root, leaf, and stem), respectively (Han et al., 2011). Additionally, a linear model and an analysis

103   of variance with the type III were performed to test the variations of C contents explained by climatic factors and life

104   forms. A linear model was used to explore the relationship of plant C content with the content of lignin and cellulose.

105   All statistical analyses were performed in the R 3.3.1 software (R core Team, 2016).

3 Results

106

3.1 Carbon content of plant organs

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108   Plant C content varied significantly among organs. Arithmetic means of C content for reproductive organ, root, leaf and

109   stem were 45.01%, 45.64%, 46.85% and 47.88%, respectively (Fig. 2, Table 1), all of which were significantly lower

110   than the default value of 50% ($p < 0.05$). Plant organ C content also varied markedly across life forms (Table 1). Among

111   herbaceous plants, C content ranged from 42.41% in stems to 44.73% in leaves; and among woody plants, C content

112   changed from 47.43% in roots to 48.56% in reproductive organs (Table 1). C contents in all four organs were

113   significantly higher in the woody species than in the herbaceous species. Across woody species, C contents in roots,

114   leaves, and stems of conifers were significantly higher than those of deciduous broad-leaved and evergreen broad-leaved

115   woody plants, respectively. In addition, the C contents of ferns, vines and bamboo ranged from 42.98% to 49.20% (Table

116   1).

3.2 Latitudinal trends of carbon content and possible driving factors

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118   Plant C contents in roots and leaves decreased with increasing latitude and decreasing MAT and MAP ($r^2 = 0.05$, $p <$

119   0.001 in all cases), while reproductive and stem C content displayed no significant latitudinal trends ($r^2 = 0.02$, $p > 0.05$;

120     $r^2 < 0.01$, $p > 0.05$; Fig. 3, Table S2).

121   The C content of plant organs was significantly affected by climatic factors ($p < 0.05$ in stem), life form and their

122   interaction ($p < 0.05$ in all cases, except for reproductive organ), respectively (Tables S3-S6). The effects of climatic

123   factors and life forms on plant C content varied largely across the plant organs (Fig. 4). The independent explanations

124   of climatic factors on the variation in the C contents of the reproductive organs, roots, leaves, and stems were 8.4%,

125   0.2%, 3.8% and 0.5%, respectively. The variation of C content in the reproductive organs, roots, leaves, and stems

126   explained independently by life forms were 19.8%, 21.5%, 7.2%, and 10.0%, respectively. The interactive explanations

127   of climatic factors and life form on the variation of C content of the reproductive organs, roots, leaves, and stems were

128   15.7%, 3.6%, 5.2%, and 0.7%, respectively. These results demonstrated that the variation of plant C content was

129   explained more by life form than by climatic factors (Fig. 4; Tables S3-S6).

130   **4 Discussion**

131   We evaluated plant C content across plant organs and life forms by establishing a global plant C content dataset. Our

132   results showed that plant C content varied remarkably among organs, which was consistent with previous studies

133   (Alriksson and Eriksson, 1998; Northup et al., 2005; Tolunay, 2009). Notably, we found that the global average C

134   contents of four organs were significantly lower than the canonical value of 50% which was widely used to convert

135   vegetation biomass to C stock at large-scales, such as in temperate forests (De vries et al., 2006), tropical forests (Lewis

136   et al., 2009; Saatchi et al., 2011), and global forests (Keith et al., 2009). In addition, C contents of stems and leaves were

137   significantly higher than another default value of 45.45% proposed by Whittaker (1975), although the C contents of roots

138   and reproductive organs showed no significantly statistical difference. Furthermore, our results showed that plant C

139   contents varied significantly among life forms (Table 1). Among woody plants, the stem C contents of broad-leaved

140   woody species (i.e. 47.69% in deciduous and 47.78% in evergreen) and conifers (51.48%) were comparable with those

141   (47.7% and 50.8%, respectively) reported by Thomas and Martin (2012). However, these data were significantly lower

142   than the values of temperate broad-leaved woody species (48%; $p < 0.001$ and $p = 0.018$) and conifers (51%; $p < 0.001$),

143   but higher than that of tropical broad-leaved woody species (47%; $p < 0.001$ and $p < 0.001$) proposed by IPCC (2006).

144   This suggested that these values from IPCC may overestimate or underestimate the stem C content for broadleaved trees

145   and conifers at global scales.

146   The variation of plant C content among organs and life forms were associated with differences in their chemical

147   compositions (Figs. 5-6). Plant organs are composed of several organic compounds with different C content, such as

148   lignin (with C content of 63% − 66%), cellulose (with C content of about 44%), and nonstructural carbohydrates (NSC)

149   (e.g. sugar or starch with C content of about 44%) (Adler, 1977; Poorter and Bergkotte, 1992). Our result was consistent

150   with previous findings that plant organs with higher lignin (e.g. stems) tend to a higher C content than organs with lower

151   lignin content (e.g. leaves, roots, and reproductive organs, Fig. 5a) (Savidge, 2000; Lamlom and Savidge, 2003; Bert

152   and Danjon, 2006; Martin and Thomas, 2011). Despite of the high lignin in roots, the C content in roots was lower than

153   that in leaves, probably because of the high proportions of protein and others C-rich compounds in leaves (Rouwenhorst

154   et al., 1991; Niinemets et al., 2002) and high content of starch in roots (Bert and Danjon, 2006). The lowest C content in

155   reproductive organs was consistent with its high quantities of NSC and low content of lignin (Barros et al., 1996). Across

156   life forms, woody plants generally require proportionally greater investments of C at the cellular level to synthesize

157   lignin to support structures with relatively low growth rate, which result in high lignin and C content (Fig. 6a). In contrast,

158   the high relative growth rate of herbs is accordant with their low lignin and C content (Armstrong et al., 1950; Johnson

159   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).

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

354

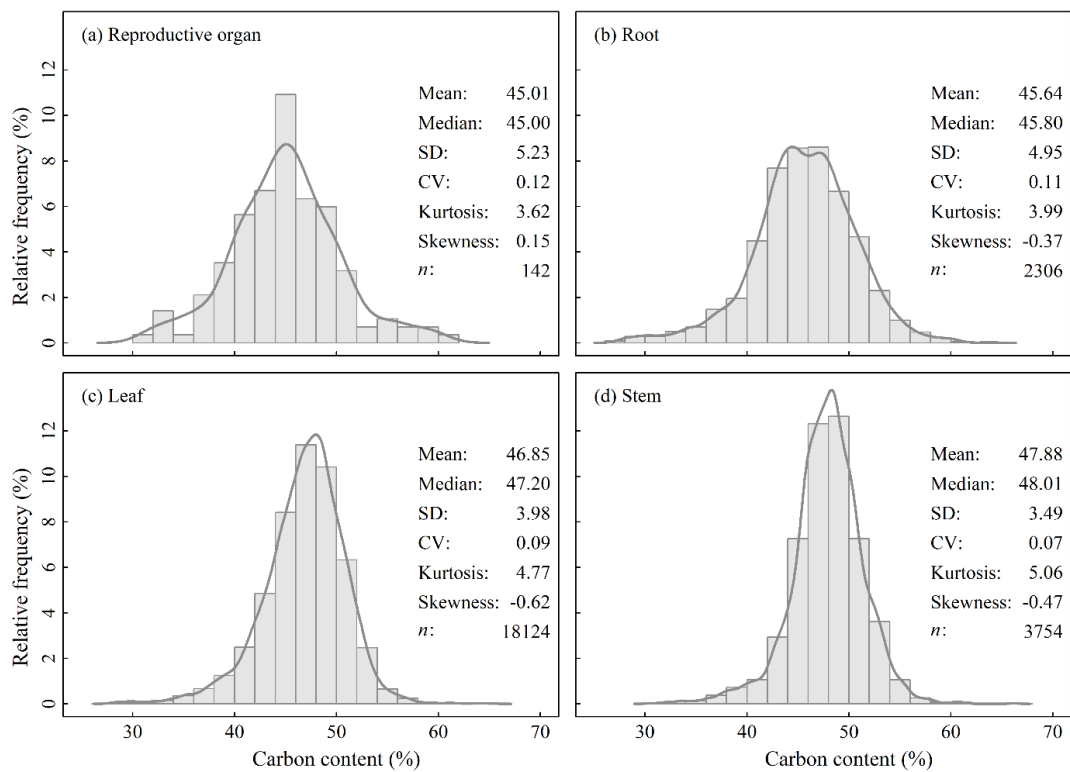| Life form	Reproductive organ		Root		Leaf		Stem	
	n	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD
Herbaceous plants	83	42.56 ± 4.57	749	42.45 ± 5.12	5181	44.73 ± 3.45	162	42.41 ± 3.54
Crop	42	42.40 ± 5.11	56	38.20 ± 5.23	85	41.32 ± 3.38	69	43.26 ± 3.15
Woody plants	57	48.56 ± 4.07	1392	47.43 ± 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

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

356

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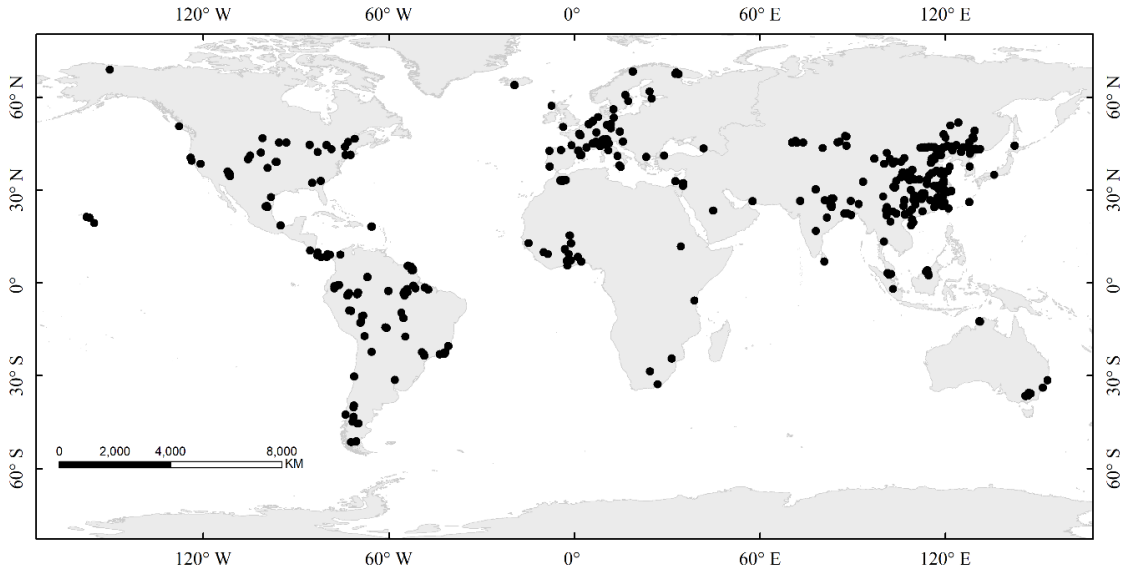
Figure 2. Histograms of carbon content of (a) reproductive organ, (b) root, (c) leaf and (d) stem. Abbreviations: SD, Standard deviation; CV, coefficient of variation. *n* indicates sample size.

(a) Reproductive organ

Mean:	45.01
Median:	45.00
SD:	5.23
CV:	0.12
Kurtosis:	3.62
Skewness:	0.15
n:	142

(b) Root

Mean:	45.64
Median:	45.80
SD:	4.95
CV:	0.11
Kurtosis:	3.99
Skewness:	-0.37
n:	2306

(c) Leaf

Mean:	46.85
Median:	47.20
SD:	3.98
CV:	0.09
Kurtosis:	4.77
Skewness:	-0.62
n:	18124

(d) Stem

Mean:	47.88
Median:	48.01
SD:	3.49
CV:	0.07
Kurtosis:	5.06
Skewness:	-0.47
n:	3754

360

361 **Figure 3.** Trends in the plant carbon contents along latitude and climate gradients. MAT, mean annual temperature;
362 MAP, mean annual precipitation. Ordinary least squares (OLS) regression lines are fit to the data. Solid lines indicate
363 the significant relationships with $p < 0.05$, and dashed lines denotes the insignificant relationships with $p > 0.05$.
364 Abbreviations: Repr carbon content, Reproductive organ carbon content. Plant carbon content in roots and leaves showed
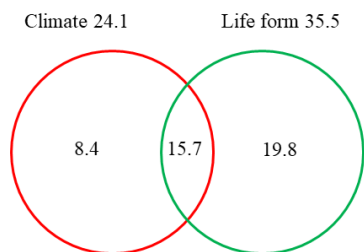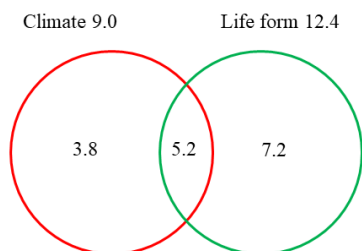365 a significant latitudinal trend.
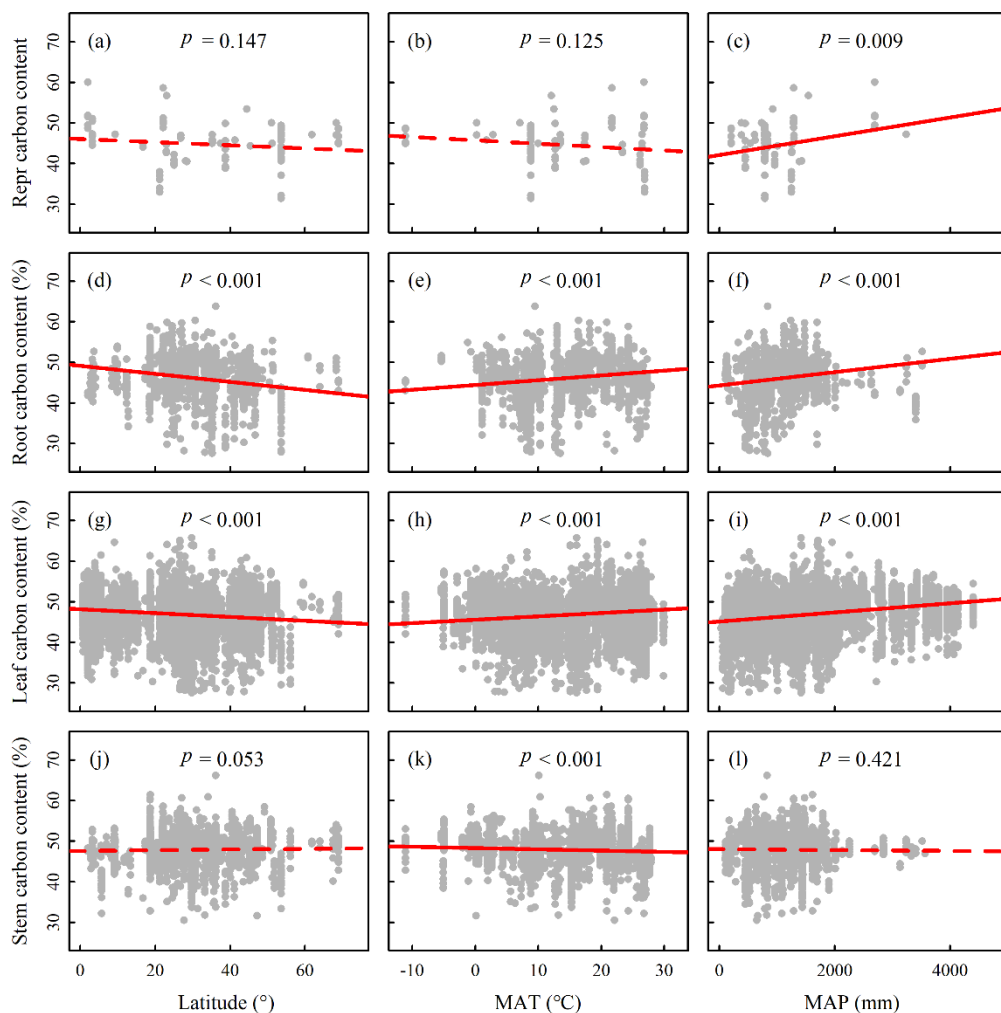
366

367 **Figure 4.** Variation partitioning (r^2) of climate and life forms in accounting for the variances in plant carbon contents
368 across different organs. (a) reproductive organ, (b) root, (b) leaf, and (d) stem. Life form independently explained more
369 variation of carbon content in each organ than climate.
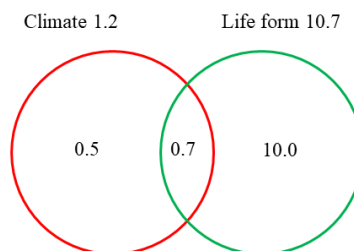370

(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
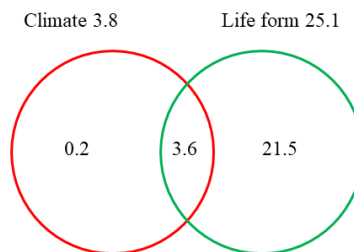
(c) Full model for leaf carbon content: 16.2 (%)

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

371

372　**Figure 5.** Relationships between plant carbon content and lignin and cellulose among three organs. Plant carbon

373　content increases significantly with the increasing lignin in plant ($r^2 = 0.29$, $p < 0.001$), whereas it is not correlated

374　with the cellulose in plants.

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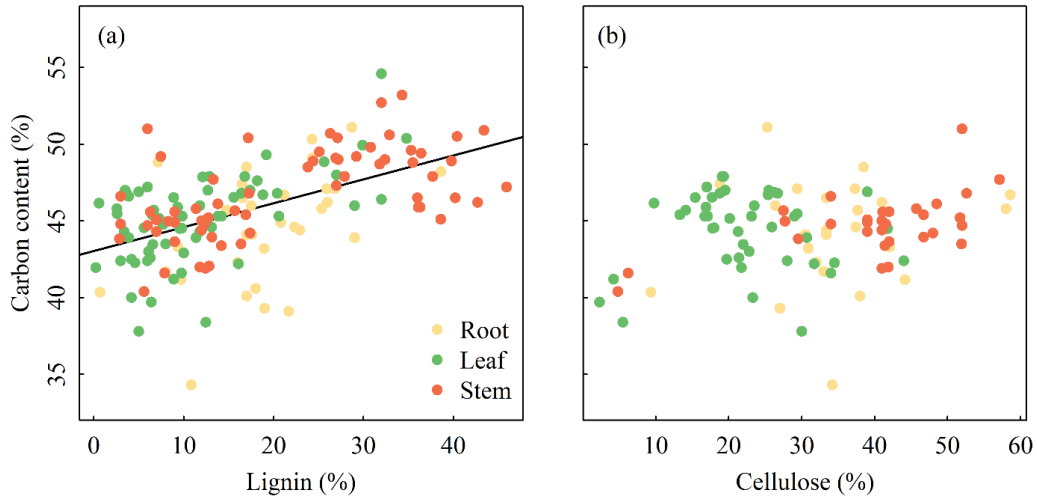
376 **Figure 6.** Relationships between plant carbon content and lignin and cellulose in woody plants and herbaceous plants.

377 Plant carbon content increases significantly with increasing lignin in plant ($r^2 = 0.29$, $p < 0.001$), whereas it is not

378 correlated with the cellulose in plants.