Authors' response to reviewer' comments on the manuscript bg-2017-322 "Variations and determinants of carbon content in plants: a global synthesis" by Suhui Ma et al.

# To the editor:

Dear Dr. Akihiko Ito,

Thank you very much for the constructive comments and suggestions from you and the two reviewers. These comments were summarized as two major points: (1) explaining the application of the C content, and (2) adding discussions on the interactive effects of climatic factors and life form on the variation of plant C content. We have carefully addressed these comments in this revised manuscript. Please find our point-to-point responses to these comments as attached at the bottom of this letter. We also attach our updated manuscript with the "track changes" option.

We are looking forward to receiving your decision.

Best wishes,

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#### **To Anonymous Referee #1:**

#### [Comment] General comments

This manuscript describes a synthesis of carbon (C) content measurements in plants i.e., the fraction of biomass that is C. This is quite important, as many researchers assume that this value is, e.g., 45-50%, without measuring it themselves, and systematic errors could bias ecosystem- to global-scale estimates of vegetation C pools. The authors assemble a large dataset from both TRY and the scientific literature and analyze the effects of plant organ, life form, latitude, etc., on reported C values. In general, I think this is a very worthy effort, and the analysis seems solid in most respects.

[**Reply**] Thank you very much for your encouragement.

**[Comment]** 1. The text says that "interactive" factors were explored, but there's no mention of interactive effects in the results, and it's not clear, for example, whether the latitudinal trends shown are independent of life form. It seems to me really important to report type III SS and interactions, so that readers understand the relative importance and relationships of the tested factors. This would also allow the text to be clearer and more prescriptive about the primary effects and what values or ranges researchers should use.

**[Reply]** Thanks. Following your suggestions, we have analyzed the interactive effects by using *varpart* function in the revised version. The interactive explanations of climatic factors and life form on the variation of the C content ranged from 0.7% in the stems to 15.7% in the reproductive organs. This indicated that the changes of plant C content along latitudinal or climatic gradient may not be independent of life form. We have added these results in the revised manuscript [Lines 126-128: "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."].

As you recommended, we have also used the general linear model (GLM) and the *anova* function in the *car* package to report the type III SS. The C content of plant organ 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 (Table S3-S6). We added in the section of Materials and methods [Lines 102-104: "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."] and Result [Lines 121-122: "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)."] in the revised manuscript.

 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).

Factor	Sum Sq	Df	F value	P value
Intercept	4771	1	366.48	< 0.001
MAT	6	1	0.46	0.50
MAP	8	1	0.61	0.44
Life form	3	2	0.10	0.91
MAT: MAP	85	1	6.66	0.01
MAT: Life form	9	1	0.65	0.42
MAP: Life form	29	1	2.25	0.14
MAT: MAP: Life form	2	1	0.14	0.71
Residuals	1172	90		

**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).

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Factor	Sum Sq	Df	F value	P value
Intercept	5831	1	359.17	< 0.001
MAT	2	1	0.12	0.73
MAP	4	1	0.27	0.60
Life form	256	3	5.25	< 0.01
MAT: MAP	5	1	0.28	0.59
MAT: Life form	328	3	6.73	< 0.001
MAP: Life form	73	3	1.49	0.21
MAT: MAP: Life form	424	3	0.87	0.46
Residuals	28717	1769		

**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).

Factor	Sum Sq	Df	F value	P value

Intercept	6517	1	510.08	< 0.001
MAT	22	1	1.72	0.19
MAP	39	1	3.09	0.08
Life form	2829	3	73.81	< 0.001
MAT: MAP	13	1	1.00	0.32
MAT: Life form	371	3	9.68	< 0.001
MAP: Life form	818	3	21.34	< 0.001
MAT: MAP: Life form	471	3	12.29	< 0.001
Residuals	222234	17393		

**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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Factor	Sum Sq	Df	F value	P value
Intercept	83	1	7.75	0.01
MAT	104	1	9.72	< 0.01
MAP	108	1	10.11	< 0.01
Life form	286	3	8.92	< 0.001
MAT: MAP	107	1	10.03	< 0.01
MAT: Life form	129	3	4.02	0.01
MAP: Life form	136	3	4.25	0.01
MAT: MAP: Life form	108	3	3.36	0.02
Residuals	35321	3311		

**[Comment]** 2. On a related note, no code or data availability is specified (and please note that "available from the authors" is not, in my opinion, acceptable). It's 2017, and I expect all code and data (at least that backing the main results) to be included as supplementary info, or posted in a repository. It's not acceptable to produce results from a black box, and there's a huge benefit to making the data (for future analyses) and code (so readers can see exactly what was done) available. At the very least, why not contribute your assembled literature data back to TRY?

**[Reply]** Thanks. We will upload the *R*-software codes and relevant data of this study in the revised manuscript. Following your suggestions, we will contribute our data to TRY to benefit more studies.

[Comment] 3. Finally, while I appreciate the difficulties of writing in a foreign language, the current manuscript has many minor errors and thus frustrating to read. Please work with either an editing service or English-fluent colleague to improve it in this respect. [Reply] Thanks. We have polished the manuscript writing with colleagues' help.

## Specific comments

[Comment] 1. Lines 23-25: unclear ending; more suitable than what? [Reply] Thanks. Specific C content values from different organs and life forms may be more suitable than the canonical value of 50% to evaluate global vegetation C stock. We have revised this sentence in the revised manuscript [Lines 22-24].

[Comment] 2. L. 44: "ignores"[Reply] Thanks. We have corrected the writing.

[Comment] 3. L. 136: can you give examples of large-scale studies that have assumed a 50% value?

**[Reply]** Thanks. According to your comments, we have added some case studies of the large-scale C stock estimations using 50% in Lines 134-136 as following: "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).".

[Comment] 4. L. 157-158: "Plant organs: are likely"[Reply] Thanks. We corrected this in the revision.

[Comment] 5. L. 163: consistent? Inconsistent?[Reply] Thanks. It is consistent. We have corrected it.

**[Comment]** 6. L. 198: how specific? Do researchers need to use latitude-weighted values? Life form weighted? It would be good to very clear: what are the most important factors for researchers to consider, if they need a C content value and aren't going to measure one themselves? E.g. "We recommend using the values given in Table 1, which are specific to plant organ and life form." **[Reply]** Thanks for your insightful comments. Our results showed that C content varied significantly among plant organs and life forms. Thus, we recommend using the values given in Table 1, which are specific to plant organ and life form. We have revised this in the revision [Lines 186-187: "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."].

## [Comment] 7. L. 356: latitudinal trend after accounting for other factors?

**[Reply]** Thanks. Similar to the statistical analysis of Han et al. (2011), we did not account for other factors, because we focused our study on exploring the biogeographical pattern of plant C content. We have made modifications in Materials and methods section [Lines 98-99: "A linear model without accounting for other factors was used to explore the biogeographical pattern of plant organ C content along the latitudinal gradient, as well as the relationships between plant organ C content and MAT and MAP (Han et al., 2011)."].

#### **To Anonymous Referee #2:**

**[Comment]** General Comments: This paper reports the findings of an extensive literature review to determine the carbon content of plants with respect to different organs in individual plants, between plant species and along a latitudinal gradient. While the review is comprehensive, I wonder how these results will be applied in any practical way? The authors present a superficial analysis of how their results are different from canonical values typically used for plant carbon content, but the reader is left to wonder how the results reported here will be used in any practical way?

One concern that I have is that this paper seems ill-fitted to the journal Biogeosciences. There's no biogeoscientific data provided and the findings are not discussed in a biogeoscientific context.

[Reply] Thanks for your comments. As we know, plant C content is critical to assessment of global C cycle and ecological stoichiometry. The most widely employed C content in plants is 50% both at the regional and global scales for the estimations of vegetation C stock (e.g. Saatchi et al., 2011; Li et al., 2016; Borchard et al., 2017). However, plant C contents varies significantly with different organs, life forms, and biomes, and even across individuals (Elias and Potvin, 2003; Tolunay, 2009; Martin and Thomas, 2011; Yao et al., 2015). Using the default value of 50% as biomass-C conversion factor can lead to biases in vegetation C stock estimations (Zhang et al., 2009; Martin and Thomas, 2011; Rodrigues et al., 2015). To reduce the uncertainty, several studies have used the species-specific organ C contents to evaluate the stand vegetation C stocks (Jones and O'Hara, 2012; Rodrigues et al., 2015; Wu et al., 2017). Nonetheless, it is hard to obtain available data of C content and biomass allocation for every species and organ in practical applications. At large scales, the generalized C contents of specific woody species provide an alternative to the realistic estimations (IPCC, 2006; Thomas and Martin, 2012; Wu et al., 2017). However, the lack of plant C contents of other life forms (such as herb, crop, vine, etc.) still constrains the accurate estimation of vegetation C stocks at large scales.

Therefore, in this paper, we explored the C content of different life forms and organs using the largest C content dataset to date. The dataset covers woody plants, herbs and other life forms plants (i.e. crop, vine, fern, bamboo). Moreover, our result can be an alternative for the IPCC guidelines to update the C fractions. The practical applications of specific C content will improve the accuracy of vegetation C stock estimations and our understanding of terrestrial C cycle. We have added these in the Introduction [Lines 32-61] and the Conclusion sections [Lines 186-190].

In addition, accurate estimation of the vegetation C stock can help us to understand the responses of global C cycles and terrestrial ecosystems to global changes, which is one of major scopes of *Biogeosciences*. Many studies focusing on the estimation of vegetation C stocks across the world's terrestrial biomes have been published in *Biogeosciences* (e.g., Fyllas et al., 2009; Petrescu et al., 2012; Guo et al., 2014; Nyirambangutse et al., 2017). Therefore, we believe that our paper is suitable to *Biogeosciences*. Thank you for your understanding.

[Comment] 1. Specific Comments: You point out that C content varies across individuals (line 57), and that your results suggest that overestimating the carbon content of plant organs could introduce errors ranging between 3.77-13.8% in regional C stock. I wonder if this 3-14% is larger than the variance between individuals, and if not, how much uncertainty does the inter-individual variation add to a regional C stock estimation? Are your findings significant compared to the uncertainty due to different C content between individuals? **[Reply]** Thanks for your comments. As you pointed out, plant C content from the same organ and the same species in one site varies across individuals (Elias and Potvin, 2003). Compared with the species-specific C content, several studies have showed that the canonical value of 50% could introduce errors ranging from 3.77% to 13.8% in regional C stock (Bert and Danjon, 2006; Tolunay, 2009; Fang et al., 2010; Rodrigues et al., 2015). Following your suggestions, we calculated the mean individual variation of plant organ C contents using the formula of Bert & Danjon (2006). Our result showed that the mean individual variations in roots, leaves and stems were -0.61% (-1.34~2.56%), 0.13% (-0.01~0.23%), and 0.19% (-0.63~1.01%), respectively, implying that variations among individuals of certain species are less than the variations among life forms (e.g. 3.77 – 13.8% in previous studies). Hence, the specific C contents of different life forms in our study could be useful in global and regional C stock estimation.

[Comment] 2. Page 7, line 148: Are the differences between your values and those used by the IPCC significant?

While I appreciate the effort to quantify the plant organ C content, if you were to consider the carbon stock of an entire plant, for example a tree, given the % mass that each organ contributes to the overall C mass of the individual tree, is 50% that far off? It's difficult to decifer this from the text, but I would imagine that this is the number that would be of most interest to someone trying to apply this data, for example, calculating a regional carbon pool.

**[Reply]** Thanks for your comments. Following your suggestions, we conducted one sample Student's t-test 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%). The stem C contents in our results were significantly lower than that of temperate broad-leaved woody species (47.7% and 47.8% *vs.* 48%; p < 0.001 and p = 0.018, respectively) and conifers (50.5% *vs.* 51%; p < 0.001), but were significantly higher than those of tropical broad-leaved woody species (47.7% and 47.8% *vs.* 47%; p < 0.001 and p < 0.001) proposed by IPCC (2006). We have added these results in the new manuscripts [Lines 93-95: "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."] and [Lines 141-143:" 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 = 0.018) 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)."].

Additionally, we have not found relavent studies that have reported the detailed biomass allocation of each plant individual in terrestrial biomes. The unclear biomass allocation limited our calculation of the biomass-weighted C contents of each organ of specific individuals. Thus, as we addressed in the Introduction section [Lines 51-52], "the generalized C contents of specific life forms provide an alternative for realistic estimations". From the perspective of practical application, the organ-specific and life form-specific C contents in our study may improve the accuracy of the estimation of regional and global vegetation C stocks.

[Comment] 3. Page 8, line 177: But your results suggest that life form is more important than climate

I'm having a tough time following your argument. If I have this right, life form is the dominant control on C, not climate. But doesn't climate influence life form, particularly along a latitudinal gradient where climate will influence the length of the growing season, water availability, photosynthetically active radiation, etc...I guess I don't understand how you can talk about life form independently from climate and attribute it to carbon content. Are you suggesting that within the same species that a latitudinal gradient exists with respect to carbon content? If so, it's unclear.

[**Reply**] Thanks for your comments. Indeed, climate affects plant physiological processes through changing the length of growing season, water availability, photosynthetically active radiation, etc., and shaping life form distribution and the community species compositions. In other words, climate is the key factor driving plant physiological processes and determining species compositions (Araújo et al., 2004; Bertrand et al., 2011). Moreover, the distributions of plant life forms are also affected by phylogenetic evolution, soil fertility, topographic condition, biotic interactions, and anthropogenic activities (Furley and Newey, 1979; Linhartyan and Grant, 2003; Wang et al., 2009).

Our result showed that the independent explanations of climatic factors (MAT+MAP) (0.2 - 8.4%) on the variation of organ C contents (analyzed by pooled data of each organ in all life forms rather than species) were lower than that of life form (7.2% - 21.5%). Thus, life form may directly drive the variation of plant C content. Further, we found that plant C content deceased with increasing latitude, which was consistent with the changes of life forms along the latitude. The proportion of woody plants tended to decrease while that of herbs increased with increasing latitude and decreasing MAT and MAP (Fig. S1). Hence, the compositions of life form of regional vegetation may largely explain the variation of plant C content at the latitude.

Our result was consistent with the previous studies that life form influenced greatly the plant C content (Fyllas et al., 2009; Zhao et al., 2016). Additionally, the universally constrained C:N:P ratios of plants shows the close relationship among C, nitrogen (N) and phosphorus (P) contents (Hessen et al., 2004; Fyllas et al., 2009; Zhao et al., 2016). At large scales, that leaf N and P stoichiometry varies remarkably among life forms also supports our conclusion (Han et al., 2011; Zhao et al., 2016; Tian et al., 2017). According to your comments, we have rewritten our discussion to avoid misunderstanding [Lines 163-181]. Thank you again!

#### Technical Corrections:

[Comment] Page 3, line 38: biogeochemical cycling? Page 3, line 44: ignores; Page 3, line 49: compared; Page 4, line 66: patterns; Page 4, line 71: literatures; Page 4, line 77: that used; Page 5, line 105: A linear model; Page 6, line 106: latitudinal gradient; Page 6, line 111: A linear model.

[**Reply**] Thanks for your comments. We have corrected all these wordings.

## [Comment] Page 6, line 125: should it be p<0.15 and p<0.05?

**[Reply]** Thanks. Their *p* values were 0.147 and 0.053, respectively. We have revised these in the new manuscript[Lines 119-120] as following: "while reproductive and stem C content displayed no significant latitudinal trend ( $r^2 = 0.02$ , p > 0.05;  $r^2 < 0.01$ , p > 0.05; Fig. 3, Table S2). "

[Comment] Page 8, line 180: Doesn't this belong in the Results section?[Reply] Yes. Following your suggestions, we have deleted this sentence in the Discussion section and rewritten the Results section.

[Comment] Page 9, line 189: shapes the biogeographic patterns... Page 9, line 199: "Besides"?

[Reply] Thanks. We deleted "Besides" in the revised manuscript.

## **Refereces:**

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

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- 15 Abstract. Plant carbon (C) content is one of the most important plant traits and is critical toin the assessment of global 16 C cycle and ecological stoichiometry-; hHowever, the global variations in plant C content remains poorly understood. 17 In this study, Www conducted a global analysis of the plant C content by synthesizing data from 4,318 species to provide 18 document specific values of C content and to assessand their variation of the C contenta across plant organs and life 19 forms. Our results showed that C content varied markedly across plant organs. Plant organ C contents ranged from 45.01% 20 in reproductive organs to 47.889% in stems at global scales, which were significantly lower than a-the widely employed 21 canonical value of 50% that has been widely employed in previous studies. Plant C content in leaves (global mean of 22 46.9%) was higher than that in roots (45.6%). Across life forms, woody plants exhibited higher C content than 23 herbaceous plants. Conifers, relative to broad-leaved woody species, had higher C content in roots, leaves and stems. 24 Plant C content tended to a decrease with the increasing latitude. The life form explained more variation of the C content 25 than climate due to plant structural requirements. Our findings suggest that specific C content values from of different 26 organs and life forms developed in our study should be incorporated into the estimations of regional and may be more 27 suitable to evaluate global vegetation biomass C stock and plant ecological stoichiometrys.
- 28 Keywords: plant, carbon content, organ, life form, climate, biogeographical pattern

## 29 **1 Introduction**

30 Carbon (C) is one of the most abundant elements in all living organisms (Hessen et al., 2004; Dietze et al., 2014). Plant 31 photosynthesis transfers C from CO<sub>2</sub> to the forms of biological compounds to maintain metabolic functions and build 32 basic structures (Dietze et al., 2014; Mart nez-Vilalta et al., 2016). This process creates a huge organic C pool in 33 terrestrial vegetation (Schlesinger and Bernhardt, 2013). The vegetation C stock, which is usually estimated by 34 multiplying total plant biomass by a corresponding biomass C conversion factor, i.e., the C content (gram of C per gram 35 of dry biomass) (Bert and Danjon, 2006; Thomas and Martin, 2012). The most widely employed C content in plants is 36 50% in the regional and global vegetation C stock estimations (De Vries et al., 2006; Keith et al., 2009; Lewis et al., 37 2009; Saatchi et al., 2011; Zhu et al., 2015, 2017). Originally, this value was calculated from an average molecular 38 formula CH<sub>144</sub>O<sub>0.66 i.e.</sub>, elemental composition of about 50% C, 6% hydrogen, 44% oxygen and trace amounts of several 39 metal ions in living plant wood (Pettersen, 1984; Bert and Danjon, 2006).

40 Therefore, C content is one of the key factors determining the assessment accuracy of global terrestrial vegetation C 41 stocks (Lamlom and Savidge, 2003; Thomas and Martin, 2012; Jones and O'Hara, 2016). Additionally, as a major 42 element in plants and contributing roughly half of dry biomass, C is relatively more stable than mineral elements in 43 plants and can be easily measured simultaneously with other key elements (Hessen et al., 2004; Han et al., 2011). Thus 44 the ratio of C, nitrogen (N), phosphorus (P) in plants is widely used in ecological stoichiometry to diagnose nutrition 45 limitation, competition, and biogeochemical cycle (Sardans et al., 2012; Liu and Sun, 2013). Further study on plant C 46 content will improve our understanding of the variation in plant key elements in ecological stoichiometry.

47 The most widely employed C content in plants is 50% in the forest C stock estimations (De Vries et al., 2006; Keith et 48 al., 2009; Lewis et al., 2009; Saatchi et al., 2011; Borchard et al., 2017). Originally, this value is calculated from an 49 average molecular formula CH144O0.66 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 50 51 Eriksson, 1998; Bert and Danjon, 2006; Yao et al., 2015), life forms (Tolunay, 2009; Fang et al., 2010; Cao and Chen, 52 2015), biomes (He et al., 2006; Martin and Thomas, 2011; Martin et al., 2015), and even across individuals (Elias and 53 Potvin, 2003; Uri et al., 2012; Martin et al., 2013). -uUsing the default value of 50% for different as biomass C 54 conversion factor which plant organs ignores the variation of C content among plant organs and life forms and may lead 55 to biases-in vegetation C stock estimation (Zhang et al., 2009; Martin and Thomas, 2011; Rodrigues et al., 2015). For 56 example, change of 1% wood C content from the canonical value of 50% can bring up to ~7 petagrams variation in 57 global vegetation C stocks, which is almost equivalent to half of the vegetation C stocks of continental USA (Dixon et 58 al., 1994; Jones and O'Hara, 2016). Therefore, accurate knowledge of plant C content is crucial for estimating the 59 potential magnitude of C sequestration in different biomes and understanding the roles of vegetation in the global C 60 cycle (Thomas and Martin, 2012).

61 <u>To reduce the uncertainty in estimation of vegetation C stocks, several studies have used the species-specific organ C</u>

62 content in regional scales (Jones and O'Hara, 2012; Rodrigues et al., 2015; Wu et al., 2017). Basically, the weighted

63 mean C content (WMCC) of plants, especially woody plants, was useful for precise C stock estimation (Zhang et al.,

64 2009). However, it is hard to obtain available data of C content and biomass allocation for every species and organ in 65 diverse vegetation. Combining the phylogenic, taxonomic and environment-dependent traits of species, the generalized 66 C contents of specific life forms provide an alternative for realistic estimations (Thomas and Martin, 2012; Wu et al., 67 2017). For instance, T the Intergovernmental Panel on Climate Change (IPCC) (2006) provided the wood C content of 68 biomass of trees in tropical/subtropical forests (47%), temperate/boreal forests (48% of and that of broad-leaved trees 69 and 51% of conifers in temperate/boreal forests (48% and 51%), respectively. Although t-which was based on chemical 70 analysis of pooled samples. The values were more accurate than do enhance the accuracy of vegetation C stock estimation 71 Compared with the default value of 50%. Nevertheless, errors was were still introduced to C stock estimation in an the 72 actual application (Martin and Thomas, 2011), especially when the uncertainty resulted from estimation using available 73 plant C contents of limited specific life forms could not be eliminated (Thomas and Martin, 2012). Thus-, the specific 74 C contents of different life form plants require explicit consideration and application in vegetation C stock evaluations. 75 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., 76 77 2009; Zhang et al., 2012).

For 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.

81 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 82 still varies significantly with different organs (Alriksson and Eriksson, 1998; Northup et al., 2005; Bert and Danjon, 83 2006; Yao et al., 2015), life forms (Tolunay, 2009; Fang et al., 2010; Cao and Chen, 2015), biomes (He et al., 2006; 84 Martin and Thomas, 2011; Martin et al., 2015), and even across individuals (Elias and Potvin, 2003; Uri et al., 2012; 85 Martin et al., 2013). This indicates a high risk of inaccurate C storage estimation at large scales. In addition, the 86 geographical pattern of plant C content has been explored by recent studies (Yuan et al., 2011; Yang et al., 2015a; Zhao 87 et al., 2016). C content in plant leaves and roots showed significant latitudinal trends in Chinese forests (Zhao et al., 88 2016). However, other studies reported no significant latitudinal trends of plant fine root and aboveground tissue (Yuan 89 et al., 2011; Yang et al., 2015a). These controversial results suggest that the geographical pattern of plant C content at 90 global scale is still unclear.

91 <u>the With-above considerationreasons</u>, we compiled a global dataset of plant organ C content to provide referable, and 92 then conducted a synthetic analysis of its global variation in plant organ C contents of plant organs in different and two 93 possible driving factors, climate and life forms. We tried, to answer the following two questions: (1) how much C do 94 specific plant organs contain? <u>a</u>And (2) what are the biogeographical patterns of plant C content and the possible driving 95 factors?

#### 96 2 Material and methods

## 97 **2.1 Data compilation**

98 We searched three databases including Google Scholar (https://scholar.google.com/), Web of Science 99 (http://isiknowledge.com) and CNKI (China National Knowledge Infrastructure) (http://www.cnki.net/) for literatures 100 reporting the C content data inof plants which were published during from 1970 to 2016. To collect reliable and 101 comparable data. We documented -315 -research paperspublications were obtained according to the following two 102 criteria: (1) the data must have been obtained infrom natural ecosystems (including wetland and mangrove) or plantation 103 ecosystems (including grassland and cropland-which were disturbed by human activities such as cultivation, fertilization 104 and grazing) were accepted, while the excluding data from laboratory grown or field control experiment grown plants 105 were excluded; and (2) dataset only included plant C content obtained detected by the two commonly used methods (i.e., 106 the  $K_2Cr_2O_7$ -H<sub>2</sub>SO<sub>4</sub> oxidation-method and the combustion methods) was included, excluding-while studies that used the 107 default value, assumption-assumed value, or values calculated from the chemical compositions for plant C contentwere 108 excluded from our data compilation. In addition, we compiled also included the data on of plant C content in specific 109 plant organs from the TRY database (https://www.try-db.org) (Kattge et al., 2011) using the aforementioned criteria 110 (Table S1).

111 Finally, a total of 24,326 records of 4,318 species in 1,694 genera and 238 families for plant organ C content from 627 112 sites in six continents-were included in our global dataset (Fig. -1), in which 36.33% were from literatures and 63.67% 113 were were from literatures from and the TRY database, respectively. The dataset is consisted of 4,318 species in 1,694 14 genera and 238 families. For each data record, we recorded documented the geographical location information (latitude, 115 longitude and altitude), Latin binomial-species name, genus and, family of species, organ type (reproductive organ, root, 16 leaf and stem), life forms, chemical compounds (lignin and cellulose), and plant C content. To provide detailed C content 117 of plant for future estimation of vegetation C stock, pPlant life forms were divided into five categories: herbaceous 118 species (herb), woody plants, fern, vine, and bamboo-in this study. Data of C crops wereas separately listed analyzed in 19 the herbaceous category. Due to the high proportion of The woody plants in the terrestrial vegetation, we were further 120 categorized-divided them into three sub categories groups: evergreen broadleaved woody plants, deciduous broadleaved 121 woody plants, and conifers. If the compiled literature showedFor those data with no information of on life forms, then 122 we documented it fromit was attained from the Flora of China (http://foc.eflora.cn), Wikipedia 123 (https://en.wikipedia.org/wiki/Wiki/), Useful Tropical Plants (http://tropical.theferns.info) or The Plant List 124 (http://www.theplantlist.org) to get accurate information of plant life form. In order to explore the biogeographic pattern 125 and the driving factors of C content oin f plant organs, we used the latitude and longitude of each site to extract data of 126 climatic variables (mean annual temperature, MAT, °C; mean annual precipitation, MAP, mm) from WorldClim 127 (http://www.worldclim.org/) (Hijmans et al., 2005). Given that plant C content can-might vary with the size-growth 128 stages of individuals (Elias and Potvin, 2003; Uri et al., 2012; Martin et al., 2013), we recorded the averaged C content 129 in of herbaceous species at across different growth stages during the annual growing season.

#### 130 **2.2 Statistical analyses**

First, wWe first calculated documented the statistical measures of plant organ C content for different life forms, central tendency and variability, including arithmetic mean (Mean), median (Median), standard deviation (SD), and 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).-), and tThus, the one sample Student's t-test was used to determine whether the plant stem C content of woody plants each organ 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, and 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.-

40 A lLinear model without accounting for other factors was used to explore the biogeographical pattern of plant organ C 41 content along latitudinal the latitude gradients as well as the relationships between plant organ C content and, MAT and 42 MAP (Han et al., 2011). To differentiate evaluate the effects of life form and climatic factors (i.e. MAT and MAP) on 43 the variations of plant C content among four organs, a partial generalized linear model was used to calculate the total 44 explanation, the independent explanation and the interactive explanation of climatic factors and life forms for four 45 different organs (i.e. reproductive organ, root, leaf, and stem), respectively (Han et al., 2011). Additionally, a linear 146 model and an analysis of variance with the type III were performed to test the variations of C contents explained by 147 climatic factors and life forms. A linear model Linear model-was used to explore the relationship of plant C content with 148 the content of lignin and the cellulose. All statistical analyses were performed in the R 3.3.1 software (R core Team, 149 2016).

#### 150 **3 Results**

#### 151 **3.1 Carbon content of plant organs**

152 Plant C content varied significantly with among organs. Arithmetic means of C content for reproductive organ, root, leaf 153 and stem were 45.01%, 45.64%, 46.85% and 47.88%, respectively (Fig. 2, Table 1), all of which were significantly lower 154 than the default value of 50% (p < 0.05 in all case). Plant organ C content also varied markedly across the life forms 155 (Table 1). Among herbaceous plants, C content ranged from 42.41% in stems to 44.73% in leaves; and among woody 56 plants, it-C content changed from 47.43% in roots to 48.56% in reproductive organs (Table 1). C contents in all four 157 organs were significantly higher in the woody species than in the herbaceous species. Across woody species, C contents 158 in roots, leaves, and stems of conifers was were significantly higher than those at of deciduous broad-leaved and 159 evergreen broad-leaved woody plants, respectively. In addition, the C contents of ferns, vines and bamboo ranged from 160 42.98% in bamboo leaves to 49.20% in bamboo stems (Table 1).

## 161 **3.2 Latitudinal trends of carbon content and possible driving factors**

- Plant C contents in roots and leaves decreased with the increasing latitude and decreasing MAT and MAP  $(r^2 = 0.05, p)$
- $63 \leq 0.001$  in all cases), while reproductive organ and stem C content displayed no significant latitudinal trends ( $r^2 = 0.02$ ,
- 64  $p > 0.05; r^2 < 0.01, p > 0.05;$  Fig. 3, Table S2 $r^2 = 0.02, p = 0.15; r^2 < 0.01, p = 0.05;$  Fig. 3, Table S2).-

165 The C content of plant organs was significantly affected by climatic factors (p < 0.05 in stem), life form and their 166 interaction (p < 0.05 in all cases, except for reproductive organ), respectively (Tables S3-S6). The effects of climatic 167 factors and life forms on plant C content varied largely across the plant organs (Fig. 4). The independent explanations 168 of climatic factors on the variation in the C contents of the reproductive organs, roots, leaves, and stems were 8.4%, 169 0.2%, 3.8% and 0.5%, respectively. The variation of C content in the reproductive organs, roots, leaves, and stems 170 explained independently by life forms were 19.8%, 21.5%, 7.2%, and 10.0%, respectively. The interactive explanations 171 of climatic factors and life form on the variation of C content of the reproductive organs, roots, leaves, and stems were 172 15.7%, 3.6%, 5.2%, and 0.7%, respectively. These results demonstrated that the variation of plant C content was 173 explained more by life form than by climatic factors (Fig. 4; Tables S3-S6).

## 174 **4 Discussion**

175 We evaluated plant C content across plant organs and life forms by using establishing a global plant C content dataset 176 established in this study. Our results showed that plant C content varied remarkably across the four among organs, which 177 is supported bywas consistent with previous studies (Alriksson and Eriksson, 1998; Northup et al., 2005; Tolunay, 2009). 178 Notably, we found that tThe global average C contents of all-four organs were significantly lower than the canonical 79 value of 50% which was widely used to convert vegetation biomass to C stock at large-scales, such as in temperate 180 forests (De vries et al., 2006), tropical forests (Lewis et al., 2009; Saatchi et al., 2011), and global forests (Keith et al., 181 2009)., In addition, -indicating that this default value could lead to the overestimation of vegetation C stocks at global 82 scales and could induce errors between 3.77 -13.8% in regional C stock estimations (Bert and Danjon, 2006; Tolunay, 83 2009; Fang et al., 2010; Rodrigues et al., 2015). Similarly, global average C contents in of stems and leaves were 84 significantly higher than the other another default value of 45.45% proposed by Whittaker (Whittaker, 1975), while 85 although the C contents of roots and reproductive organs showed no significantly statistical differences with 45.45%. 86 respectively. This means that the canonical value of 50% or other values (e.g. 45.45%) may also introduce errors to 87 vegetation C stock estimations due to the ignorance of the variation of plant C content among organs.

188 AdditionallyFurthermore, our results showed that plant C contents varied significantly among life forms (Table 1). This 89 implies that using the canonical value of 50% could ignore the variances of C contents across life formsAmong woody 90 plants, the stem C contents of broad-leaved woody species (i.e. 47.69% in deciduous and 47.78% in evergreen) and 91 conifers (51.48%) in this study were comparable with that those (47.7% and 50.8%, respectively) reported by Thomas 92 and Martin (2012). However, these dataour results were significantly lower than the default values of temperate broad-93 leaved woody species (48%; p < 0.001 and p = 0.01848%) and conifers (51%; p < 0.001), and but higher than the default 94 value that of tropical broad-leaved woody species (47%; p < 0.001 and p < 0.001) proposed by IPCC (2006). This 95 suggesteds that these values from IPCC may overestimate or underestimate the stem C content for broadleaved trees and 196 conifers at global scales.

197 that these values may overestimate or underestimate the stem C content for broadleaved trees and conifers at global 198 scales due to the uncertainty caused by data scarcity. Furthermore, our study also estimated the C content of herbaceous 199 species, vines, ferns and bamboo, which were seldom studied at large scale (Thomas and Martin, 2012). Our results may 200 improve the accuracy of vegetation C stock model and our understanding of the contribution of terrestrial vegetation to 201 global C budgets (Zhang et al., 2009).

202 The variation of plant C content among organs and life forms were associated with differences in their chemical 203 compositions (Figs. 5-and Fig. 6). Plant organs consist are composed of several organic compounds with different C 204 content, such as lignin (with C content of 63% - 66%205 and nonstructural carbohydrates (NSC) (e.g., sugar or starch, with about 44% of C content of about 44%) (Adler, 1977; 206 Poorter and Bergkotte, 1992). Our result was consistent with previous findings that pPlant organs with higher lignin (e.g., 207 stems) tendis likely to ahave higher C content than organs with lower lignin content in this study (e.g., leaves, roots, and 208 reproductive organs,- see-Fig. 5a)- This is consistent with the previous results (Poorter and Bergkotte, 1992; Savidge, 209 2000; Lamlom and Savidge, 2003; Bert and Danjon, 2006; Martin and Thomas, 2011). Despite of the high lignin in roots, 210 the C content in roots was lower than that in leaves, probably because of which is likely due to the high proportions of 211 protein and others C-rich compounds in leaves (Rouwenhorst et al., 1991; Niinemets et al., 2002) and high content of 212 starch in roots (Bert and Danjon, 2006). The lowest C content in reproductive organs was in consistent with its high 213 quantities of NSC and but low content of little lignin (Barros et al., 1996). Across life forms,

214 C content of woody plants was higher than that of herbs (Table 1). This is consistent with their different lignification. 215 wWoody plants generally requirehave low relative growth rate and need proportionally greater investments of C at the 216 cellular level to synthesize lignin for theto supporting structures with relatively low growth rate, which result in leads to 217 a-high lignin and C content (Fig. 6a). This also is supported by previous results (Lambers and Poorter, 1992; Poorter and 218 Bergkotte, 1992; Sariyildiz and Anderson, 2005; Majdi, 2007; Poorter et al., 2012; Mart nez-Vilalta et al., 2016). In 219 contrast, herbs generally showthe high relative growth rate of herbs is accordant with their and high NSC 220 (Mart nez-Vilalta et al., 2016). Thus herb has low lignin and C content (Armstrong et al., 1950; Poorter and Bergkotte, 221 1992; Johnson et al., 2007). Furthermore, our results show that the difference in stem C contents of broad-leaved woody 222 plants (i.e., 47.69% in deciduous and 47.78% infor deciduous and evergreen species, respectively) was lower than that 223 of and conifers (50.48%) could also be explained by their corresponding differences in chemical compositions, which 224 might be due to higher lignin in coniferous stems than that of broad leaved woody stems (Lamlom and Savidge, 2003; 225 Thomas and Martin, 2012).

226 Our results showed that C contents in roots and leaves decreased significantly with the increasing latitude (Fig. 3). This 227 is was inconsistent with previous studies reporting that C content of global plant fine root showed no the latitudinal trend 228 (Yuan et al., 2011), but was consistent with the latitudinal trends ofs in plant C contents of in roots and leaves in China's 229 forests (Zhao et al., 2016). Generally, climatic factors (i.e. temperature and precipitation) regulate elemental contents in 230 plant organs by influencing the associated plant metabolism and functioning (Reich and Oleksyn, 2004; Reich, 2005; 231 Zhang et al., 2012). In our study, Climate and life form may be potential causes for the biogeographical pattern of plant 232 C content in roots and leaves (Zhao et al., 2016). The climatic factors explained independently less variation of plant C 233 contents of four organs (0.2 - 8.4%), see Fig. 4) than other factors. The climatic factors – and life form ean-together

- explain<u>ed relatively higher proportion of large parts of the variation in C contents of roots and leaves (25.3% and 16.2% in, see Fig. 4), while it 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. 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.
  </u>
- 239 <u>Our data showed that The C content of reproductive organs showed no significant latitudinal trend may be due to scarcity</u>
   240 of data (Table S2).
- 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 fiez–Vilalta et al., 2016).
- 247 In addition, the life form independently explained independently more variation of plant C content of four organs (7.2 – 248 21.5%, see-Fig. 4), which was consistent with the results of Fyllas et al. (2009) and other studies about plant nutrient 249 stoichiometry at global scales (Han et al., 2011; Zhao et al., 2016; Tian et al., 2017). Further, the interactive effects of 250 climatic factors with life forms were higher than the independent explanations of climate (0.7 - 15.7%, Fig. 4). These 251 results conjointly revealed the important role of plant life form in shaping plant C content, suggests that life form mainly 252 shape the biogeographic patterns of plant C content. which implied that tThe shift of the species composition in regional 253 vegetation along the latitudinal gradients influenced by climate could partly explain the biogeographic pattern of plant 254 C content. Generally, resonates with this biogeographical pattern. The proportion of woody plants (i.e. species with high 255 <del>C content)</del> tends to a decrease with the increasing latitude, while that of herbs (i.e. species with low C content) increases 256 with the-increasing latitude and decreasing MAT and MAP (Fig. S1). Hence, the variation in life forms grouping in 257 different biomes further corroborates our results of the biogeographic pattern of plant C content., which possibly result 258 in the decreasing latitudinal trend of plant C content. Furthermore, we found that life form explained more variation in 259 the plant C content across organs than climate (Fig. 4). This suggests that ontogenetic differences between plants had a 260 stronger effect on the variation of plant C content than climate due to structural requirements.

# 261 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
 suggesting that the canonical values of 50% may underestimate and overestimate the C content of in stems and leaves
 of conifers and in all organs of overestimate of C content of other life forms, respectively. Thus, specific plant C contents
 given in Table 1 should be used in the estimations of the regional and global C stocks. Besides, global C content of plants

267 may give provided an alternative reference to IPCC for their guidelines to update the plant C fractions and	could improve
268 the accuracy of vegetation C stock estimations. Furthermore, plant C content showed significant lat	itudinal trends
269 induced by optogenetic differences among life forms climatic factors and life forms. This suggests that the	nese latitudinal
270 trends and driving factors should be incorporated into the research in of plant ecological stoic	chiometry and
271 biogeochemical modeling should take these latitudinal trands and driving factors into consideration	momeny and
biogeochemical model <u>mg.</u> should take these faithdunar tiends and driving factors into consideration.	

# 273 Supporting information

.74	Figure S1. Changes in the species composition along the gradients of latitude, mean annual temperature (MAT) and
.75	mean annual precipitation (MAP). The percentage of woody plants decreased with increasing latitude and with
76	decreasing MAT and MAP. Herbs showed the opposite trends with woody plants. Other life forms showed no significant
.77	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.
- 280 Table S2. Model summary for the ordinary least squares (OLS) regression of plant carbon content on three factors
- 281 (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).
- 290 <u>Competing interests</u>
- 291 <u>The authors declare that they have no conflict of interest.</u>

## 292 Funding

293 This work was supported by the National Natural Science Foundation of China (31330012, 31621091).

## 294 Acknowledgments

- 295 We thank Peng Li, Chengjun Ji and Zhiyao Tang for their helpful suggestions for data collection and analysis. We thank
- Aaron Hogan, Anwar Eziz, Jianxiao Zhu, Qiong Cai and Ming Ouyang for a friendly review of the manuscript. We also
- thank the TRY initiative on plant traits (http://www.try-db.org). The TRY database is hosted at the Max Planck Institute
- 298 for Biogeochemistry (Jena, Germany) and supported by DIVERSITAS/Future Earth, the German Centre for Integrative
- 299 Biodiversity Research (iDiv) Halle-Jena-Leipzig and EU project BACI (grant ID 640176).

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

Life form	Reproductive organ		Root		Leaf		Stem	
	n	Mean $\pm$ SD	n	$Mean \pm SD$	n	Mean $\pm$ SD	n	Mean ±SD
Herbaceous plants	83	$42.56 \pm 4.57$	749	$42.45 \pm 5.12$	5181	44.73 ±3.45	162	42.41 ±3.54
Crop	42	$42.40 \pm 5.11$	56	$38.20\pm5.23$	85	41.32 ±3.38	69	$43.26 \pm 3.15$
Woody plants	57	$48.56 \pm 4.07$	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	$48.25 \pm 2.56$	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	$45.83 \pm 0.33$	38	$46.25 \pm 4.46$	251	45.74 ±4.77	82	46.73 ±2.69
Bamboo	-	-	23	$45.06 \pm 4.28$	30	$42.98 \pm 5.09$	39	$49.20 \pm 3.54$
All	142	45.01 ±5.23	2306	45.64 ±4.95	18124	$46.85 \pm 3.98$	3754	47.88 ±3.49

Figure 1. Geographic distribution of sample points sites used in this synthesis. The samples are from size is 627 sites.
 469



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



473

474 **Figure 3.** Trends in the plant carbon contents along latitude and climate gradients. MAT, mean annual temperature; 475 MAP, mean annual precipitation. Ordinary least squares (OLS) regression lines are fit to the data. Solid lines indicate 476 the significant relationships with p < 0.05, and dashed lines denotes the insignificant relationships with p > 0.05. 477 Abbreviations: Repr carbon content, Reproductive organ carbon content. Plant carbon content in roots and leaves showed 478 a significantly latitudinal trends.



- **Figure 4.** Variation partitioning  $(r^2)$  of climate and life forms in accounting for the variances in plant carbon contents 481 across different organs. (a) reproductive organ, (b) root, (b) leaf, and (d) stem. Life form independently explained more 482 variation of carbon content in each organ than climate.



Figure 5. The <u>rR</u>elationships 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 <u>it</u> is no<u>t</u> correlated with the cellulose in plant<u>s</u>.



Figure 6. The rRelationships 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 it is not correlated with the cellulose in plants.



#### 494 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 the increasing latitude and with the decreasing MAT and MAP. Herb 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 content. References cited in this

499 Table S1. Data sets in TRY that contributed to our global dataset of plant carbon content. References cited in this 500 table are attached below.

501 **Table S2.** Model summary for the ordinary least squares (OLS) regression of plant carbon content on three factors

502 (Latitude, MAT and MAP). Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation.