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Tissue carbon concentration of 175 Mexican forest species

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Reliable calculations of carbon stocks in forest ecosystems are crucial for proper implementation of global warming mitigation policies. Accurate estimations depend upon applying the correct factor of carbon (C) concentration for different forest species and tissues instead of the often assumed 50% carbon content. Despite the high forest species richness in Mexico and the increasing CO_2 emissions, data on carbon concentrations in forest plant tissues are scarce. In this study, we determined variation in C concentration of different tissues for 175 plant species common in Mexican forests. C contents were estimated and contrasted for plant distribution, taxa, and plant structure (main stems, branches, twigs, bark, leaves, buds, fruits, roots and root cuticles). The mean C concentration across species was 44.7%. Species significantly differed in C concentration by tissue, environment and taxa. These multi-species data contribute to improve precision on estimates of C balance in terrestrial ecosystems, reducing the uncertainty in C inventories in Mexico and elsewhere.

Keywords: Carbon Sink, Plant Tissue C, Multi-species C, Global Warming

Introduction

Estimates of carbon stocks of terrestrial ecosystems are complex (Murray-Tortarolo et al. 2016), due to a large species and ecosystem diversity caused by the convergence of Nearctic and Tropical regions (Rzedowski 1991), climate heterogeneity (Sarukhán et al. 2009), and complex geological and climatic history (Espinosa-Organista et al. 2008).

Knowledge on carbon (C) concentration of different plant species and plant tissues is essential to accurately estimate C stocks in forest ecosystems (Thomas & Martin 2012) and thus understanding of C dynamics. Studies in different parts of the world and in Mexico often use a constant value for C concentration (usually 50%) to model C stocks in different ecosystems and taxa (Návar 2009, Vieilledent et al. 2011, Rojas-García et al. 2015). Other authors, however, argue that such generalization can under- or over-estimate real C stocks (Yerena-Yamallel et al. 2011, Jiménez-Pérez et al. 2013), causing uncertainty in the potential of forests as C sinks (Lamlom & Savidge 2003).

Variations in C concentration between species is influenced by phylogeny and the environment (biotic and abiotic) in which plant species grow (Thomas & Malczewski 2007). Different plant species may have a specific chemical composition and carbon compounds due to their metabolism, as physiology and morphology are linked to an optimal functioning under the ecological conditions where they have evolved (Sardans & Peñuelas 2014). Within a given individual, C concentration varies between tissues (Yeboah et al. 2014), depending to a larger extent on the chemistry of such tissues (Savidge 2003) than on plant age or size (Bert & Danjon 2006). This study presents C concentration values for 175 plant species in 18 families from temperate, tropical, subtropical, arid and semiarid zones in Mexico to establish whether and how biomass C concentration differed across environments, taxa and plant tissues. Such dataset will help determine if the use of the generalized assumption of 50% C content is applicable for Mexican forests and similar ecosystems and species in other parts of the world.

Material and methods

Experimental design and C concentration determinations

A selective sampling of 175 representative forest species (Pompa-García et al. 2017) was carried out across Mexican environments. Sites were selected trying to encompass the large environmental variation but restricted by logging and accessibility. Temperate, tropical/subtropical and arid/semiarid ecosystems were targeted as per González-Medrano (2003). In 68 localities in 17 states (Fig. S1 in Supplementary materials), at least three individuals from each of the 175 species, a sample of ca. 50 g (fresh mass) was taken from different plant parts following Henry et al. (2011): leaves (L), buds (Bd), fruits (F), branches (B), bark from branches (Bb), twig (< 5 cm in diameter – T), bark from twig (Bt), stem (S), bark from stem (Bs), roots (R) and root cuticles (Rc). Only undamaged trees with no deformities were included in the study.

Samples were taken to the lab following the procedures described in Karlik & Chojnacky (2014), and immediately (<24 hours) were placed and dried in the lab at room temperature to avoid loss of volatile substances (Avendaño et al. 2009, Martin & Thomas 2011). Following the procedure by Lamlom & Savidge (2003), we broke down the samples into small particles to better

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Tab. 1 - Carbon concentration for Mexican forest species studied by region and moisture regime. (n): number of species. Different letters indicate significantly different means (p<0.05) after Tukey's test.

Region	Moisture regime	n	C Concentration (%, mean ± sd)
Temperate Zone	Semidry	9	44.14 ± 0.54 [ab]
	Semihumid	52	45.81 ± 0.36 [a]
Tropical and Subtropical zones	Humid	72	44.35 ± 0.23 [ab]
	Semidry	6	42.79 ± 0.37 [b]
	Subhumid	4	44.16 ± 0.30 [ab]
Arid and semiarid zones	Semidry	22	43.95 ± 0.34 [ab]
	Dry	10	44.23 ± 0.50 [ab]

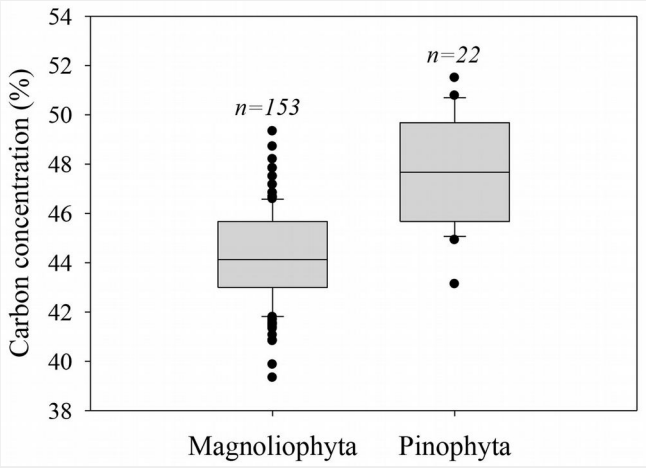

Fig. 1 - Differences in Carbon concentration between Magnoliophyta and Pinophyta. A higher C concentration for species of Pinophyta was observed.

Tab. 2 - Mean and standard error of carbon concentration for 18 families. Only families with enough replicates were used in this analysis. Different letters indicate different means (p<0.05) after Tukey's test.

Order	Family	Number of species	Carbon concentration (%, mean ± sd)
Pinophyta	Cupressaceae	5	45.68 ± 0.83 [bcd]
	Pinaceae	16	48.29 ± 0.50 [a]
Magnoliophyta	Asparagaceae	3	42.79 ± 1.01 [e]
	Anacardiaceae	7	45.01 ± 0.69 [bcde]
	Arecaceae	5	43.58 ± 0.74 [de]
	Bignoniaceae	4	44.40 ± 0.74 [cde]
	Boraginaceae	4	43.10 ± 0.56 [de]
	Burseraceae	4	43.54 ± 0.72 [de]
	Combretaceae	3	42.82 ± 0.52 [e]
	Ericaceae	4	47.15 ± 0.77
	Fabaceae	39	44.53 ± 0.28 [ab]
	Fagaceae	17	44.29 ± 0.41 [cde]
	Malvaceae	4	43.00 ± 0.81 [e]
	Meliaceae	3	43.41 ± 1.21 [de]
	Moraceae	8	43.41 ± 0.55 [de]
	Rubiaceae	5	44.81 ± 0.49 [bcde]
	Salicaceae	3	45.68 ± 0.83 [bcd]
	Sapotaceae	3	48.29 ± 0.50 [a]

Tab. 3 - Mean and standard error of carbon concentration of some of the genera sampled. Different letters indicate different means (p<0.05). (*): Genera with at least tree sampled species were included to comply with assumptions of analysis of variance.

Genus*	Number of species	Carbon concentration (%, mean ± sd)
Acacia	7	43.93 ± 0.42 [b]
Bursera	3	42.89 ± 0.44 [b]
Cordia	3	43.08 ± 0.79 [b]
Ficus	6	43.08 ± 0.53 [b]
Pinus	12	48.96 ± 0.51 [a]
Pithecellobium	3	43.92 ± 0.96 [b]
Quercus	17	44.29 ± 0.41 [b]

estimate C content using a pulverizing mill, (Fritsch Pulverisette 2®, Idar-Oberstein, Germany), which yields fractions smaller than 10 µg. Total carbon concentration (TCC) was obtained using a Solids TOC Analyzer (model 1020A®) with catalytic combustion method from O·I·Analytical (College Station, TX, USA) in the Soils and Fertility lab in Postgraduate College.

Statistical analyses

As classification resulted in different sample sizes, data were subjected to an unbalanced ANOVA, using the general linear model (GLM) procedure of SAS version 9.1 (SAS 2009). Differences between taxa (division, family and genus) and ecosystems were tested by one-way unbalanced ANOVAs, in which only groups with at least three samples were considered. Differences in concentration of C between tree tissues were evaluated, analyzing separately the two divisions: Magnoliophyta and Pinophyta. In all analyses the carbon concentration values were transformed with the arcsine function to satisfy the assumptions of normality and homogeneity of variances. A multiple comparison between means was carried out with the *post-hoc* Tukey's test at P = 0.05 level.

Results

The mean C concentration across species and plant parts was 44.7% (Tab. S1 in Supplementary material), varying from 44.1% to 45.8% for temperate zone species, 42.8% to 44.3% for species from tropics and subtropics and from 43.8% to 44.2% for species in arid and semiarid zones (Tab. 1). Tree species from different biomes significantly differed in C concentration ($F = 9.07$, $p = 0.0002$). Species from the temperate zone had the highest C concentration (45.8%) and those from tropical and subtropical zones the lowest (42.8%).

Different taxa also significantly differed in C concentration ($F = 58.41$, $p < 0.0001$). The highest C concentration was found for Pinophyta (47.5%), while Magnoliophyta had 3.3% less C concentration (44.2% – Fig. 1). Asparagaceae and Arecaceae had the lowest C concentration (43.1%).

Carbon concentration varied between families ($F = 6.72$, $p < 0.0001$), from 42.8% for Asparagaceae to 48.3% for Pinaceae (Tab. 2). Within family variation in C concentration was relatively low with a mean standard deviation of 1.45%. Carbon concentration also differed between genera ($F = 17.43$, $p < 0.0001$). Two main groups could be identified (Tab. 3): the first included the genus *Pinus*, with the highest concentration (48.96%), while *Acacia, Quercus, Bursera, Cordia, Pithecellobium* and *Ficus* were in the second group.

Carbon concentration between plant structure differed for Pinophyta ($F = 2.36$, $p = 0.0128$) and Magnoliophyta ($F = 10.36$, $p < 0.0001$). For conifers, fruits, buds and bark had carbon concentrations close to 50% (Fig. 2), which were significantly higher

than those of dead tissue of roots and branches (44.8% to 45.3%). For broad-leaved species, C concentration was higher in stem and leaves (Fig. 2).

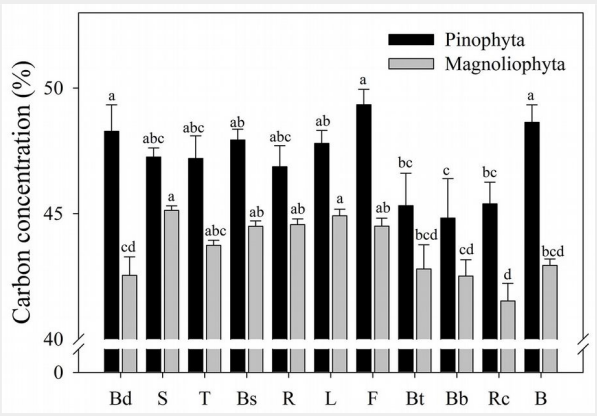

Fig. 2 - Carbon concentration for plant tissues grouped by taxonomic division. Different letters between bars of the same color indicate different means ($p<0.05$). Leaves (L), buds (Bd), fruits (F), branches (B), bark from branches (Bb), twig (<5 cm in diameter – T), bark from twig (Bt), stem (S), bark from stem (Bs), roots (R) and root cuticles (Rc).

Discussion

The common C-concentration constant used for the aerial parts of the trees is 50%. This is still broadly used in large scale models of C fluxes and sinks (Becker et al. 2012, Martin et al. 2013, 2015, Gao et al. 2016). In our study, all values for C concentration of 175 Mexican forest plants were below 50% with an average value of 44.7%. In agreement with other multi-species studies (Zhang et al. 2009, Martin & Thomas 2011, Castaño-Santamaría et al. 2013), we suggest to use specific estimations for different genera and ecosystems instead of the 50% assumption. We also recommend to test the overestimation stemming from the adoption of such assumption in other ecosystems and species.

C concentration was higher in temperate than in tropical tree species, which could be a result of C rich volatile substances (Thomas & Malczewski 2007, Gao et al. 2016), and lignin (Lamlom & Savidge 2003) in species of temperate environments. In contrast, tropical trees might have less C due to differences in cellulose and lignin contents (Elias & Potvin 2003, Martin & Thomas 2011).

C concentration was higher for Pinophyta than for Magnoliophyta, likely due to high contents of resins and other C rich organic compounds in the former (Savidge 2000). Variations in C concentration between biomes were small, suggesting that C concentration is relatively constant for species across environments, as already reported in other studies (Martin & Thomas 2011, Watzlawick et al. 2014). Moreover, a large within-family variations in C content was observed. This is in agreement with findings that C concentration is not a strongly phylogenetically-conserved trait (Martin & Thomas 2011). In our study the larger within-family variation was found in Pinaceae, coinciding with the findings of Yerena-Yamallel et al. (2012a). This is possibly due to differences in chemical composition of cellulose, lignin, hemicellulose, and starches (Martin et al. 2013). The high C content found in leaves compared with other tissues might be the result of higher rates of volatile compounds, as suggested by Yerena-Yamallel et al. (2012b). Other studies have also found variations of C concentration between plant tissues, with higher values in leaves (Zhang et al. 2009, Durkaya et al. 2013, 2015). Because leaves differ in their longevity, their role as C stocks must vary between evergreens and deciduous species (Martin & Thomas 2011, Martin et al. 2013). The high values of C (ca. 50%) found in bark and cones of Pinophyta in this study, could be the result of C-rich lignin and suberin in these structures (Franceschi et al. 2005).

Other studies have observed variations in C concentration in dead or decaying tissue. For instance Harmon et al. (2013) found that uncertainties associated to forest C inventories may be reduced using specific detritus C coefficient for each taxon, instead of using the generalized 50% assumption. In dead conifer trees, as decomposition takes place, a slight increase in C concentration occurs (Cousins et al. 2015, Köster et al. 2015). Other authors argue about the relative importance of intra- *vs.* inter-specific variation in wood C for forest C assessments. For instance, Martin et al. (2015) suggest that variations in C concentration between tissues of the same species are less important than variations between species for modelling C dynamics in forest ecosystems. Improvement and validation of models for given ecosystems could be a viable solution, using wood density as an independent variable as suggested by some authors (Urquiza-Haas et al. 2007, Chave et al. 2014).

Reliable C concentration estimations are crucial for determining the role of forests in the global C cycle (Bombelli et al. 2009). The results from this study contribute to more accurate estimations of carbon concentration of plant tissues across a large number of tree species in Mexico. Even though differences between the 50% common assumption and actual findings are small, these differences would mean gross C overestimations at the scale of stands, forests or biomes (Gao et al. 2016). These could lead to C content overestimations in studied Mexican forests in the order of 1.5 Mg ha^{-1} (Yerena-Yamallel et al. 2012b) or 3.9 Mg ha^{-1} (Aguirre-Calderón & Jiménez-Pérez 2011). Taxa-specific results contribute to a more realistic assumptions of C sinks in different ecosystems (Cartus et al. 2014, Matula et al. 2015) with implications for other countries where the studied species occur and challenges the current assumption of a 50% C concentration of plant tissues across forests worldwide.

Conclusions

The C concentration of plant tissues for Mexican tree species differed between environments, taxa and plant tissues. Our results show that the generalized assumption of 50% C content is consistently slightly above real values for the species studied. This overestimation, though small in some cases, could lead to errors of 3.9 Mg ha^{-1} in some Mexican forests. To improve estimations of C reserves, our values should be used for the studied genera. Given the large number of species studied, it would be important to test whether the generalized 50% assumption does apply in other environments. It is not practical to use C concentration for each plant tissue, therefore more research that models C concentration indices is still necessary, especially to distinguish dead or decaying tissues. Our study contributes to a better understanding of C concentration in forest ecosystems and provides a large dataset for Mexican species that can be contrasted across environments elsewhere.

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Supplementary Material

Fig. S1 - Distribution of 68 localities in Mexico from where samples were collected for C concentration in 175 species.

Tab S1 - Carbon concentration to the nearest 1% for the 175 Mexican forest species studied and their tissues.

Link: Pompa-Garcia_2421@suppl001.pdf