Forests **2012**, *3*, 332-352; doi:10.3390/f3020332

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Review

Carbon Content of Tree Tissues: A Synthesis

Sean C. Thomas and Adam R. Martin *

Faculty of Forestry, University of Toronto, Earth Sciences Building, 33 Willcocks Street, Toronto, ON, M5S 3B3, Canada; E-Mail: sc.thomas@utoronto.ca

* Author to whom correspondence should be addressed; E-Mail: adam.martin@utoronto.ca; Tel.: +1-416-978-1044; Fax: +1-416-978-3834.

Received: 12 April 2012; in revised form: 24 May 2012 / Accepted: 11 June 2012 / Published: 19 June 2012

Abstract: Assessing the potential for forest carbon (C) capture and storage requires accurate assessments of C in live tree tissues. In the vast majority of local, regional, and global assessments, C content has been assumed to be 50% of tree biomass; however, recent studies indicate that this assumption is not accurate, with substantial variation in C content among tree species as well as among tissue types. Here we conduct a comprehensive literature review to present a global synthesis of C content in tissues of live trees. We found a total of 253 species-specific stem wood C content records in 31 studies, and an additional 34 records of species with C content values of other tissues in addition to stem wood. In all biomes, wood C content varied widely across species ranging from 41.9–51.6% in tropical species, 45.7–60.7% in subtropical/Mediterranean species, and 43.4–55.6% in temperate/boreal species. Stem wood C content varied significantly as a function of biome and species type (conifer, angiosperm). Conifer species exhibited greater wood C content than angiosperm species (50.8 ± 0.7% (95% C.I.) and 47.7 ± 0.3%, respectively), a trend that was consistent among all biomes. Although studies have documented differences in C content among plant tissues, interspecific differences in stem wood appear to be of greater importance overall: among species, stem wood C content explained 37, 76, 48, 81, and 63% respectively of the variation in bark, branch, twig, coarse root, and fine root C content values, respectively. In each case, these intraspecific patterns approximated 1:1 linear relationships. Most published stem wood C content values (and all values for other tree tissues) are based on dried wood samples, and so neglect volatile C constituents that constitute on average 1.3–2.5% of total C in live wood. Capturing this volatile C fraction is an important methodological consideration for future studies. Our review, and associated data compilation, provides empirically supported wood

C fractions that can be easily incorporated into forest C accounting, and may correct systematic errors of ~1.6–5.8% in forest C assessments.

Keywords: carbon; forest; tree; volatile carbon; wood chemistry; carbon accounting; tropical forest; temperate forest; subtropical forest; boreal forest

1. Introduction

Accurate knowledge of carbon (C) content in live wood is essential for converting estimates of forest aboveground biomass (AGB) into forest C stocks. By extension, quantifying wood C content in tree species from a range of forest types is critical for understanding the potential of forests for C capture and storage [1–3]. Although recent studies have documented high interspecific variation in wood C content among co-occurring tree species [1–3,4], accounting for this variation has largely been overlooked as an important consideration in measuring forest C stocks [5–7]. A small number of studies have incorporated species-specific C fractions into forest C assessments [2,8–11], but by and large, factors used to convert forest, or tree, AGB to C have only been vaguely generalized in forest C accounting methodologies.

Overwhelmingly, the generic assumption that AGB consists of 50% C on a mass/mass basis remains commonplace in forest C estimates. This value has been used in large-scale estimates of C pools and fluxes in natural tropical [12–15] and temperate forests [16–19], as well as smaller-scale estimates of C stocks in managed forests [20], agroforestry systems [21], tree plantations [22–24], and experimental forest sites [25]. However, recent data indicates that the 50% assumption introduces errors of ~5% in forest C stock estimates [2,3,26,27]. For example, in a previous study from a natural Panamanian forest, we found that using a 50% AGB-C conversion factor lead to a systematic overestimate of ~6.8 Mg C ha^{-1} [2]. Similarly, previous research has shown assuming wood contains 50% C can either over- or underestimate temperate forest C stocks by ~6–8% [1,3,28,29].

Prominent forest C accounting methodologies, such as those offered by the Intergovernmental Panel on Climate Change [30], suggest more precise C fractions for trees of different provenances (e.g., tropical/subtropical trees, temperate/boreal angiosperms and conifers) that are based on chemical analyses of woody tissues. These values have been incorporated into a few estimates of forest C stocks [31,32]; in tropical forests in particular, IPCC guidelines may reduce biases in forest C stock estimates by ~2% when compared to a 50% C fraction assumption [2]. However, since the IPCC [30] protocols were published, a number of studies have made available more detailed species-specific wood C data for trees from a much wider range of forest types. As a result, evidence from tropical forests suggest IPCC protocols still may overestimate forest C stocks by 3.3%: an overestimate equivalent to ~4.1 Mg C ha^{-1} [2]. Fortunately, compared to other sources of error in forest C accounting [33], redressing accuracies in AGB-C conversion factors (or wood C fractions) is relatively tractable through a comprehensive synthesis of existing literature. However to our knowledge no such effort has been made to date.

In addition to accounting for interspecific variation, recent studies have also pointed to a critical methodological consideration when deriving wood C fractions through elemental analysis. First

identified by Lamlom and Savidge [1], studies have shown that the traditional method of oven-drying wood prior to elemental analysis significantly underestimates observed wood C content. For example, in 59 tropical angiosperm species we found oven drying wood leads to underestimates in wood C content of 2.5 ± 1.3% S.D. [2]. Similarly, oven-drying samples has been found to result in 2.2% underestimates of wood C in six Chinese temperate species [3]. Carbon that is lost upon heating has been referred to as the "volatile C fraction" (C_{vol}) which, for the purposes of this review, specifically refers to low molecular weight compounds such as phenolics, alcohols and terpenoids that are lost upon heating of woody tissue [1–3]. Capturing the contribution of C_{vol} to total wood C has primarily been done by comparing C content found in freeze-dried or desiccated wood samples *vs.* oven-dried samples [1–3]. Although only a small number of studies have approximated C_{vol}, because new data is quickly being amassed, it is important to review and highlight the contribution of C_{vol} to total wood C content.

In this study, we sought to comprehensively review the existing literature in order to (1) evaluate variation in wood C content across biomes and tree types in a global dataset; (2) calculate wood C fractions that are biome- and "type"-specific (*i.e.*, angiosperm *vs.* conifer); (3) evaluate variation in C_{vol} content across biomes and tree types; (4) assess differences in C content of major tree tissue types, and (5) make available a comprehensive wood C dataset that includes species-specific data. In doing so, we aim to provide synthesis of data that can then be easily integrated into estimates of forest C stocks and fluxes in forest systems generally.

2. Methods

2.1. Data Collection

To identify studies in peer-reviewed journals that provide species-specific stem wood C content data, we searched three databases (Web of Science, Web of Knowledge, Google Scholar) using the search terms "carbon" and "tree", and for "carbon" and major tree tissue types (including "wood", "bark", "root" and "stem"). Additional studies were then identified in the reference sections of papers found in the databases. We included papers that were published or in press as of April 1, 2012. To ensure that only reliable and comparable data was used, studies incorporated into our analyses: (1) provided Latin botanical species names in order to avoid uncertain species assignments; (2) provided data from trees that were ≥10 cm diameter at breast height (dbh) to avoid confounding interspecific variation with size-dependent variation (e.g., differences in wood C between saplings and large conspecific trees [34]. See also discussion on within-stem variation below); and (3) explicitly described field- and lab methodologies. In cases where a single publication had two or more wood C records for the same species [35] we calculated the average value for use in our analysis. When conducting our search, we also found a small number of studies provided wood C data taken from different trunk heights. Here we chose to report data taken from 1.3 m dbh because this was the most commonly replicated sample methodology, and because the effect of sample height location on C content tended to be small (<1%) and non-significant [36–38]. In nearly all cases data was taken directly from tables, with two exceptions: figures were used to estimate wood C content for 32 tropical species (see Figure 1 in [4]), and to estimate C_{vol} for 7 temperate species (see Figure 4 in [1]).

For each published record we classified each species "type" as (1) angiosperm, or (2) conifer, and recorded species "biome" (or provenance) as (1) tropical, (2) subtropical/Mediterranean or (3) temperate/boreal. Provenance was determined based on the location where the trees were sampled, and not the species' biogeographical origin (e.g., tropical angiosperm species sampled by Telmo *et al.* [39] in subtropical/Mediterranean Portugal, were classified as subtropical/Mediterranean). Temperate and boreal species were combined under one classification due to boreal records being found strictly in general analyses of North American trees [1] or Scandinavian studies that sampled south of the boreal zone [40].

In addition to reviewing published estimates of stem wood C content, we compiled data from studies presenting tissue-specific C content. In addition to the criteria noted above, we considered only studies that presented data on two or more of the following tissue types: (1) stem wood; (2) branch wood (as described by authors); (3) twigs (as described by authors); (4) bark; (5) coarse roots (>5 mm diam.); (6) fine roots (<5 mm diam.); (7) leaves. Some studies provide analyses of additional tree tissues and wood anatomical features, but insufficient data were reported to support a cross-species analysis.

2.2. Data Analysis

All statistical analyses were conducted using R v. 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria). Our first analysis step was to evaluate variation in species wood C content as a function of biome and species type. Our literature review found uneven sample sizes (in terms of species) and sampling effort (in terms of number of references) across different biome/type groupings (Table 1). Therefore we tested the effect of biome and type on wood C content using analysis of variance with *F*-tests based on Type III sum of squares, in the "car" R package [41]. Our next analysis step was to directly compare average wood C values among the biome/type groupings. Again, because of unbalanced sample sizes these comparisons were done by calculating a least squares mean (or the "population marginal mean" *sensu* Searle *et al.* [42]) for total wood C for each of the six biome/type groups. Least squares means were calculated by performing a generalized least squares regression in the "nlme" R package [43], and using the regression parameters to calculate predicted values for each biome/type groupings.

We then compared our estimated wood C mean values for each biome/type species groups to corresponding values suggested by IPCC [30] forest C accounting protocols. Agreement between wood C values derived from the literature and those from the IPCC [30] were statistically evaluated by testing the linear hypothesis that IPCC values perfectly predict mean wood C values from the literature (where the *y* intercept = 0 and the slope (or regression coefficient for IPCC values) = 1). This test was performed in the "car" R package, and was performed on a total of seven data points: six biome/type group values, and overall mean wood C value (corresponding to the "default" value of the IPCC).

We also found uneven sample sizes for records of C_{vol}, therefore we conducted the same least squares means calculations and analysis of variance tests on C_{vol} data. In a final analysis step, we also tested if C_{vol} (when grouped by biome/type) made a significant contribution to total wood C content. This was done using a one-sided *t* test that compared mean C_{vol} values against a population with a mean of 0.

Table 1. Peer-reviewed publications containing species-specific C content data. Numbers in square brackets following author names correspond to citations listed in the final reference list, and studies presenting data for tissues other than stem wood are noted with an asterisk. The species-specific dataset is deposited in the Dryad Repository [44].

Reference	Biome	Location	Species (*N*)
Arias *et al.* 2011* [45]	tropical	Costa Rica	6
Becker *et al.* 2012 [35]	tropical	Uganda, Kenya	17
Bert and Danjon 2006* [38]	temperate/boreal	France	1
Castaño-Santamaria and Bravo 2012* [46]	subtropical/Mediterranean	Spain	2
Correia *et al.* 2010* [47]	subtropical/Mediterranean	Portugal	1
Elias and Potvin 2003 [4]	tropical	Panama	32
Fang *et al.* 2007* [48]	temperate/boreal	China	1
Fukatsu *et al.* 2008 [49]	temperate/boreal	Japan	3
Herrero de Aza *et al.* 2011* [50]	subtropical/Mediterranean	Spain	3
Huet *et al.* 2004* [51]	temperate/boreal	France	1
Jacobs *et al.* 2009 [52]	temperate/boreal	United States	3
Janssens *et al.* 1999* [53]	temperate/boreal	Belgium	1
Jones and O'Hara 2012 [29]	temperate/boreal	United States	1
Joosten and Shulte 2002 [54]	temperate/boreal	Germany	1
Joosten *et al.* 2004 [55]	temperate/boreal	Germany	1
Kort and Turnock 1998 [56]	temperate/boreal	Canada	4
Kraenzel *et al.* 2003* [36]	tropical	Panama	1
Laiho and Laine 1997* [40]	temperate/boreal	Finland	3
Lamlom and Savidge 2003 [1]	temperate/boreal	Canada	41
Li *et al.* 2011* [57]	temperate/boreal	South Korea	1
Martin and Thomas 2011 [2]	tropical	Panama	59
Peri *et al.* 2010* [58]	temperate/boreal	Argentina	1
Rana *et al.* 2010 [59]	tropical	Philippines	5
Telmo *et al.* 2010 [39]	subtropical/Mediterranean	Portugal	17
Thomas and Malczewski 2007 [3]	temperate/boreal	China	14
Tolunary 2009 [60]	temperate/boreal	Turkey	1
van Geffen *et al.* 2010 [61]	tropical	Bolivia	15
Xing *et al.* 2005*	temperate/boreal	Canada	1
Zabek and Prescott 2006* [62]	temperate/boreal	Canada	1
Zhang *et al.* 2009* [28]	temperate/boreal	China	10
Zheng *et al.* 2008* [63]	subtropical/Mediterranean	China	5

As in the case of stem wood, we compiled data from studies presenting values for C content of other plant tissues, in all cases using data presented in tables or text. Where multiple tissue-specific values were presented within a given study, we computed an average across all values presented in table form. Where multiple studies presented values for the same species (and tissue type) we computed a simple unweighted mean across studies (using the subset of studies presenting C content values across multiple tissue types). For each tissue type with sufficient sample size ($N > 9$) we tested significance of the relationship between tissue-specific C content and the corresponding species mean stem wood C content, using standard major axis regression. We also tested for non-linearity of these

relationships on the basis of a second-order polynomial term in a least squares regression in which stem wood was considered the independent variable. To test for deviations of the relationship from a linear 1:1 pattern, we computed the standardized major axis regression to test for deviations of the intercept from zero and slope from 1. Differences in tissue-stem C relationships between conifers and angiosperms were also evaluated using analysis of covariance in which C content of a given tissue type was the dependent variable, and stem wood C content and tree type were independent variables; an interaction term was also included in the model to test for heterogeneity of slopes.

3. Results

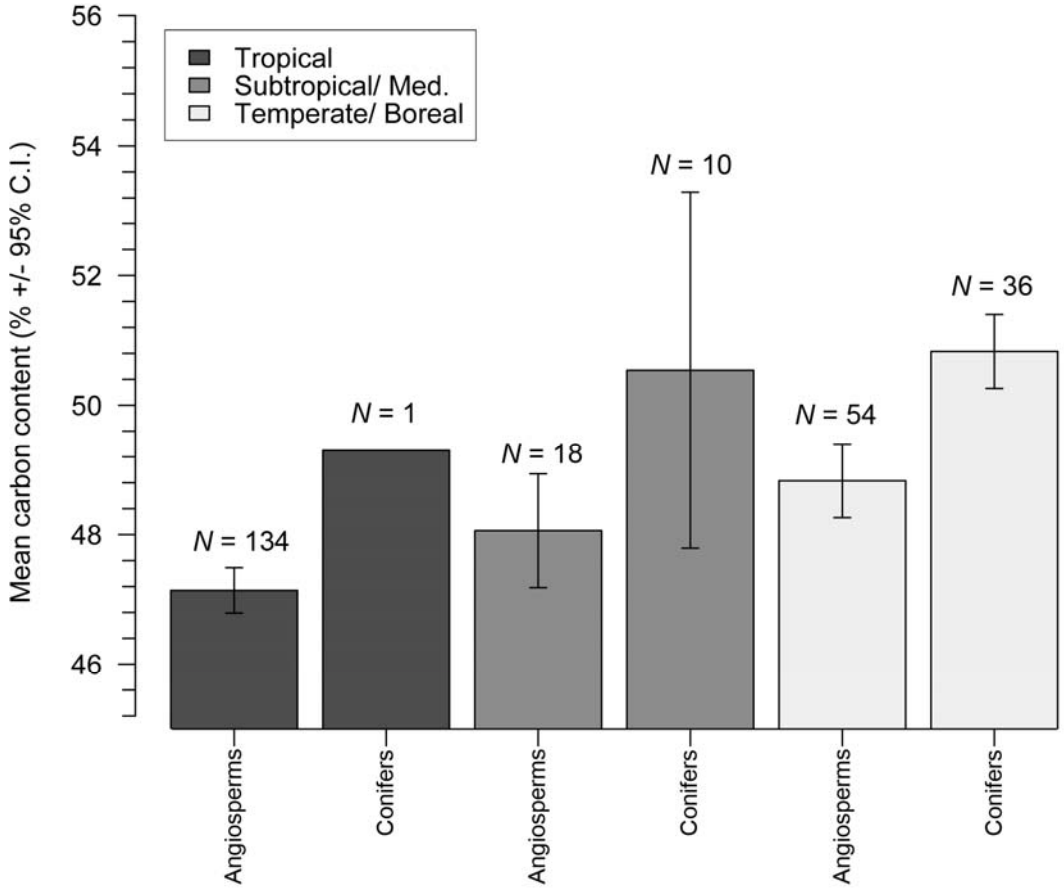
3.1. Stem Wood Carbon Content

We found a total of 31 published studies reporting species-specific C content data for stem wood, representing 253 species-specific C records (Table 1, see also [44]). Of these, only seven studies provided data for ≥10 species, with the largest dataset including 59 species-specific records (Table 1). Overall subtropical/Mediterranean regions are the most poorly represented, with only 28 total species-specific records available, owing to five peer-reviewed studies (Tables 1 and 2, Figure 1). Tropical angiosperm species were the most-well represented group with 134 species-specific records found from seven published studies (Table 2), while tropical conifers had the poorest representation with only one species-specific record for *Pinus caribaea* available (Table 2). In total, angiosperms were better represented compared to conifer species, with 206 *vs*. 47 species-specific records available, respectively (Table 2).

Table 2. Summary data for mean stem wood C and mean volatile C fraction (C_{vol}) for angiosperms and conifers, from three provenances. Error terms represent 95% confidence intervals.

Biome	Type	*N* (References)	*N* (Species)	Observed mean C fraction (%)	IPCC (2006) C fraction (%)	C_{vol} (%)
Tropical	angiosperm	7	134	47.1 ± 0.4	49	2.5 ± 0.3
Tropical	conifer	1	1	49.3	49	N.A.
Subtropical/ Mediterranean	angiosperm	3	18	48.1 ± 0.9	49	N.A.
Subtropical/ Mediterranean	conifer	3	10	50.54 ± 2.8	49	N.A.
Temperate/Boreal	angiosperm	10	54	48.8 ± 0.6	48 ± 2	1.3 ± 0.6
Temperate/Boreal	conifer	13	36	50.8 ± 0.6	51 ± 4	2.1 ± 1.4
All biomes	angiosperm	N.A.	206	47.7 ± 0.3	N.A.	2.3 ± 0.3
All biomes	conifer	N.A.	47	50.8 ± 0.8	N.A.	2.1 ± 1.4
Complete dataset	N.A.	31	253	48.3 ± 0.3	47	2.3 ± 0.3

Figure 1. Comparisons of wood carbon content for 253 trees species grouped across three biomes (tropical, subtropical/Mediterranean, temperate/boreal) and two tree types (angiosperms, conifers). Height of each bar represents a mean wood C content for each grouping estimated as least squares means, and error bars represent 95% confidence intervals. Sample sizes (*N* species) for each grouping are represented above each bar.



In all biomes wood C content varied across species by ~10–15%, ranging from 41.9–51.6% in tropical species, 45.7–60.7% in subtropical/Mediterranean species, and 43.4–55.6% in temperate/boreal species (data not shown, but see [44]). Mean wood C content varied significantly as a function of both biome ($F_{2, 249} = 12.02$, $p < 0.0001$) and species type ($F_{1, 249} = 29.21$, $p \leq 0.0001$; Table 3). Tropical species showed significantly lower wood C content than subtropical/Mediterranean and temperate/boreal species, while subtropical/Mediterranean and temperate/boreal species tested were not statistically different in terms of mean wood C content (Table 4). Our analysis showed that across the whole dataset, conifer species exhibited mean wood C content (50.8 ± 0.7%, 95% C.I.) that was ~3% greater on average than angiosperm species (47.7 ± 0.3%; Table 4), a trend consistent in all biomes when considered independently (Figure 1). Subtropical/Mediterranean and temperate/boreal conifers showed the highest mean wood C content at 50.54 ± 2.8% and 50.8 ± 0.6% respectively (Figure 1). Tropical angiosperms maintained the lowest wood C fractions with an average of 47.1 ± 0.4% (Table 2).

Table 3. Analysis of variance for wood C content and the volatile C fraction (C_{vol}) as a function of biome (tropical, subtropical/Mediterranean, temperate/boreal) and type (conifer, angiosperm).

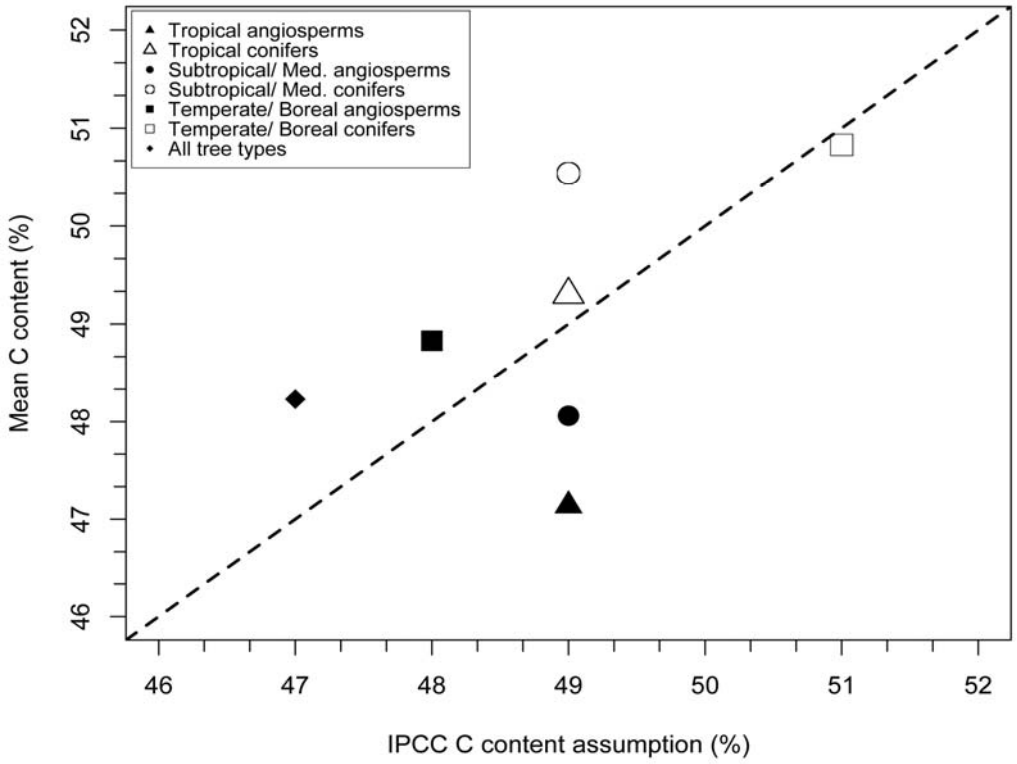
Term		Type III SS	D.F.	*F* value	*p* value
Wood C content	Intercept	57864	1	12455.66	< 0.0001
	Biome	112	2	12.02	< 0.0001
	Type	136	1	29.21	< 0.0001
	Residuals	1157	249	-	-
C_{vol}	Intercept	12.78	1	8.34	0.005
	Biome	10.33	1	6.74	0.012
	Type	1.49	1	0.97	0.328
	Residuals	102.67	67	-	-

Table 4. Parameter estimates from a generalized least squares regression predicting wood C and the volatile C fraction (C_{vol}) as a function of biome and type.

Term		Estimate	Std. Error	*t* value	*p* value
Wood C content	Intercept	48.18	0.43	111.61	< 0.0001
	Temperate	0.59	0.47	1.26	0.209
	Tropical	−1.04	0.47	−2.21	0.028
	Conifer	2.16	0.40	5.41	< 0.0001
C_{vol}	Intercept	1.26	0.44	2.89	0.005
	Tropical	1.21	0.47	2.59	0.012
	Conifer	0.83	0.84	0.99	0.328

Taken together, the IPCC suggested values [30] did not significantly match wood C values found in the literature (linear hypothesis test $F_{0,7}$ = 0.499, p = 0.634; Figure 2); the degree of discrepancy between suggested values differed substantially among biome/type classifications (Figure 2). Specifically, IPCC [30] C fractions were within 1% of observed wood C values, only slightly underestimating wood C content in tropical conifers (0.3% underestimate), subtropical/Mediterranean angiosperms (0.9% underestimate), and temperate/boreal angiosperms (0.8% underestimate). IPCC values only provided a slight overestimate (0.2%) for wood C for temperate/boreal conifers (Table 2, Figure 2). Differences between IPCC [30] wood C fractions and observed C fractions were much larger for tropical angiosperms where IPCC values represent a 1.86% overestimate, and in subtropical/Mediterranean conifers where IPCC values represent a 1.54% underestimate (Table 2, Figure 2). The global wood C value of 47% suggested by the IPCC [30] represents a 1.2% underestimate of the global average wood C value (48.2 ± 0.3%) calculated from available literature (Table 2, Figure 2).

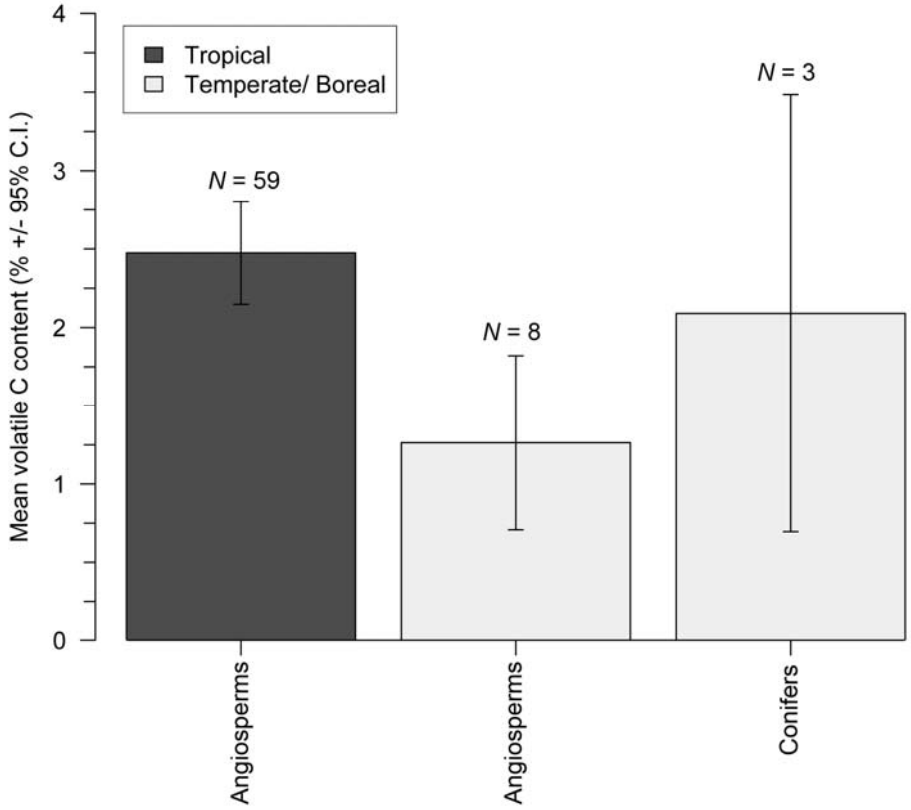
Figure 2. Comparison of wood C fractions suggested by IPCC forest C accounting protocols [30], and mean wood C data found through our literature review (Tables 1 and 2). Comparisons are presented for tropical (triangles), subtropical/Mediterranean (circles), and temperate/boreal (squares) biomes, grouped by angiosperms (filled symbols) and conifer species (open symbols). Also presented is a general value (closed diamond), corresponding to the "default value" suggested by the IPCC [30], and the grand mean calculated from N = 253 species found in the literature (Tables 1 and 2). Dashed line represents a 1:1 relationship between IPCC values and observed wood C content (where y intercept = 0 and slope = 1): a linear expectation (where y intercept = 0 and slope = 1) did not fit the relationship ($F_{0,7}$ = 0.499, p = 0.634).



3.2. Volatile Carbon Content

We found only 70 species-specific records for C_{vol}, owing to three studies [1–3]. Of these, our previous assessment of C_{vol} in 59 tropical trees [2] is the only to provide data for more than seven species (Figure 3); Chinese and North American temperate/boreal species comprised the remaining 11 species-specific records for C_{vol} [1,3]. We found C_{vol} varied significantly as a function of biome ($F_{1,67}$ = 6.74, p = 0.012; Table 3), but did not differ significantly between angiosperm and conifer species ($F_{1,67}$ = 0.97, p = 0.328; Table 3). Results from one-sided t tests showed contributions of C_{vol} were significantly greater than 0 in all groups tested (tropical angiosperms, t_{58} = 14.85, p < 0.0001; temperate/boreal angiosperms, t_7 = 4.45, p = 0.002; temperate/boreal conifers, t_2 = 2.94, p = 0.05). When grouped by biome and type, tropical species exhibited the highest mean C_{vol} (2.5 ± 0.3%), followed by temperate/boreal conifers (2.1 ± 1.4%), and temperate/boreal angiosperms (1.3 ± 0.6%; Table 2, Figure 3).

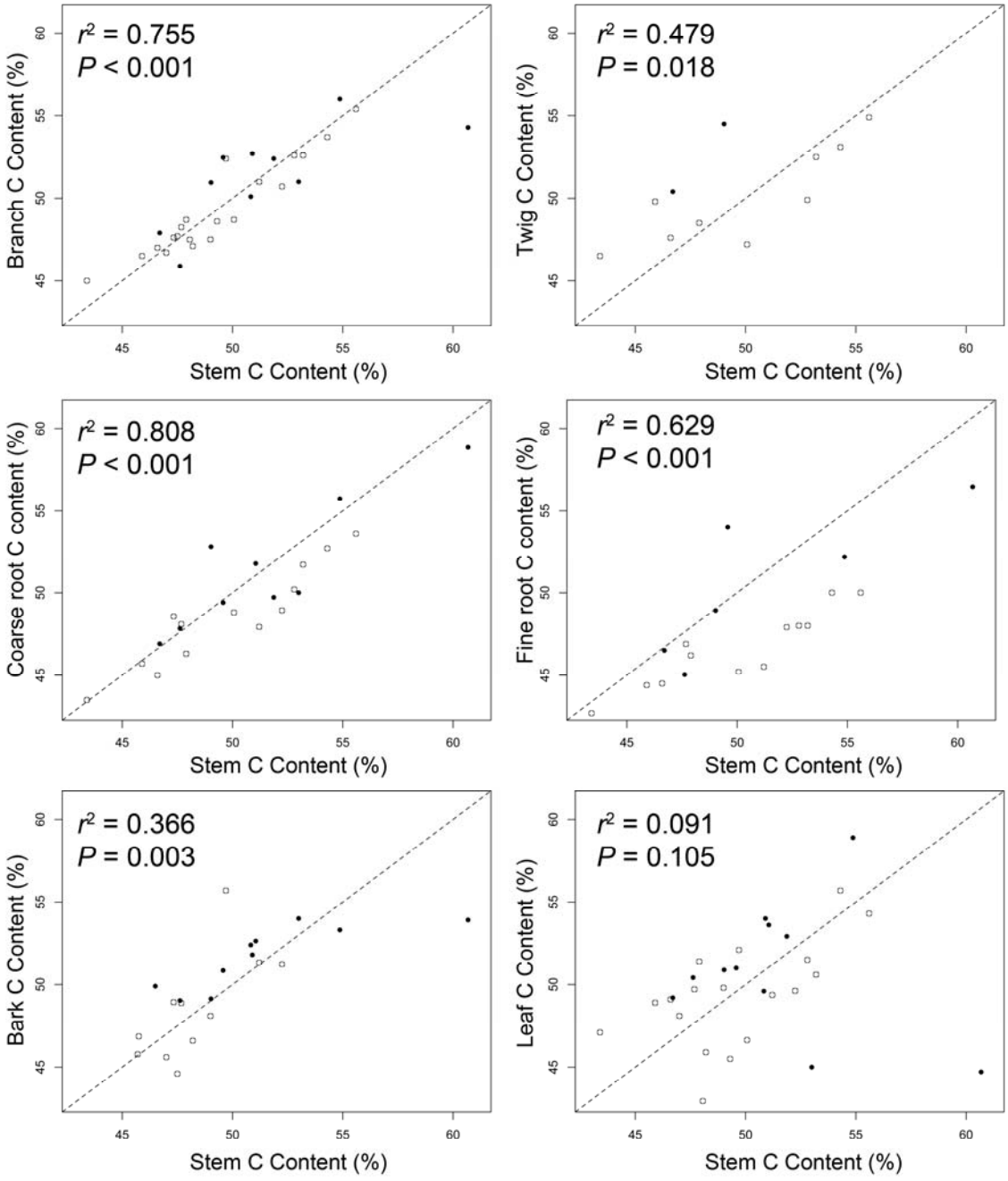
Figure 3. Comparisons of the volatile C fraction [*sensu* 1,3] across two biomes (tropical, temperate/boreal) and two tree types (angiosperms, conifers). Height of each bar represents the mean C_{vol} estimated as least squares means for each grouping, and error bars represent 95% confidence intervals (Table 2). Sample sizes (*N* species) for each grouping are represented above each bar.



3.3. Tissue Comparisons

In analyses of tissue-specific C content values, all tissues with the exception of leaves showed statistically significant linear relationships with stem wood C content (Figure 4); in no case was a significant non-linear trend detected. Considering pooled data sets (angiosperms and conifers), all of the standardized major regressions did not differ significantly from a 1:1 relationship (showing a *y* intercept not significantly different from 0 and a slope not significantly different from 1). A number of relationships are remarkably tight: 80% of the variation in coarse root C content, and 75% of the variation in branch C content is explained by stem C content. In spite of this, there is some evidence for systematic differences in these relationships between angiosperms and conifers. There was significant heterogeneity of slopes detected for branch and leaf C ($p = 0.05$ and $p = 0.03$, respectively); and a difference in intercept for twig C ($p = 0.028$), coarse root C ($p = 0.03$), and fine root C ($p = 0.003$). The cases of heterogeneity of slopes are driven entirely by a single outlying species (*Pinus massoniana*), for which very high stem C is reported [63]. In all cases showing differences in intercept value, the pattern is consistently of higher C content values for a given tissue in conifers than in angiosperms, given the observed stem C value.

Figure 4. Carbon content of major tree biomass components as a function of the carbon content of carbon content of main stem wood, based on data compiled from the literature review. Standard major axis regressions do not differ significantly from a 1:1 relationship (shown as dotted lines) in any case; open circles indicate angiosperms and closed circles conifers. The species *Pinus massoniana* (with a stem C content of 60.7%—data from [63]) is an outlier for several relationships. Excluding this species increases the r^2 value for branch, bark, and leaf comparisons (analyses excluding *Pinus massoniana*—branch C: $r^2 = 0.816$; $p < 0.001$; coarse root C: $r^2 = 0.722$; $p < 0.001$; fine root C: $r^2 = 0.460$; $p = 0.003$; bark C: $r^2 = 0.383$; $p = 0.003$; leaf C: $r^2 = 0.307$; $p = 0.002$).



4. Discussion

Our review of existing literature yielded a total of 253 species-specific stem wood C fractions, owing to 31 peer-reviewed publications; 16 of these presented tissue-specific C fractions among 34 tree species (Table 1). For stem wood values, tropical angiosperms were the best represented group with 134 species-specific records found, while only one record was found for a tropical conifer species (Table 2). In contrast, tissue-specific analyses are available mainly for temperate/boreal species (Table 1), with only one study presenting values for tropical species. Our analysis found wood C content ranges by ≥10% across species of the same provenance [44]. We also found significant variation in wood C content across biomes, and between conifers and angiosperms (Table 3). Subtropical/Mediterranean trees displayed the highest wood C content on average, tropical forest trees the lowest and temperate/boreal species intermediate values (Table 2, Figure 1).

Our analysis is consistent with previous literature [1,3] in finding that conifers have higher wood C content than angiosperms, a trend that was consistent when all biomes were considered individually (Table 2, Figure 1). Four of the wood C fraction values suggested by the IPCC [30] were within 1% of values obtained from our literature review (Figure 2). However, updating IPCC wood C fractions with data from current literature could reduce the error associated with AGB-C conversion by ~2.5–3.7%, with the most notable increases in conversion accuracy likely to be found in tropical and subtropical/Mediterranean forest C accounting (Table 2, Figure 2). We found only a small number of studies (N = 3 studies) reporting volatile carbon (C_{vol}) data (N = 70 species). C_{vol} averaged 2.5 ± 0.3% in tropical angiosperms, 1.3 ± 0.6% in temperate/boreal angiosperms, and 2.1 ± 1.4% in temperate/boreal conifers (Table 2, Figure 3), a non-trivial contribution from a C accounting perspective.

4.1. Tissue-Specific Wood C Values

Analyses of tissue-specific wood C values indicate that stem wood C provides a surprisingly good direct approximation for C content in other tissues (Figure 4), particularly those tissues that represent the most important biomass fractions in large trees after stem wood (namely branches and coarse roots). This result suggests that in spite of tissue-specific functional demands, there are important constraints on genetic determination of the key chemical traits of woody tissues (such as lignin-cellulose ratio and non-structural carbohydrate content) that determine C content. Although the pooled relationships between stem wood C and other tissues did not differ from a 1:1 linear function, we did find significant differences between conifers and angiosperms in several cases. In each instance, conifers show higher than expected tissue-specific C content than do angiosperms, at a given value of stem wood C content (Figure 4). Likely explanations for this pattern are a higher relative degree of lignification of tissues in conifers [64], differences in conifer *vs*. angiosperm lignin chemistry [65], and/or higher relative concentrations of non-structural carbohydrates in stem wood of angiosperms [66].

One important consideration not addressed quantitatively in this review is differences in wood C content within stems, among different wood types: in particular differences between sapwood and heartwood, between juvenile wood and mature wood, and changes due to reaction wood formation. Heartwood is expected to show high C content due to chemical transformations occurring during

formation, including deposition of phenolic compounds and reductions in starch and other non-structural carbon compounds [38]. Observations that heartwood can have an appreciably higher C content than sapwood date back to the late 19th century [67]; however, we were able to locate only six peer-reviewed studies on seven tree species that present relevant data, and differences/trends in wood C between the tissue types are not consistent. For example, in *Pinus pinaster*, Bert and Danjon [38] found heartwood to contain ~1–4% higher C content than sapwood; a trend that depended strongly on height of sampling. Similar differences in the 1–7% range have found in both conifers and angiosperms, including *Pinus sylvestris* (52.3% *vs.* 45.3% C for heartwood and sapwood, respectively [50]), *Pinus pinaster* (49.5% *vs.* 45.8% [50]), and *Nothofagus antarctica* (53.0% *vs.* 51.5% [58]). However, other studies have reported only small differences (<1%): *Sequoiadendron giganteum* (55.2% *vs.* 54.7% [1]), *Quercus petraea* (46.0 *vs.* 45.5% [46]), and *Quercus pyrenaica* (45.8 *vs.* 45.6% [46]). Thus, while heartwood may have appreciably higher C content then sapwood, this appears to be strongly taxon-specific, with by far the largest differences reported for pines, and the lowest differences generally reported for angiosperms [see also 37]. Moreover, data from Lamlom and Savidge [1] suggests the trend of increased wood C in heartwood *vs*. sapwood is a generalization of a much more complex pattern: in *Sequoiadendron giganteum*, the zone of transition wood (mean wood C 52.5%) between heartwood (mean wood C 55.2%) and sapwood (mean wood C 54.7%) was not intermediate in terms of wood C content. Instead, in *Sequoiadendron giganteum* changes in wood C from pith to bark were non-monotonic [1]. Since studies quantifying chemical changes from pith to bark tend to overlook this transition zone [68], we suggest a careful evaluation of the expected pattern that wood C decreases linearly from pith (*i.e.*, heartwood) to bark (*i.e.*, sapwood) is needed. Extractives deposited in heartwood may commonly include volatile C constituents, and thus analyses that include the volatile C fraction are particularly important for this question. Along these lines, Lamlom and Savidge [1] report sapwood C values slightly higher than heartwood values for conventionally dried samples of *Thuja occidentalis*, but the reverse pattern for desiccated wood samples prepared to retain volatile C.

Another important confounding factor we do not address is differences between juvenile wood and mature wood. Predictable changes in wood properties are often assumed to occur between juvenile and mature wood, with much of the evidence for these patterns coming from commercially viable North American conifer species [reviewed by 68]. With respect to wood C, juvenile wood generally has a higher lignin: cellulose ratio, and is thus expected to have a higher C content [34,38,68]. However, here we also caution against generalizations, as expected chemical differences between juvenile and mature wood have tended to be determined based on categorical comparisons that overlook the relatively large transition zone between pith and bark [68]. Lastly, an additional source of within-stem variation in wood chemistry that has received little attention is the effect of reaction wood (compression wood in conifers and tension wood in angiosperms). Development of reaction wood is expected to have large effects on wood chemistry [69], but we are unaware of data on C content in relation to reaction wood formation.

4.2. Incorporating Wood C Data into Forest C Accounting

Our review has some important implications to high-level forest C accounting protocols as supported by the IPCC ("Tier 2" or "Tier 3" carbon accounting [30]). In documenting that wood C

ranges by ≥10% across species of the same provenance, and finding that wood C varies across biomes and species types, our data support IPCC protocols suggesting that region- or species-specific wood C fractions should be used when converting AGB to C (Figure 1; [44]). Recent studies have shown it is technically tractable to incorporate species-specific C fractions into forest C accounting when detailed inventories are available [2,70]. However, it would clearly be challenging to incorporate species-specific C fractions into large-scale forest C accounting, especially in diverse tropical forests (such as western Amazonian or Bornean rainforests) that may contain ~250 tree species ha^{-1} in the ≥10 cm dbh size class alone [71,72]. Incorporation of species-specific wood C data may be also particularly challenging, given that recent progress in estimating forest AGB relies heavily on remotely sensed data [73,74]. Such technologies may be able to discriminate species in temperate forests [75], but are likely to perform only limited species- or tree functional type discrimination in diverse tropical forests [76].

Despite these limitations, biome/type-specific wood C fractions found in this review represent the most current data that can be incorporated into forest C accounting. Currently, the largest discrepancies between IPCC values and existing data are primarily attributable to the IPCC conflating tropical and subtropical/Mediterranean species (Figure 2). In doing so, IPCC protocols may result in an overestimate of ~3.7% in wood C of tropical forests that have little or no conifer component. This finding is consistent with a previous study where we found IPCC wood C fractions overestimated Panamanian forest C stocks by 3.3% [2]. Based on our review here, we also suggest the IPCC wood C fractions may currently underestimate C stocks in subtropical/Mediterranean forests by 3.7% (Figure 2). However, examining the magnitude of this error with forest inventory data (similar to [2]) would be needed to confirm this. Our review indicates that the general "default value" of 47% C suggested by the IPCC is low, since existing data suggest a value of 48.2 ± 0.3% (95% C.I.). However, given the large consistent differences between conifers and angiosperms, and availability of wood C data for both groups in all three provenances defined here (Table 2), there appears no reason to continue use of generalized global wood C values.

4.3. Methodological Considerations for Wood C Determinations

Consistent with previous studies [1–3], our analysis indicates that C_{vol} is a non-negligible component of total wood C content. Overlooking C_{vol} in analysis of woody tissues underestimates total wood C content by 1.3–2.5% (Figure 3): in tropical forests, this error leads to underestimates of forest C on the order of 6.6 Mg C ha^{-1} [2]. By convention, tree biomass is expressed in terms of dry mass, the standard protocol involving drying tissues to constant mass at 65 °C [77–80]. Biomass stocks are then converted to C stocks by multiplying the oven-dried biomass (*i.e.*, biomass without the volatile constituents) by species- or forest-type-specific carbon fractions. Accurate C fractions determined from wood samples should represent both the volatile- and non-volatile C mass as a percentage of oven-dried biomass. Therefore, to correct for the effects of differences in drying treatments (and to account for the contribution of C_{vol}) it is important to account for the mass loss associated with loss of volatile constituents during the drying process.

C determinations based on elemental analysis are calculated as:

$$C_{tot} = (M_C/M_S) \times 100 \quad (1)$$

where C_{tot} is the percentage mass of C in a wood sample (mass/mass basis); M_C is the mass of C in the sample (dried at a given temperature; most commonly 60–70 °C but see [44]), and M_S is the total sample mass (dried at the same temperature as M_C).

Therefore to make these values applicable to AGB estimates based oven-dried samples, we have proposed a "carbon conversion factor" (C_{conv}) that corrects for mass and C loss during sample drying [2]. Specifically, we suggest for the purposes of estimating forest C stocks and fluxes, wood C content should be calculated as:

$$C_{conv}=[M_C/(M_F-(VMF\times M_F))]\times 100 \quad (2)$$

where M_C is the mass of C in a sample following freeze-drying; M_F represents the mass of the freeze-dried sample, and VMF represents the volatile mass fraction, calculated as:

$$VMF=(M_F-M_H)/M_F \quad (3)$$

where M_F is as in Equation (2); and M_H represents mass of the same sample used for M_F determination, after oven-drying to constant mass (at 65 °C).

This proposed C_{conv} calculation has been used in only two studies to date [2,34], both of which only analyze stem wood. We reiterate our suggestion that if volatile C is to be included in forest carbon assessments, this should be done on the basis of the C_{conv} parameter described above to correctly express total live C in tree tissues as a proportion of conventionally determined measures of biomass. In the absence of additional comparative studies, data from our tropical comparative study [2] may be used to derive a function to approximate C_{conv} on the basis of C content determined from conventionally dried samples (C_{heat}):

$$C_{conv}=1.053\times C_{heat} \quad (4)$$

(Least squares regression constrained to have *y* intercept = 0; $N = 59$; adjusted $r^2 = 0.74$; $p < 0.001$).

4.4. Future Research and Data Needs

Although our review found more than 200 species-specific wood C records (Table 1, Figure 1), there is still clearly a need to accumulate more species-specific wood chemical information. There currently exists 8, 412 species-specific records of wood density, which are readily (and freely) available in large databases [81]. This database resource has proven critical for refining estimates of forest- and tree AGB, by providing wood density data that is readily incorporated into tree allometric models [78,82]. While we provide a starting point for creating a similar database that contains species-specific wood C data (see [44]), clearly more sampling effort is needed. For example, in the wood density database [81], the number of Mexican species alone ($N = 221$) closely rivals the entire wood C dataset here ($N = 253$; Table 2).

In addition, our biome classifications may mask important variation among forest regions and taxonomic groups that are especially poorly represented (if not completely unrepresented) in terms of species-specific wood C data. Common rainforest trees of southeast Asia, such as those in canopy-dominant Dipterocarpaceae family (that constitute ~40% of total forest basal area [72]), are represented by only five species in our dataset (Table 1). Southeast Asian tropical forests are likely the most carbon-dense pantropically [7,15], and most dynamic in terms of forest C stocks and fluxes [32].

Similarly, although Becker *et al.* [35] provide data for Kenyan and Ugandan trees (Table 1), our review found no species-specific wood C data for trees from the Congo basin, a forested region that is likely the most C-rich in continental Africa [7,15]. Geographical discrepancies in wood C data availability are even more pronounced for the subtropical/Mediterranean region: of the five references presenting data for 28 subtropical/Mediterranean species, only one study representing five species was outside of Mediterranean Europe [63]. In addition, our review did not find published species-specific C content values for many important taxonomic and functional groups of woody plants including lianas, hemi-epiphytes, palms, tree ferns, and non-conifer gymnosperms (such as cycads and *Gnetum*), some of which may be increasing with respect to their contribution to total forest biomass [83].

4.5. Conclusions

The overarching goal in this review was to evaluate existing literature in order to amass and analyze wood C content data across a global dataset. We also identify methodological considerations that should be taken into account when measuring wood C content. We suggest that information on wood C content from a wider range of species is needed to inform forest C accounting in a number of forest types. Our synthesis and data compilation provides a starting point for a database on tree C content. However, there is a pressing need for additional species-specific wood C data. Amassing such data represents an opportunity to refine our understanding of the role forests may play in C capture and storage at spatial scales ranging from individual trees to the biosphere.

Acknowledgments

The authors thank the Natural Sciences and Engineering Research Council of Canada, and the Jeanne F. Goulding Fellowship program at the University of Toronto for providing financial support for this research.

Conflict of Interest

The authors declare no conflict of interest.

References

1. Lamlom, S.H.; Savidge, R.A. A reassessment of carbon content in wood: Variation within and between 41 North American species. *Biomass Bioenergy* **2003**, *25*, 381–388.
2. Martin, A.R.; Thomas, S.C. A reassessment of carbon content in tropical trees. *PLoS One* **2011**, *6*, e23533:1–e23533:9.
3. Thomas, S.C.; Malczewski, G. Wood carbon content of tree species in eastern China: Interspecific variability and the importance of the volatile fraction. *J. Environ. Manag.* **2007**, *85*, 659–662.
4. Elias, M.; Potvin, C. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. *Can. J. For. Res.* **2003**, *33*, 1039–1045.
5. Qureshi, A.; Pariva, R.B.; Hussain, S.A. A review of protocols used for assessment of carbon stock in forested landscapes. *Environ. Sci. Policy* **2012**, *16*, 81–89.

6. Brown, S. Measuring carbon in forests: Current status and future challenges. *Environ. Pollut.* **2002**, *116*, 363–372.
7. Gibbs, H.K.; Brown, S.; Niles, J.O.; Foley, J.A. Monitoring and estimating tropical forest carbon stocks: Making REDD a reality. *Environ. Res. Lett.* **2007**, *2*, 1–13.
8. Feldpausch, T.R.; Rondon, M.A.; Fernandes, E.C.M.; Riha, S.J.; Wandelli, E. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. *Ecol. Appl.* **2004**, *14*, 164–176.
9. Hughes, R.F.; Kauffman, J.B.; Jaramillo, V.J. Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. *Ecol. Appl.* **2000**, *10*, 515–527.
10. Ruiz-Jaen, M.C.; Potvin, C. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytol.* **2011**, *189*, 978–987.
11. Bradford, J.B.; Fraver, S.; Milo, A.M.; D'Amato, A.W.; Palik, B.; Shinneman, D.J. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. *For. Ecol. Manag.* **2012**, *267*, 209–214.
12. Chave, J.; Condit, R.; Muller-Landau, H.C.; Thomas, S.C.; Ashton, P.S.; Bunyavejchewin, S.; Co, L.L.; Dattaraja, H.S.; Davies, S.J.; Esufali, S.; *et al.* Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol.* **2008**, *6*, 455–462.
13. Lewis, S.L.; Lopez-Gonzalez, G.; Sonke, B.; Affum-Baffoe, K.; Baker, T.R.; Ojo, L.O.; Phillips, O.L.; Reitsma, J.M.; White, L.; Comiskey, J.A.; *et al.* Increasing carbon storage in intact African tropical forests. *Nature* **2009**, *457*, 1003–1006.
14. Pyle, E.H.; Santoni, G.W.; Nascimento, H.E.M.; Hutyra, L.R.; Vieira, S.; Curran, D.J.; van Haren, J.; Saleska, S.R.; Chow, V.Y.; Carmago, P.B.; *et al.* Dynamics of carbon, biomass, and structure in two Amazonian forests. *J. Geophys. Res.* **2008**, *113*, G00B08:1–G00B08:20.
15. Saatchi, S.S.; Harris, N.L.; Brown, S.; Lefsky, M.; Mitchard, E.T.A.; Salas, W.; Zutta, B.R.; Buermann, W.; Lewis, S.L.; Hagen, S.; *et al.* Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 9899–9904.
16. Fang, J.Y.; Chen, A.P.; Peng, C.H.; Zhao, S.Q.; Ci, L. Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* **2001**, *292*, 2320–2322.
17. Kurz, W.A.; Dymond, C.C.; White, T.M.; Stinson, G.; Shaw, C.H.; Rampley, G.J.; Smyth, C.; Simpson, B.N.; Neilson, E.T.; Trofymow, J.A.; *et al.* CBM-CFS3: A model of carbon-dynamics in forestry and land-use change implementing IPCC standards. *Ecol. Model.* **2009**, *220*, 480–504.
18. Kauppi, P.E.; Tomppo, E.; Ferm, A. C and N storage in living trees within Finland since 1950s. *Plant Soil* **1995**, *168*, 633–638.
19. Fang, J.Y.; Oikawa, T.; Kato, T.; Mo, W.H.; Wang, Z.H. Biomass carbon accumulation by Japan's forests from 1947 to 1995. *Glob. Biogeochem. Cycles* **2005**, *19*, GB2004:1–GB2004:10.
20. Blanc, L.; Echard, M.; Herault, B.; Bonal, D.; Marcon, E.; Chave, J.; Baraloto, C. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecol. Appl.* **2009**, *19*, 1397–1404.
21. Soto-Pinto, L.; Anzueto, M.; Mendoza, J.; Ferrer, G.J.; de Jong, B. Carbon sequestration through agroforestry in indigenous communities of Chiapas, Mexico. *Agrofor. Syst.* **2010**, *78*, 39–51.

22. Beets, P.N.; Brandon, A.M.; Goulding, C.J.; Kimberley, M.O.; Paul, T.S.H.; Searles, N. The inventory of carbon stock in New Zealand's post-1989 planted forest for reporting under the Kyoto protocol. *For. Ecol. Manag.* **2011**, *262*, 1119–1130.
23. Redondo-Brenes, A.; Montagnini, F. Growth, productivity, aboveground biomass, and carbon sequestration of pure and mixed native tree plantations in the Caribbean lowlands of Costa Rica. *For. Ecol. Manag.* **2006**, *232*, 168–178.
24. Redondo-Brenes, A. Growth, carbon sequestration, and management of native tree plantations in humid regions of Costa Rica. *New For.* **2007**, *34*, 253–268.
25. Fahey, T.J.; Siccama, T.G.; Driscoll, C.T.; Likens, G.E.; Campbell, J.; Johnson, C.E.; Battles, J.J.; Aber, J.D.; Cole, J.J.; Fisk, M.C.; *et al.* The biogeochemistry of carbon at Hubbard Brook. *Biogeochemistry* **2005**, *75*, 109–176.
26. Saner, P.; Loh, Y.Y.; Ong, R.C.; Hector, A. Carbon stocks and fluxes in tropical lowland Dipterocarp rainforests in Sabah, Malaysian Borneo. *PLoS ONE* **2012**, *7*, e29642:1–e29642:11.
27. Melson, S.L.; Harmon, M.E.; Fried, J.S.; Domingo, J.B. Estimates of live-tree carbon stores in the Pacific Northwest are sensitive to model selection. *Carbon Balance Manag.* **2011**, *6*, 1–16.
28. Zhang, Q.Z.; Wang, C.K.; Wang, X.C.; Quan, X.K. Carbon concentration variability of 10 Chinese temperate tree species. *For. Ecol. Manag.* **2009**, *258*, 722–727.
29. Jones, D.A.; O'Hara, K.L. Carbon density in managed coast redwood stands: implications for forest carbon estimation. *Forestry* **2012**, *85*, 99–110.
30. IPCC. Forest lands. *Intergovernmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories*; Institute for Global Environmental Strategies (IGES): Hayama, Japan, 2006; Volume 4, p. 83.
31. Mascaro, J.; Asner, G.P.; Muller-Landau, H.C.; van Breugel, M.; Hall, J.; Dahlin, K. Controls over aboveground forest carbon density on Barro Colorado Island, Panama. *Biogeosciences* **2011**, *8*, 1615–1629.
32. Pan, Y.D.; Birdsey, R.A.; Fang, J.Y.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; *et al.* A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988–993.
33. Clark, D.A.; Brown, S.; Kicklighter, D.W.; Chambers, J.Q.; Thomlinson, J.R.; Ni, J. Measuring net primary production in forests: Concepts and field methods. *Ecol. Appl.* **2001**, *11*, 356–370.
34. Martin, A.R.; Thomas, S.C.; Zhao, Y. Size-dependent changes in wood chemical traits: A comparison of neotropical saplings and large trees. *Oikos* **2012**, in review.
35. Becker, G.S.; Braun, D.; Gliniars, R.; Dalitz, H. Relations between wood variables and how they relate to tree size variables of tropical African tree species. *Trees Struct. Funct.* **2012**, in press. doi: 10.1007/s00468-00012-00687-00466.
36. Kraenzel, M.; Castillo, A.; Moore, T.; Potvin, C. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. *For. Ecol. Manag.* **2003**, *173*, 213–225.
37. Lamlom, S.H.; Savidge, R.A. Carbon content variation in boles of mature sugar maple and giant sequoia. *Tree Physiol.* **2006**, *26*, 459–468.
38. Bert, D.; Danjon, F. Carbon concentration variations in the roots, stem and crown of mature *Pinus pinaster* (Ait.). *For. Ecol. Manag.* **2006**, *222*, 279–295.

39. Telmo, C.; Lousada, J.; Moreira, N. Proximate analysis, backwards stepwise regression between gross calorific value, ultimate and chemical analysis of wood. *Bioresour. Technol.* **2010**, *101*, 3808–3815.
40. Laiho, R.; Laine, J. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. *For. Ecol. Manag.* **1997**, *93*, 161–169.
41. Fox, J.; Weisberg, S. *An R Companion to Applied Regression*, 2nd ed.; SAGE: Thousand Oaks, CA, USA, 2011.
42. Searle, S.R.; Speed, F.M.; Milliken, G.A. Population marginal means in the linear-model—An alternative to least-squares means. *Am. Stat.* **1980**, *34*, 216–221.
43. *Nlme: Linear and Nonlinear Mixed Effects Models*, version 3.3.1; Software for mixed-effects models; José Pinheiro and Douglas Bates: Murray Hill, NJ, USA, 2012.
44. Thomas, S.C.; Martin, A.R. Dryad wood carbon content database. *Dryad* **2012**, doi: 10.5061/dryad.69sg2. Available online: http://dx.doi.org/10.5061/dryad.69sg2 (accessed on 18 June 2012).
45. Arias, D.; Calvo-Alvarado, J.; Richter, D.D.; Dohrenbusch, A. Productivity, aboveground biomass, nutrient uptake and carbon content in fast-growing tree plantations of native and introduced species in the southern region of Costa Rica. *Biomass Bioenergy* **2011**, *35*, 1779–1788.
46. Castaño-Santamaría, J.; Bravo, F. Variation in carbon concentration and basic density along stems of sessile oak (*Quercus petraea* (Matt.) Liebl.) and Pyrenean oak (*Quercus pyrenaica* Willd.) in the Cantabrian Range (NW Spain). *Ann. For. Sci.* **2012**, in press. doi:10.1007/s13595-012-0183-6.
47. Correia, A.C.; Tome, M.; Pacheco, C.A.; Faias, S.; Dias, A.C.; Freire, J.; Carvalho, P.O.; Pereira, J.S. Biomass allometry and carbon factors for a Mediterranean pine (*Pinus pinea* L.) in Portugal. *For. Syst.* **2010**, *19*, 418–433.
48. Fang, S.; Xue, J.; Tang, L. Biomass production and carbon sequestration potential in poplar plantations with different management patterns. *J. Environ. Manag.* **2007**, *85*, 672–679.
49. Fukatsu, E.; Fukuda, Y.; Takahashi, M.; Nakada, R. Clonal variation of carbon content in wood of *Larix kaempferi* (Japanese larch). *J. Wood Sci.* **2008**, *54*, 247–251.
50. De Aza, C.H.; Turrion, M.B.; Pando, V.; Bravo, F. Carbon in heartwood, sapwood and bark along the stem profile in three Mediterranean *Pinus* species. *Ann. For. Sci.* **2011**, *68*, 1067–1076.
51. Huet, S.; Forgeard, F.; Nys, C. Above- and belowground distribution of dry matter and carbon biomass of Atlantic beech (*Fagus sylvatica* L.) in a time sequence. *Ann. For. Sci.* **2004**, *61*, 683–694.
52. Jacobs, D.F.; Selig, M.F.; Severeid, L.R. Aboveground carbon biomass of plantation-grown American chestnut (*Castanea dentata*) in absence of blight. *For. Ecol. Manag.* **2009**, *258*, 288–294.
53. Janssens, I.A.; Sampson, D.A.; Cermak, J.; Meiresonne, L.; Riguzzi, F.; Overloop, S.; Ceulemans, R. Above- and belowground phytomass and carbon storage in a Belgian Scots pine stand. *Ann. For. Sci.* **1999**, *56*, 81–90.
54. Joosten, R.; Schulte, A. Possible effects of altered growth behaviour of Norway spruce (*Picea abies*) on carbon accounting. *Clim. Change* **2002**, *55*, 115–129.
55. Joosten, R.; Schumacher, J.; Wirth, C.; Schulte, A. Evaluating tree carbon predictions for beech (*Fagus sylvatica* L.) in western Germany. *For. Ecol. Manag.* **2004**, *189*, 87–96.
56. Kort, J.; Turnock, R. Carbon reservoir and biomass in Canadian prairie shelterbelts. *Agrofor. Syst.* **1998**, *44*, 175–186.

57. Li, X.; Yi, M.J.; Son, Y.; Park, P.S.; Lee, K.H.; Son, Y.M.; Kim, R.H.; Jeong, M.J. Biomass and carbon storage in an age sequence of Korean Pine (*Pinus koraiensis*) plantation forests in central Korea. *J. Plant Biol.* **2011**, *54*, 33–42.
58. Peri, P.L.; Gargaglione, V.; Pastur, G.M.; Lencinas, M.V. Carbon accumulation along a stand development sequence of *Nothofagus antarctica* forests across a gradient in site quality in Southern Patagonia. *For. Ecol. Manag.* **2010**, *260*, 229–237.
59. Rana, R.; Langenfeld-Heyser, R.; Finkeldey, R.; Polle, A. FTIR spectroscopy, chemical and histochemical characterisation of wood and lignin of five tropical timber wood species of the family of Dipterocarpaceae. *Wood Sci. Technol.* **2010**, *44*, 225–242.
60. Tolunay, D. Carbon concentrations of tree components, forest floor and understorey in young *Pinus sylvestris* stands in north-western Turkey. *Scand. J. For. Res.* **2009**, *24*, 394–402.
61. Van Geffen, K.G.; Poorter, L.; Sass-Klaasssen, U.; van Logtestijn, R.S.P.; Cornelissen, H.C. The trait contribution to wood decomposition rates of 15 neotropical tree species. *Ecology* **2010**, *91*, 3686–3697.
62. Zabek, L.M.; Prescott, C.E. Biomass equations and carbon content of aboveground leafless biomass of hybrid poplar in coastal British Columbia. *For. Ecol. Manag.* **2006**, *223*, 291–302.
63. Zheng, H.; Ouyang, Z.Y.; Xu, W.H.; Wang, X.K.; Miao, H.; Li, X.Q.; Tian, Y.X. Variation of carbon storage by different reforestation types in the hilly red soil region of southern China. *For. Ecol. Manag.* **2008**, *255*, 1113–1121.
64. Minami, E.; Saka, S. Comparison of the decomposition behaviors of hardwood and softwood in supercritical methanol. *J. Wood Sci.* **2003**, *49*, 73–78.
65. Campbell, M.M.; Sederoff, R.R. Variation in lignin content and composition—Mechanism of control and implications for the genetic improvement of plants. *Plant Physiol.* **1996**, *110*, 3–13.
66. Hoch, G.; Richter, A.; Korner, C. Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ.* **2003**, *26*, 1067–1081.
67. Daube, W. Chemische analysen des kernund splintholzes wichtiger waldbäume. *Forstli. Blätter* **1883**, *20*, 177–192.
68. Lachenbruch, B.; Moore, J.R.; Evans, R. Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence. In *Size- and Age-Related Changes in Tree Structure and Function*; Meinzer, F.C., Dawson, T., Lachenbruch, B.J., Eds.; Springer-Verlag: Berlin, Germany, 2011; pp. 121–164.
69. Du, S.; Yamamoto, F. An overview of the biology of reaction wood formation. *J. Integr. Plant Biol.* **2007**, *49*, 131–143.
70. Potvin, C.; Mancilla, L.; Buchmann, N.; Monteza, J.; Moore, T.; Murphy, M.; Oelmann, Y.; Scherer-Lorenzen, M.; Turner, B.L.; Wilcke, W.; *et al.* An ecosystem approach to biodiversity effects: Carbon pools in a tropical tree plantation. *For. Ecol. Manag.* **2011**, *261*, 1614–1624.
71. Valencia, R.; Condit, R.; Foster, R.B.; Romoleroux, K.; Villa-Munoz, G.; Svenning, J.C.; Magard, E.; Bass, M.; Losos, E.C.; Balslev, H. Yasuni forest dynamics plot, Ecuador. In *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*; Losos, E.C., Leigh, E.G., Eds.; University of Chicago Press: Chicago, IL, USA, 2004; pp. 609–620.

72. Lee, H.S.; Tan, S.; Davies, S.J.; La-Frankie, J.V.; Ashton, P.S.; Yakamura, T.; Itoh, A.; Ohkubo, T.; Harrison, R. Lambir forest dynamics plot, Sarawak, Malaysia. In *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*; Losos, E.C., Leigh, E.G., Eds.; University of Chicago Press: Chicago, IL, USA, 2004; pp. 527–539.
73. Asner, G.P. Tropical forest carbon assessment: Integrating satellite and airborne mapping approaches. *Environ. Res. Lett.* **2009**, *4*, 034009:1–034009:11.
74. Patenaude, G.; Hill, R.A.; Milne, R.; Gaveau, D.L.A.; Briggs, B.B.J.; Dawson, T.P. Quantifying forest above ground carbon content using LiDAR remote sensing. *Remote Sens. Environ.* **2004**, *93*, 368–380.
75. Brandtberg, T. Classifying individual tree species under leaf-off and leaf-on conditions using airborne lidar. *ISPRS J. Photogramm. Remote Sens.* **2007**, *61*, 325–340.
76. Asner, G.P.; Martin, R.E. Airborne spectranomics: Mapping canopy chemical and taxonomic diversity in tropical forests. *Front. Ecol. Environ.* **2009**, *7*, 269–276.
77. Bond-Lamberty, B.; Wang, C.; Gower, S.T. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Can. J. Forest Res.* **2002**, *32*, 1441–1450.
78. Chave, J.; Andalo, C.; Brown, S.; Cairns, M.A.; Chambers, J.Q.; Eamus, D.; Folster, H.; Fromard, F.; Higuchi, N.; Kira, T.; *et al.* Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **2005**, *145*, 87–99.
79. Wang, C.K. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. *For. Ecol. Manag.* **2006**, *222*, 9–16.
80. Jenkins, J.C.; Chojnacky, D.C.; Heath, L.S.; Birdsey, R.A. National-scale biomass estimators for United States tree species. *For. Sci.* **2003**, *49*, 12–35.
81. Zanne, A.E.; Lopez-Gonzalez, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L.; Miller, R.B.; Swenson, N.G.; Wiemann, M.C.; Chave, J. Towards a worldwide wood economics spectrum. *Dryad Digital Repository* **2009**, doi:10.5061/dryad.234/1. Available online: http://hdl.handle.net/10255/dryad.235 (accessed on 11 June 2012).
82. Flores, O.; Coomes, D.A. Estimating the wood density of species for carbon stock assessments. *Methods Ecol. Evol.* **2011**, *2*, 214–220.
83. Schnitzer, S.A.; Bongers, F. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecol. Lett.* **2011**, *14*, 397–406.