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Variation of main terrestrial carbon stocks at the landscape-scale are shaped by soil in a tropical rainforest

Armando Navarrete-Segueda[a,*], Miguel Martínez-Ramos[b], Guillermo Ibarra-Manríquez[b], Lorenzo Vázquez-Selem[c], Christina Siebe[a]

[a] Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Circuito de la Investigación Científica s/n, Delegación Coyoacán, Ciudad de México CP 04510, México

[b] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro No. 8701, Col. San José de la Huerta, CP 58190 Morelia, Michoacán, México

[c] Instituto de Geografía, Universidad Nacional Autónoma de México, Ciudad Universitaria, Circuito de la Investigación Científica s/n, Delegación Coyoacán, Ciudad de México CP 04510, México

A R T I C L E I N F O

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A B S T R A C T

Economic incentives to offset carbon dioxide (CO_2) emissions associated with deforestation and other human activities affecting forest ecosystems depend on robust estimates of changes in forest carbon (C) stocks. Such stocks are difficult to assess in heterogeneous landscapes where the soil properties and the forest structure and functionality vary in space and time. Here we show that geopedological mapping is useful to quantify the above- and belowground C stocks in the different land units of the Lacandon tropical rainforest, southeast Mexico. We used an ordination method to recognize major gradients in the soil and we applied regression analyses to identify relationships between soil properties and AGB. Total forest C stocks differed among land units (287 to 478 Mg C ha^{-1} in limestone mountains and fluvial terraces, respectively). Soil constrains like rooting depth (ranging from 0.13 to 1.34 m), available water storage capacity (ranging from 32.3 to 161.4 L m^{-2}) and Al saturation in the ion exchange complex (0 to 22.6% Al_{sat}) were correlated with the aboveground biomass (AGB) C stock by affecting the stem size and density of trees. Soil organic carbon (SOC) in the *solum* represented 22 to 46% of the total forest C stock in the different landscape units, of which 28 to 45% was stored below 30 cm depth. Therefore, an accurate assessment of forest C stocks must consider not only the variation between land units with contrasting soil properties, but also the *solum* depth. Our results indicate that stratified sampling based on geopedologic mapping is useful to allocate incentives assessment of C storage at relatively low costs and with reasonable effort.

1. Introduction

Tropical rainforests are the most productive terrestrial ecosystems accounting for the largest carbon dioxide (CO_2) uptake per area unit (Beer et al., 2010; King et al., 1997). Thus, these ecosystems play a significant role for global terrestrial C storage in their different components (van der Sande et al., 2017). However, the C balance of tropical ecosystems remains uncertain, since it is largely affected by deforestation and forest degradation (Baccini et al., 2017; Gibbs et al., 2010), causing these forests to become a carbon source for the atmosphere (Baccini et al., 2012, 2017). Despite there are other factors affecting CO_2 concentration in the atmosphere, as the residence time (Archer et al., 2009; Chapin et al., 2011) and the fact that terrestrial ecosystems have a finite capacity to store C (Mackey et al., 2013), the terrestrial C storage remains as one of the main strategies to mitigate the atmospheric increases in CO_2 concentrations (Asner et al., 2014). Therefore, tropical developing countries have created economic incentives to reduce deforestation and forest degradation rates and their associated C emissions (Gibbs et al., 2007; Griscom et al., 2009).

Establishing reliable finance schemes oriented to maintain or increase terrestrial C stocks requires robust estimates of these stocks (Berenguer et al., 2015; Gibbs et al., 2007; Houghton, 2005; Saatchi et al., 2011). Five main stocks are differentiated by the IPCC (2006): aboveground biomass (AGB), belowground biomass (BGB), dead wood (or necromass), litter, and soil organic carbon (SOC). The AGB and SOC are the largest stocks in tropical forests (Berenguer et al., 2015; Gibbs

* Corresponding author.
E-mail addresses: anavarretesegueda@yahoo.com.mx (A. Navarrete-Segueda), mmartinez@cieco.unam.mx (M. Martínez-Ramos), gibarra@cieco.unam.mx (G. Ibarra-Manríquez), lselem@igg.unam.mx (L. Vázquez-Selem), siebe@unam.mx (C. Siebe).

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et al., 2007; Ngo et al., 2013) -although the contribution of belowground biomass remains uncertain since to estimate this stock usually root to shoot ratios are applied (Delaney et al., 1997; Djomo et al., 2011; Saatchi et al., 2011)-. The AGB can be estimated by remote sensing techniques and is often used to derive other C stocks (e.g., BGB or litter) (Gibbs et al., 2007; Saatchi et al., 2011). Therefore, many studies have focused only on the remotely sensed AGB stock to maximize the cost-effectiveness of C assessments (Gibbs et al., 2007, 2010; Saatchi et al., 2011). This approach overlooks the SOC stock, notwithstanding the fact that the lack of SOC estimates may seriously underestimate total forest C stock. Soil studies to 100 cm depth in neotropical rainforests indicate that SOC may comprise 50%–75% of the total forest C stock (e.g. Delaney et al., 1997; Fonseca et al., 2011; Hughes et al., 1999; Kauffman et al., 2009).

Accurate C stock estimates are difficult to compile in tropical forests since they often face a high biotic and abiotic heterogeneity. Remote-sensing options that provide AGB estimates with low to medium uncertainty by Light Detection and Ranging (LiDAR) images (Gibbs et al., 2007) do not allow to estimate the SOC stock nor the soil properties which are necessary to calculate it, such as SOC concentration, soil bulk density, percentage of coarse fragments and soil depth (Jobbágy and Jackson, 2000; Lal, 2005). The dense canopy of tropical rainforest limits the usefulness of remote-sensing options to assess the SOC stock (Rasel et al., 2017; Vaudour et al., 2016).

Tree community stand structure parameters such as the basal area and the number of large trees are among the most important factors explaining the spatial variation in AGB of tropical rainforests (Alves et al., 2010; Banin et al., 2014; Baraloto et al., 2011; Berenguer et al., 2015; Slik et al., 2013). The spatial variation of these tree community parameters is also determined by soil properties that constrain tree growth (Alves et al., 2010; Paoli et al., 2008) or stimulate the development of specific taxonomic tree groups (families, genera, etc.) (Banin et al., 2014; De Castilho et al., 2006). Therefore, soil properties that drive SOC accumulation may also regulate the spatial variation of AGB of tropical forests (Baldeck et al., 2013; De Castilho et al., 2006; Laurance et al., 2010; Quesada et al., 2012; Sullivan et al., 2017).

Stratified sampling has proved to be useful to more accurately estimate the AGB-carbon considering landscape variation (landforms) since it includes the landscape variability of topography and geology (and the soil derived from it) (Laumonier et al., 2010). In this study we analyzed how soil properties determine site quality -the latter, defined by Daniel et al. (1979) as the sum of all the environmental factors affecting the biotic community of an ecosystem- and, thereby, the variation of C stocks in the Lacandon tropical rainforest in southeast Mexico. Particularly we aimed to assess: 1) the contribution of SOC stock in the *solum* (A and B horizons) to the terrestrial forest C stock in distinct land units with contrasting landform and parent material, and 2) to investigate how the variation in soil properties affects the AGB stock across the landscape. We studied a neotropical forest covering a landscape with contrasting soil-topographic conditions under the same climate (Ibarra-Manríquez and Martínez-Ramos, 2002; Siebe et al., 1995) (Table 1). The Lacandon tropical rainforest represents one of the most extensive tropical rainforest in North America (Mendoza and Dirzo, 1999). Previous AGB-C stock estimates in the study area ranged from 94.0 ± 26.3 (Balvanera et al., 2005) to 233.4 ± 52.3 Mg C ha^{-1} (De Jong et al., 2000). A preliminary study identified differences in tree density and standing biomass across geopedological land units (Siebe et al., 1995). Ibarra-Manríquez and Martínez-Ramos (2002) reported that smaller tree diameters are related to poor soil drainage and small available water storage capacity along the different geopedologic land units.

We hypothesized that the AGB and SOC stocks, as well as their contribution to the forest C stock, will differ among geopedologic land units. On the other hand, we expected that if soil properties variation (i.e., soil nutrient contents, soil drainage conditions or soil water storage capacities) influences the stem size and density, it will indirectly regulate AGB production across the landscape. Because a forest inventory at the field scale is the most direct method to quantify forest C stocks (Gonzalez et al., 2014), this study aimed to provide guidance for AGB, litter and SOC stock assessments in heterogeneous forest landscapes.

Table 1
Range in soil-topographic attributes and tree community characteristics at the Lacandon rainforest in southeast Mexico. Average pH was measured with samples taken from soil profiles of indicated depth. Modified from Siebe et al. (1995) and Ibarra-Manríquez and Martínez-Ramos (2002).

	Geopedologic land units		
	Fluvial terraces	Low-hills	Limestone mountains
Soil			
Rooting depth (cm)	65–100	55–65	12–20
pH	5.8	4.7	7
Drainage	Moderate to well drained	Moderate to deficiently drained	Well drained
Soil unit classification (IUSS Working Group WRB, 2014)	Fluvic Cambisol	Vertic-Stagnic Cambisol and Cutanic Acrisol	Rendzic Leptosol
Topography			
Slope	Flat (< 2°)	Moderate steep (< 15–30°)	Very steep (30–40°)
Tree community characteristics			
Tree density (individuals ha^{-1})	318–376	344–524	426–578
Basal area (m^2 ha^{-1})	22.6–37.6	16.6–29.8	21.6–27.0
Number of tree species per 0.5 ha	43–58	50–81	70–74

2. Materials and methods

2.1. Study area

This study was conducted in the surroundings of the Chajul Tropical Biological Station, in the southern part of the Montes Azules Biosphere Reserve (MABR) (16°04′ N; 90° 45′ W), within the Lacandon region, southeast Mexico (Fig. 1). The MABR was established as a nature protection zone in 1978. The difficult access to the region maintained a low population density in the neighbor communities of the MABR, however in the year 2000 the construction of a highway connecting the region with urban centers caused a population increase to 12.6 inhabitants per km^2 in 2010 (Carabias et al., 2015; INEGI, 2016). According to Zermeño-Hernández et al. (2015), the region south of the MABR is covered by 34% by preserved old-growth forest fragments, 16% by secondary forest patches, and the rest by cattle pastures and crops. Mean annual precipitation (MAP) is 3000 mm and the mean annual temperature (MAT) 22 °C. There is a short dry season from February to April (< 100 mm per month) (Martínez-Ramos et al., 2009). The area is covered by a mosaic of vegetation types that include mainly tropical rainforests of medium high canopy (< 30 m) (dominant species *Bravaisia integerrima*, *Dialium guianense*, *Quararibea funebris* among others) to high canopy (> 30) (*Brosimum alicastrum*, *D. guianense*, *Licania hypoleuca* among others), and savannah type vegetation with *Byrsonima crassifolia* and *Curatella americana* as main dominant tree species (Ibarra-Manríquez and Martínez-Ramos, 2002; Ochoa-Gaona and Domínguez-Vázquez, 2000).

Siebe et al. (1995) differentiated three main geopedologic land units in the study area, i.e., land units with contrasting lithologic and topographic conditions on which distinct soils occur, namely: 1) limestone mountain ranges with steep slopes (> 30°) and shallow soils (< 20 cm) which classify as Rendzic Leptosols (IUSS Working Group WRB, 2014), 2) low hills of folded claystone-sandstone sequences, with moderately

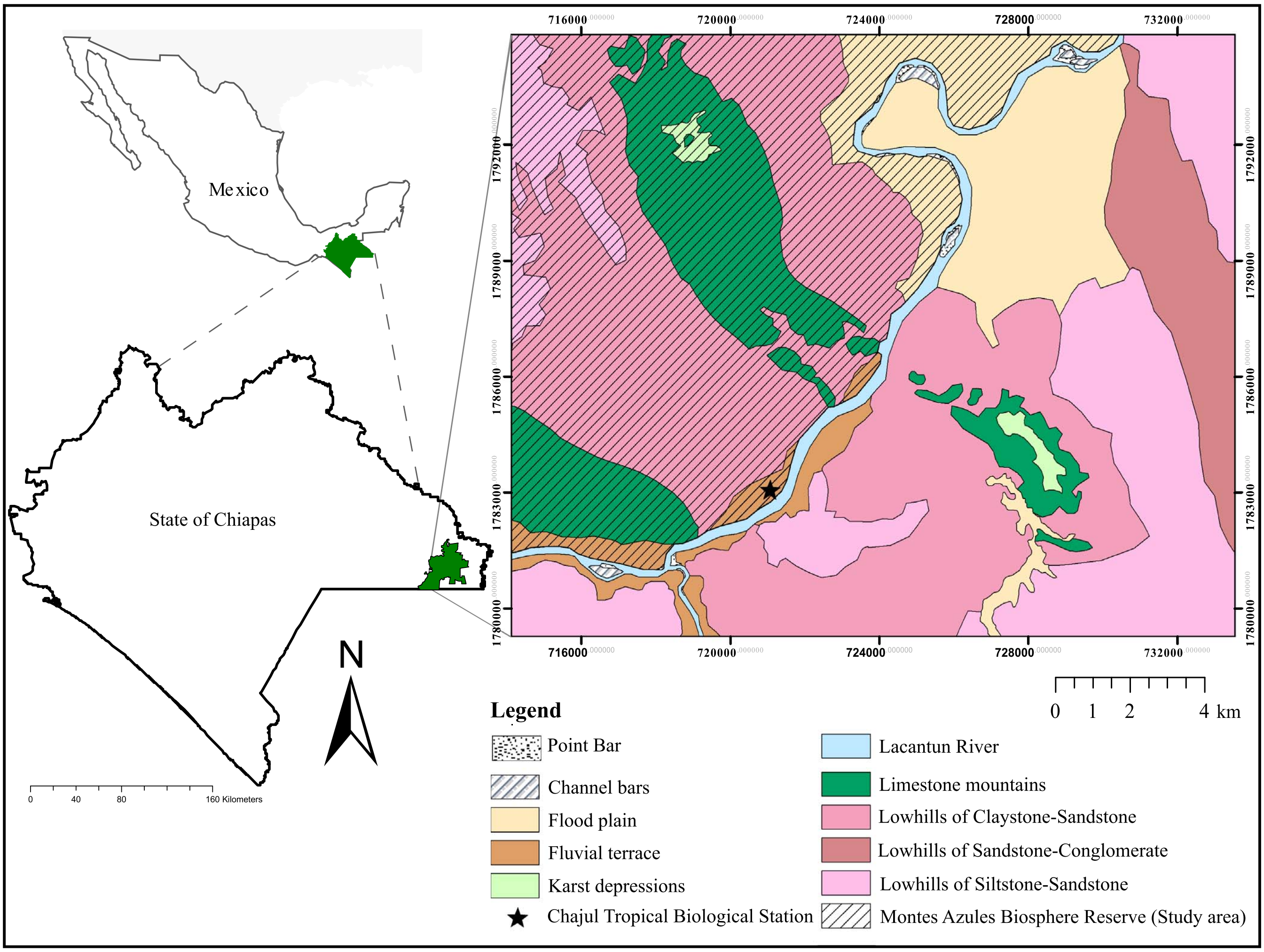

Fig. 1. Geopedologic land units delineated in Lacandon rainforest, southern Mexico.

steep slopes (15–30°) and medium deep soils (55–65 cm), the parent material changes in tenths of meters distance (Siebe et al., 1995), the soils classify as Vertic-Stagnic Cambisols associated with Cutanic Acrisols and, 3) fluvial terraces and plains (associated with fluvial deposits), i.e., nearly flat (< 2°) alluvial surfaces with deep soils (65–100 cm) which classify as Fluvic Cambisols.

2.2. Site quality classification

Major landscape units were determined by the hierarchical classification system proposed by Zinck (1988). Map units were obtained by visual interpretation of the external features of landforms (Zinck et al., 2016) in 1: 20,000 scale aerial photographs and using a 1:50,000 digital elevation model. Geological information (Servicio-Geológico-Mexicano, 1997) and soil information (Celedón, 2006; Siebe et al., 1995) were included to delineate seven major geopedologic land units (Fig. 1). We selected limestone mountains, low hills of claystone-sandstone and fluvial terraces since these units cover the major landscape surface in the study area.

2.3. Estimation of carbon stocks

Within each geopedologic land unit, three plots of 20 × 250 m each were established, to determine AGB, BGB, litter and SOC stocks. In each plot, the stem diameter of all trees with diameter ≥ 10 cm at breast height (dbh, 1.3 m above ground) was measured. For big trees with large buttresses, stem diameter was taken above such structures. In each plot, AGB was estimated based on dbh measurements using a generic tropical rainforest equation proposed by Brown (1997) and modified by Rügnitz et al. (2008). This equation was used because the available site-specific and species-specific equations (Rojas-García et al., 2015) cover < 20% of the species that are present within the studied plots, and do not include the more abundant species. We considered that it was more appropriate to use a generic model so that the error is equal for all species. The use of generalized allometric relationships by grouping all species has proven to be very effective in the tropics (De Jong et al., 2000; Lewis et al., 2013; Poorter et al., 2015; Willcock et al., 2014) since dbh alone explains > 95% of the variation in AGB tropical forest C stocks (Brown, 2002; Gibbs et al., 2007). In this study, we omitted trees with dbh < 10 cm because their contribution to the AGB may be < 2% as has been described by Berenguer et al. (2015) and Hughes et al. (1999). To calculate the ABG of each tree (AGB_{tree}) with dbh > 10 cm, we chose the allometric model based on a regression equation for estimating biomass of tropical trees [Eq. (1)] for MAP between 2000 and 4000 mm (Brown, 1997; Rügnitz et al., 2008):

$$AGB_{tree}\,(\text{kg dry mass}) = \exp\left[-2.289 + 2.649 * ln(\text{dbh}) - 0.021 * (ln(\text{dbh}))^2\right] \quad (1)$$

where AGB_{tree} is the AGB (kg) of each tree, dbh is the diameter at breast height (cm). To estimate the AGB per ha we used the Eq. (2):

$$AGB_{plot}\,(\text{Mg dry mass ha}^{-1}) = \left(\sum \text{at}/1000\right) \times (10,000/A) \quad (2)$$

where AGB_{plot} is the total AGB by plot in Mg ha^{-1}, Σat is the sum of the dry mass of all trees in the plot in kg; 1000 is the factor to convert kg into Mg; 10,000 is the factor to convert meters in hectares; and A is the surface of the plot (m^2). To transform AGB into AGB-C stock, the Eq. (3) of Somogyi et al. (2008) was used:

$$\text{AGB-C} = \text{AGB}_{plot} \times \text{CF} \quad (3)$$

where AGB-C is the aboveground C stock (in $Mg\ C\ ha^{-1}$) of the AGB, AGB_{plot} is the total AGB per hectare (in $Mg\ ha^{-1}$), CF is the C fraction of the dry AGB ($Mg\ C\ Mg^{-1}$). We assumed that 50% of the AGB mass was C (Ngo et al., 2013). We used the Eq. (4) proposed by Saatchi et al., 2011 to estimate BGB from AGB_{plot} in $Mg\ ha^{-1}$.

$$\text{BGB} = 0.489\text{AGB}_{plot}{}^{0.89} \quad (4)$$

where BGB is the belowground biomass (in $Mg\ ha^{-1}$) and AGB_{plot} is the total AGB (in $Mg\ ha^{-1}$) by plot. To convert BGB into BGB-C stock, the Eq. (5) of Somogyi et al. (2008) was used:

$$\text{BGB-C} = \text{BGB} \times \text{CF} \quad (5)$$

where BGB-C is the belowground C stock (in $Mg\ C\ ha^{-1}$), BGB is the dry below ground biomass (in $Mg\ ha^{-1}$) estimated from the Eq. (4), CF is the C fraction of the dry biomass ($Mg\ C\ Mg^{-1}$). We assumed that 50% of the dry mass was C (Ngo et al., 2013).

Three soil pits (1 m wide × 1.5 m long and between 0.3 to 1.4 m deep) were dug in the middle of each plot for soil description. The sampling was performed in the same slope-position to reduce micro-topographic effects of erosion and deposition. After describing the soil, one disturbed soil sample was taken from each genetic horizon of the *solum*, and three undisturbed 100 mL core samples were taken in each horizon for bulk density determination. In the laboratory, the disturbed samples were air dried and sieved (< 2 mm) prior to analysis. Total C (TC) was determined in air dried, sieved and ground (< 0.05 mm) subsamples in the laboratory with an elemental CHNS/O analyzer (Perkin Elmer 2400 series II). None of the soils of low hills and fluvial terraces contained carbonates so we considered that SOC was equal to TC. In the case of limestone mountains, the total inorganic C (TIC) was measured with a TC analyzer equipped with a solid sample combustion unit SSM- 5000A (Shimadzu) by an infrared gas analyzer, which determined the CO_2 produced after adding an acid solution, in such a way that SOC was calculated as the difference TC-TIC. The stone content in vol (%) was estimated in the field (FAO, 2006), and bulk density was determined gravimetrically in the 100 mL core samples after drying the samples at 105 °C (MacDicken, 1997). The SOC stock ($Mg\ C\ ha^{-1}$) in each horizon within the *solum* (A and B horizons) was calculated using the IPCC (2003) Eq. (6) as follows:

$$\text{SOC}_{horizon}(\text{Mg C ha}^{-1}) = \text{C (g kg}^{-1}) \times \text{T (m)} \times \text{BD (Mg m}^{-3}) \times (1-\text{frag}) \times 10 \quad (6)$$

where C is the concentration of organic C obtained by the laboratory analysis (the data was reported on a dry mass basis by correction for soil moisture content determined on sample aliquots dried at 105 °C), T is the horizon thickness, BD is the bulk density and frag is the percentage of coarse fragments/100, 10 is the factor to convert m^2 into hectares and kg into Mg.

The forest floor litter (i.e., the L horizon consisting of leaves, fruits, seeds, bark, and wood < 2.5 cm diameter) was sampled once in microplots of 50 × 50 cm (Hughes et al., 1999) placed along three linear transects (at a distance of 6 m each) distributed longitudinally along each plot ($n = 6$ per plot). The samples were dried at 60 °C, weighted and ground (< 1 mm), and their C concentration was determined in the laboratory with an elemental CHNS/O analyzer (Perkin Elmer 2400 series II). The C litter stock (L-C) per hectare was determined using the Eq. (7) of Rügnitz et al. (2008), which multiplies the C fraction of the litter sample (CF-L) (obtained in laboratory) by the total weight of the same sample dried at 60 °C. The C of the litter stock (L-C) in Mg C per ha was calculated with Eq. (8).

$$\text{C mass litter (Kg C)} = \text{mass (Kg)} \times \text{CF-L} \quad (7)$$

$$\text{L-C (Mg C ha}^{-1}) = (10,000/0.25\ \text{m}^2) \times ((\Sigma_{\text{C-samples}}/\text{number of samples})/1000) \quad (8)$$

where L-C is the C stock in the litter, 10,000 is the conversion factor meters into hectares, 0.25 m^2 corresponds to the microplot surface, 1000 is the factor to convert kilograms of dry mass into Mg of dry mass and $\Sigma_{C\text{-samples}}$ is the amount of C in all samples of 50 cm × 50 cm (0.25 m^2) divided by six (samples collected per plot).

2.4. Soil analyses

The following analyses were performed on air-dried soil samples following standard procedures (Van Reeuwijk, 1992; Schlichting et al., 1995). Results are reported on a dry mass basis by correction for soil moisture content determined on sample aliquots dried at 105 °C. The pH was measured in 0.01 m $CaCl_2$ in the supernatant of a 1: 2.5 (wt:vol) soil suspension with an Aqua Lytic Senso Direct pH 24 potentiometer equipped with a combined glass/calomel electrode. Total nitrogen (TN) was determined using a CHNS/O elemental analyzer (Perkin Elmer 2400 series II). Extractable phosphorus (P_{ex}) was determined by the method of Bray-Kurtz and quantified by colorimetry (Van Reeuwijk, 1992). Exchangeable base cations (X_{ex}) were extracted with 1 N ammonium acetate buffered at pH 7, and Ca_{ex} and Mg_{ex} were quantified by AAS in an air-acetylene flame (Perkin Elmer 3100). K_{ex} and Na_{ex} by flame emission (Corning). Exchangeable acidity (H_{ex} plus Al_{ex}) was determined in 1 M KCl extracts by titration with 0.01 N NaOH and 4% NaF (H^+), or by AAS in a nitrous oxide-acetylene flame (Al^{3+}). The Al saturation (Al_{sat}) in the cation exchange complex was calculated as follows (Eq. (9)):

$$\text{Al}_{sat}(\%) = (\text{Al}_{ex}(\text{cmol kg}^{-1}) / \Sigma\ (\text{Ca}_{ex}, \text{Mg}_{ex}, \text{K}_{ex}, \text{Na}_{ex}, \text{H}_{ex}, \text{Al}_{ex}(\text{cmol kg}^{-1})) \times 100 \quad (9)$$

Soil texture was determined by the combined sieve and pipette method (Schlichting et al., 1995; Soil Survey Staff, 2011) after destroying organic matter with peroxide, dissolving $CaCO_3$ with diluted HCl, and dispersing the sample with sodium hexametaphosphate.

The available water holding capacity (AWHC) and the aeration capacity of each soil horizon were estimated and interpreted using AG-Bodenkunde (2005), and Siebe et al. (1996), which consider soil texture, soil organic matter content and bulk density determined in the laboratory (as are described above), as well as the percentage of coarse fragments and horizon thickness estimated in the field.

2.5. Data analysis

In order to detect and classify meaningful variables related to the SOC stock and to identify significant gradients that may affect the AGB at landscape scale, we used a principal component analysis (PCA) as ordination method to minimize the dimensionality of the collected data. The PCA has been used as ordination method to describe major gradients in the soil related with AGB in tropical rainforest (De Castilho et al., 2006; Laurance et al., 1999; Lewis et al., 2013). The PCA additionally reduces the number and collinearity of variables (Laurance et al., 1999; Slik et al., 2013). The PCA was performed with the software R (R Core Team, 2015) after log-transformation of the data to homogenize the variances (Breulmann, 2011). Subsequently regression analyses were applied to the resulting data of the PCA to identify significant relationships with the AGB and to select predictors (De Castilho et al., 2006; Paoli et al., 2008; Unger et al., 2012). The variables that we considered were pH, Ca^{2+}, Mg^{2+}, K^+, TN, P_{ex}, Al sat., aeration capacity, AWHC, field capacity, rooting depth, slope and stoniness. In order to compare soil nutrient storage among the different plots, we calculated the stocks of the soil nutrients Ca, Mg K and N within the *solum*

(Horizons A and B) considering the nutrient concentrations and the bulk densities determined in the laboratory as well as the stoniness and the thickness of each horizon measured in the field.

To determine if the average C stocks differed among geopedological land units, we computed one way ANOVA with post hoc Tukey tests when datasets met normal criteria. Otherwise we computed the parametric equivalent pairwise comparisons using Tukey and Kramer (Nemenyi) tests with Tukey-Dist approximation for independent samples Kruskal-Wallis, using R (R Core Team, 2015). The effects were regarded as significant at $P < 0.05$. To determine the contribution of plant community attributes on AGB stocks, we assessed independently the effect of size (10–20, 20–30, 30–40, 40–50 and ≥ 50 cm dbh) and tree density to total AGB-C stock between geopedologic land units. We computed linear models with AGB-C as dependent variable. Then, we performed a stepwise multiple linear regression analysis between soil properties derived from the PCA and the tree structure attributes (density and size) that influenced the AGB. This analysis allowed us to evaluate whether or not these plant community attributes responded to soil properties.

3. Results

3.1. Site quality

Several soil properties differed among geopedologic land units (Table 2). The fluvial terraces were characterized by the highest water storage capacity (field capacity and AWHC). In this unit, we found higher rooting depth as well as a higher K stock than in the other land units. The other units did not present significant differences with respect to these properties. Fluvial terraces had a high sand content that apparently improved soil drainage since no reductomorphic features were observed in the soil profile. The low hills have rooting depth restrictions since they are moderately to deficiently aerated, when developed on clay stones (evidenced by redoximorphic features at medium depths observed in the field), or strongly acidic and with a large Al saturation in the cation exchange complex, when developed on sand stones (Table 2). The low hills were highly heterogeneous not only in terms of slope gradient (Table 1). The soils at the steep slopes of the limestone mountains had a high surface stoniness (40%) (mean depth of 0.45 m), and were dominantly shallow and rocky, having a small AWHC and field capacity (Table 2). In the field, we observed that only in sinkholes of few square meters, where the rock dissolution had proceeded, soils reached up to 85 cm depth.

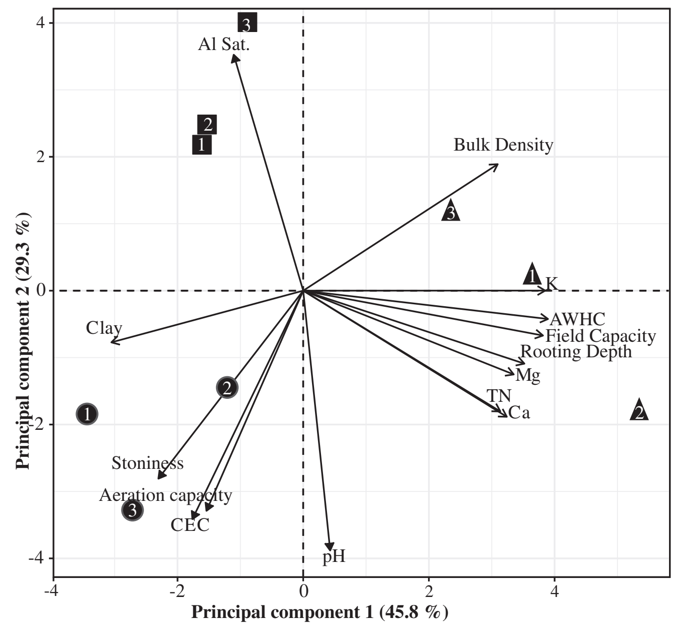

Fig. 2. Principal Component Analysis of soil properties among geopedological units. Squares represent Low hills; circles represent Limestone mountains and triangles represent Fluvial Terraces. The numbers 1 to 3 represent the plot number of each unit. Al Sat. = aluminum saturation; AWHC = available water holding capacity; CEC = cation exchange capacity; TN = total nitrogen.

The PCA analysis indicated clear differences in site quality among the soils of the three geopedologic land units (Fig. 2). The first axis of PCA (explaining 45.8% of the variance) separated the soils of the fluvial terraces, which have no site quality constrains (i.e. highest water and nutrient stocks), from those which have rooting depth constrains (Appendix A). The second axis (explaining 29.3% of the variance) separated the plots with shallow rooting depth as well as low AWHC due to large stone contents (at the limestone mountains) from those plots with poor drainage and chemical constrains indicated by acid pH and a high Al saturation (at low hills).

Table 2
Mean and standard error (± SE) values of soil properties determined in soil profile samples (N = 9), till the rooting depth of three geopedologic land units at the Lacandon forest. Means with the same superscript are not statistically different (ANOVA and Tukey posthoc < 0.05) among geopedologic land units.

Soil properties	Fluvial terraces		Low hills		Limestone mountains	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
SOC (Mg C ha^{-1})	103.9[a]	30.0	132.0[a]	23.9	68.1[a]	14.3
Total N (Mg N ha^{-1})	12.2[a]	3.0	4.8[a]	0.6	7.4[a]	2.0
Extractable P (mg P kg^{-1})	9.2[a]	1.9	6.4[a]	3.3	9.9[a]	6.2
Ca (mol m^{-2})	77.2[a]	27.7	14.5[a]	2.6	34.0[a]	7.9
Mg (mol m^{-2})	34.9[a]	13.7	7.6[a]	0.5	11.4[a]	5.6
K (mol m^{-2})	1.4[b]	0.2	0.5[a]	0.0	0.2[a]	0.0
Field capacity (L m^{-2})	269.0[b]	29.2	59.7[a]	2.2	75.0[a]	43.2
AWHC (L m^{-2})	161.4[b]	16.7	34.6[a]	3.9	32.3[a]	16.1
Rooting depth (m)	1.34[b]	0.01	0.13[a]	0.02	0.45[a]	0.21
Al saturation (%)	2.1[b]	2.1	22.6[a]	2.0	0.0[b]	0.0
pH (water)	5.4[b]	0.4	4.1[a]	0.1	5.9[b]	0.2
Clay (%)	24.3[a]	4.3	36.4[ab]	6.8	64.3[b]	8.5
Sand (%)	27.4[b]	7.6	16.3[ab]	8.8	1.8[a]	0.4
Stoniness (vol%)	0.00[a]	0.0	0.60[a]	0.3	67.50[b]	5.2

AWHC: available water holding capacity.

3.2. Carbon stocks among geopedologic land units

The total forest C stock (Mg C ha^{-1}) was significantly larger in fluvial terraces (Table 3). This unit had also the largest AGB-C and BGB-C stocks among the three geopedologic land units. The AGB-C stocks in low hills and limestone mountains was of 59% and 42%, lower than those of the fluvial terraces, respectively. There were no significant

Table 3
Carbon stocks (Mg C ha^{-1}) of the main geopedologic land units of the Lacandon forest. Means (n = 3 plots per land unit) with the same superscript are not statistically different (Nemenyi < 0.05) (CV: coefficient of variation. AGB-C: above ground carbon; BGB-C: below ground carbon; L-C: litter C stock; SOC: soil organic carbon in the solum).

Geopedologic land unit		AGB-C	BGB-C	SOC	L-C	Sum
Fluvial terraces	Mean	301[a]	73[a]	104[a]	0.36[a]	478.1[a]
	Range	277–344	67–81	65–163	0.31–0.38	416–509
	CV (%)	12	11	39	11	11
Low hills	Mean	122[b]	33[b]	132[a]	0.39[a]	287[b]
	Range	109–130	29–34	98–178	0.19–0.57	238–342
	CV (%)	9	8.08	40	49	18
Limestone mountains	Mean	174[b]	45[b]	68[a]	0.4[a]	287[b]
	Range	141–223	37–55	45–94	0.35–0.46	295–343
	CV (%)	24	22	36	14	8

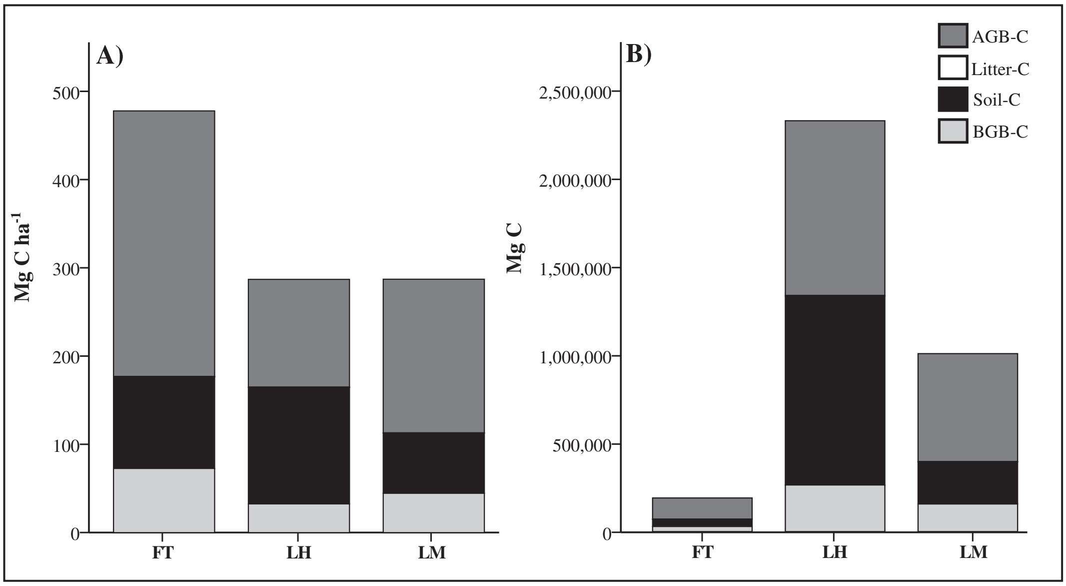

Fig. 3. Forest carbon stocks (Mg C) at the Lacandon Rainforest per hectare (A) and in total for each geopedologic land unit (B), FT = fluvial terraces; LH = Low hills; LM = limestone mountains.

differences in SOC stock in the *solum* and litter carbon stock (L-C) among geopedologic land units. The litter contributed < 0.2% to the total C stock in all land units. In fluvial terraces, SOC stock in the *solum* represented 22% of the total C stock, while in limestone mountains and low hills it represented 24% and 46%, respectively. Notably, SOC stock in low hills contributed significantly more (ANOVA test < 0.05 with Tukey contrast) to the total C stock than in fluvial terraces and limestone mountains.

Although fluvial terraces had the largest total C stock, their relative contribution to C stock of this rain forest area (138.4 km^2) was small, since this land unit only covered 2% of the whole study area (Fig. 3). Low hills, which had a smaller total C stock, cover the largest proportion of the study area, namely 59%, followed by limestone mountains (26% of the surface).

3.3. Site quality and AGB C stocks

Most of the AGB-C was stored in large trees (ranging 50 cm to 186 cm dbh) (Figs. 4 and 5a). In fluvial terraces, this tree size contributed almost 75% of the AGB-C stock, and 37% and 50% in lower hills and limestone mountains, respectively. Through regression analysis we identified a strong positive relationship between AGB-C stocks and C stored in trees of > 50 cm dbh ($\beta = 0.97$, $R^2 = 0.991$, P-value < 0.001). In limestone mountains, the trees of 20–30 cm dbh stored significantly more C than trees of the same size class in the fluvial terraces (Fig. 5d). The C stock stored in all other dhb categories was not different among the land units (Fig. 5b–e). Conversely, there was no significant difference in the tree densities in all size classes of trees ≥ 30 cm (Fig. 5f–h). Nevertheless, we found a significantly greater number of small trees (< 30 cm dbh) in these old growth forest plots, and particularly of stems of 10–20 cm, in low hills and limestone mountains in comparison to the fluvial terraces (Fig. 5i–j). The AGB-C stock of this tree size category (10–20 cm) was negatively correlated with the total AGB-C stock (β −0.890; adjusted R^2: 0.792, P-value 0.001).

Among the soil properties assessed in this study, rooting depth and soil extractable phosphorus were the most important explanatory variables influencing AGB-C stocks in the study area (adjusted R^2: 0.92), particularly, rooting depth was strongly and positively associated with AGB-C stock (P value < 0.01). Additionally, regression analysis indicated that soil rooting depth had a strong significant positive relationship with bigger trees (> 50 cm) (adjusted R^2: 0.88, P value 0.01). Soil AWHC, field capacity, pH and nutrient stock (Ca, Mg, K) were excluded from the analysis since they showed collinearity.

3.4. Vertical distribution of SOC among geopedological units

Fig. 6 indicated that the first 20 cm of the soil depth accounted for almost 50% of *solum* SOC stock. However, the SOC vertical distribution varied across geopedologic land units. The decrease was gradual in low hills, where the first 30 cm accounted for 64% of the *solum* SOC stock. A similar pattern was found at limestone mountains. In contrast, in fluvial terraces, the SOC showed an irregular depth distribution, declining below 20 cm depth and then increasing again between 60 and 80 cm depth.

4. Discussion

4.1. Site quality and C stocks at the Lacandon forest

We evaluated forest C stocks in land units of contrasting site qualities determined mainly by their soil properties, landform and lithology attributes within a tropical rainforest with relatively homogeneous climatic conditions. The mean AGB-C stocks among geopedologic land units varied widely but in a range similar to the one reported in other studies of neotropical old growth forest forests (Berenguer et al., 2014; Delaney et al., 1997). However, we found differences in the forest C stock between geopedologic land units with contrasting site quality. Our results agree with Baraloto et al. (2011), who found contrasting patterns of AGB among forest habitat types, it would be expected that the AGB-C stock would change as a result of the changes in AGB due to the strong positive relationship between both variables (Brown, 1997). In earlier studies De Jong et al. (2000) and Balvanera et al. (2005) quantified AGB-C stocks in the same forest with very contrasting results. The range of AGB-C stocks we determined in the fluvial terraces is consistent with the one reported by De Jong et al. (2000), while the one we found in low hills, is in line with the results of Balvanera et al. (2005). Therefore, the results of the previous studies diverge most probably because their sampling was conducted predominantly in different geopedological units, namely fluvial terraces and low hills, respectively.

We hypothesized that the AGB-C and SOC stocks would differ

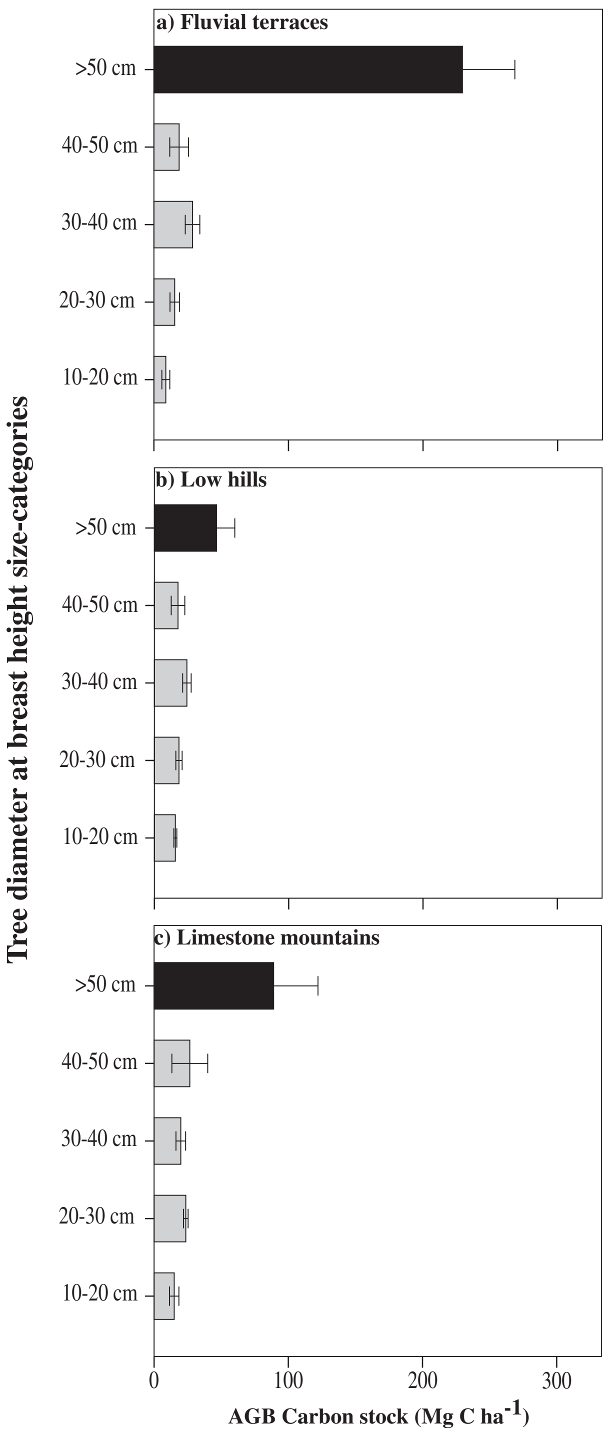

Fig. 4. Contribution of the different tree diameter at breast height size classes to the AGB-C stock (Mg C ha^{-1}) in each geopedologic land unit. Error bars indicate standard error. Black bars represent significant differences ($P < 0.05$).

among geopedologic land units. This was true only for AGB-C stock, which was significantly higher in fluvial terraces (Table 3). Contrary to our hypothesis, and although SOC concentrations differed markedly among land units (supplementary material), we did not find significant differences in SOC stock between land units. These results may be explained by the effect of soil volume (Olson and Al-Kaisi, 2015), and the variation in soil depth and stoniness (Table 2) in the three land units. Limestone mountains had shallow, stony soils with high SOC concentrations, while fluvial terraces and low hills had deeper soils with smaller SOC concentrations, so that the larger soil volume yields a higher SOC stock in these units. Lime-rich soils are known for their high capacity to store SOC, since Ca^{2+} fosters the stabilization of aggregates and the formation of organo-mineral complexes, which in turn protect organic C from microbial degradation (Blanco-Canqui and Lal, 2004; Kalbitz et al., 2000). Soils of the low hills seem to have larger iron-oxide contents, evidenced by their red colors. The SOC stabilization mechanisms were apparently different between these two soils -affected by clay content and Ca^{2+} in limestone mountains and by inhibition of microbial activity in low hills-, which deserve to be studied in more detail in the future.

4.2. Site quality effect on AGB-C variation between landscape units

We found that AGB-C stock variation between geopedologic land units corresponded mainly to changes in the basal area and density of trees. These patterns have been extensively proven in old growth tropical forests (Berenguer et al., 2014; Kauffman et al., 2009; Lü et al., 2010; Slik et al., 2013). Our results are in agreement with previous studies that show that larger trees are responsible for storing the largest fraction of AGB, and therefore, a greater amount of C (Aldana et al., 2017; Baraloto et al., 2011; Berenguer et al., 2014; Slik et al., 2013). This was expected because the tropical rain forests tend to have large trees with high basal areas and therefore higher AGB (Baraloto et al., 2011; Slik et al., 2013). In this regard, Berenguer et al. (2015) suggested that sampling of stems ≥ 20 cm dbh without taxonomic identification can predict the AGB with a high confidence in a fast and cost-effective way. In the Lacandon rainforest, the stems ≥ 20 cm dbh accounted for 92, 87 and 92% of the AGB-C stocks in fluvial terraces, low hills and limestone mountains, respectively. Particularly, the variation of AGB-C stocks is strongly affected by trees ≥ 50 cm dbh, which accounted for more than two thirds of this C stock in fluvial terraces but less than half in low hills. Therefore, the trees with smaller dbh contribute proportionally more to the AGB-C stock in low hills and limestone mountains since they accounted for more than half of the AGB-C in these landscape units. These results are in line with those by De Castilho et al. (2006), who indicated that it is difficult to establish causal relationships between AGB and topography because the latter is a composite variable that covaries and nest other abiotic variables and biotic interactions. Nevertheless, the mentioned authors found that AGB in slopes is concentrated mostly in trees of small size, while in flat areas, the AGB is determined by fewer but much bigger trees of a central Amazonian forest.

The influence of environmental factors on AGB is highly dependent on the spatial scale of the assessment (Baraloto et al., 2011; Berenguer et al., 2014). In neotropical and pantropical forests, previous studies at the landscape scale have shown a significant effect of soil properties on the AGB (Baker et al., 2009; Laurance et al., 1999; Quesada et al., 2012; Slik et al., 2013). As indicated above, our results suggest that this soil effect on the AGB can be manifested in the AGB-C amount. On the one hand, the changes in AGB-C in our area could be a direct consequence of soil extractable P and rooting depth affecting the variation of net primary production as reported previously by King et al. (1997). The positive role of soil P on AGB accumulation has been documented in other tropical rainforests, especially for bigger size trees (Paoli et al., 2008; Quesada et al., 2012). The lowest AGB-C amount was found in low hills, where the low pH values, as well as the high aluminum saturation may lead to P retention in insoluble forms for plants (Chapin et al., 2011). Similarly, the relationship found between soil thickness and AGB has been reported in other ecosystems (Belcher et al., 1995; Meyer et al., 2007). In our study area, the available climatic data (SMN-CNA, 2010), show that evaporation exceeds precipitation during two months of the year, during which plants growing in the shallow soils of the limestone mountains probably suffer water stress (the average deficit is 55 mm by month). This may limit tree growth and, thus, AGB-C because plants may respond with a low stem size at sites with small AWHC (Chapin et al., 2011; Gregory, 2006; Quesada et al., 2012).

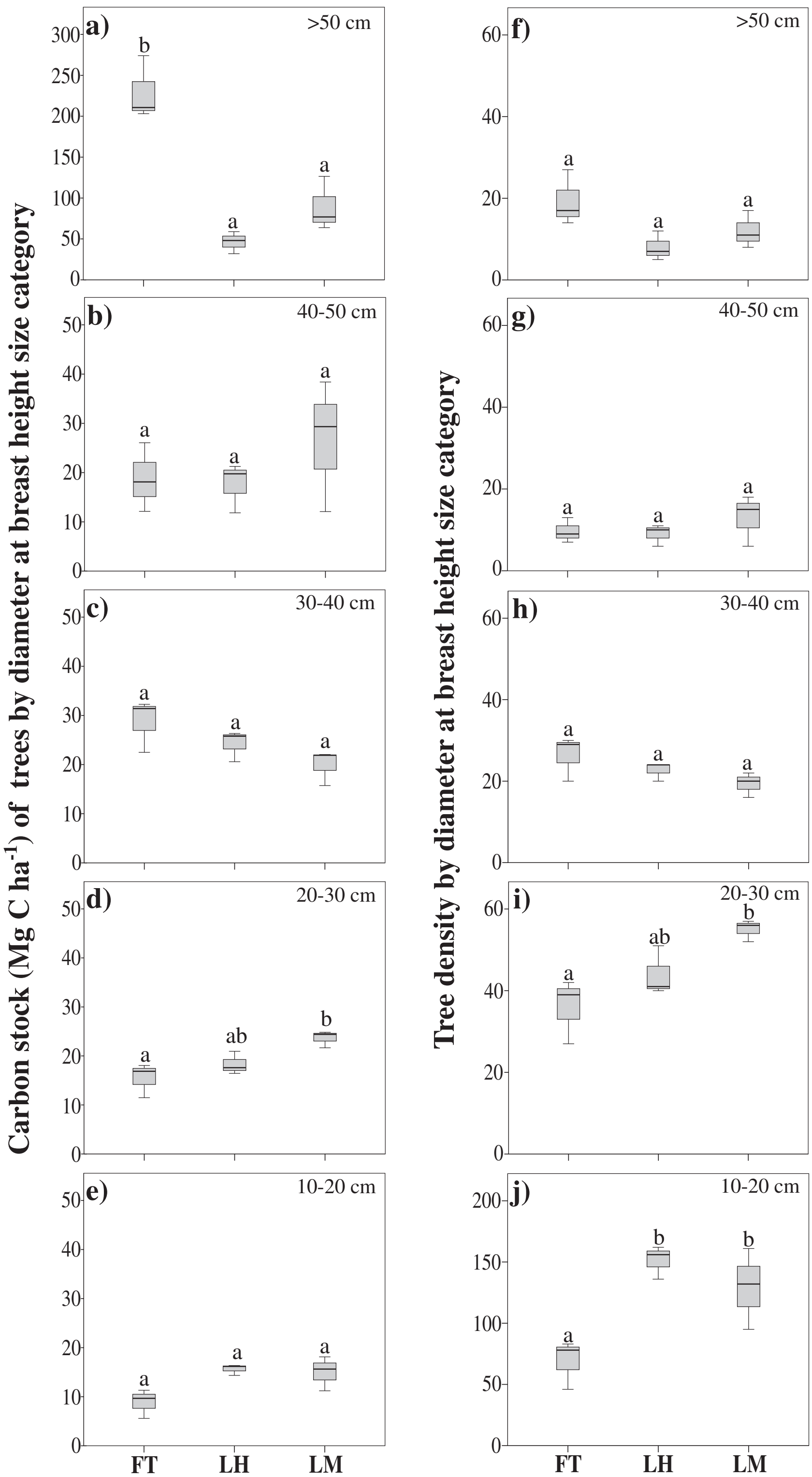

Fig. 5. AGB-C stocks (Mg C ha^{-1}) (left) and number of trees (right) within each tree diameter at breast height size class in the study area. FT = fluvial terraces; LH = Low hills; LM = limestone mountains. Error bars indicate standard error. Letters represent significant differences ($P < 0.05$) between geopedological units.

Similarly, several features may limit the AGB-C accumulation in low hills, namely the high percentage of Al saturation in the ion exchange complex, the small availability of phosphorus and nutrients as Mg and K. These, in tandem with the acidic pH, reduce the growing length of the roots, limiting the plants ability to absorb water and nutrients (Gregory, 2006; Kidd and Proctor, 2001).

On the other hand, the variation of AGB-C stocks among geopedologic land units can be an ecological response of tree community parameters to soil constraints (De Castilho et al., 2006), hindering plant development or stimulating in different degree the competition among plants. For example, in fluvial terraces we found more favorable conditions for plant development, as larger rooting depth, larger AWHC, slightly acidic pH with large base cation saturation in the ion exchange complex and favorable soil aeration conditions, that may allow a few competitive species to exclude other species (Huston, 1980; Peña-Claros et al., 2012) and to store large AGB-C stock. Likewise, in other type of forests (Meyer et al., 2007), a positive relationship has been found between soil depth and basal area. In contrast, in low hills and

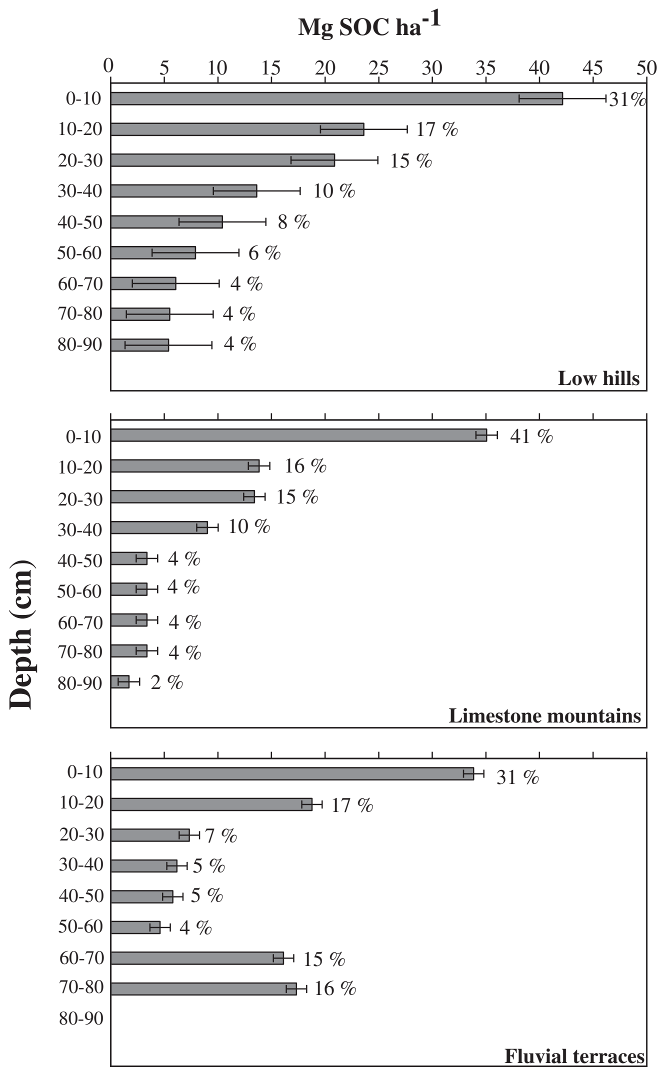

Fig. 6. Comparison of the vertical distribution of the soil organic carbon stock (Mg C ha $^{-1}$) between geopedologic land units. Weighted averages for each 10 cm of soil increment and standard error bars are shown. The relative contribution to the total SOC stock is given in percentage.

limestone mountains with several limitations for tree growth (large Al saturation in the exchange complex and small AWHC, respectively) we found a higher tree density of small size, which was negatively correlated with AGB-C stocks.

4.3. SOC contribution to forest C stock among geopedologic land units

Previous studies in neotropical forest of the Amazon Basin (Berenguer et al., 2015) and Mexico (Hughes et al., 1999, 2000) have shown that the greatest amount of C is stored in the AGB of old growth forests, but also a large amount of C is stored as SOC. The profile SOC stock accounted for at least 50% of the forest C stock (Kauffman et al., 2009). Although we consider only the SOC of the *solum*, our results are in line with this statement in low hills. We expected that the SOC stock would differ among geopedologic land units, but stocks were not significantly different (Table 3). What did change between land units was the relative contribution of SOC to the total forest C stock, being larger in low hills (46%), than in fluvial terraces (22%), and evidencing the greater importance of acknowledging SOC stocks additional to AGB-C in land units having constraints for plant growth.

Most of the SOC was stored in the first 20 cm which is consistent with results of Jobbágy and Jackson (2000), who found that the first 20 cm of soil in tropical evergreen forests accounted for 44% of soil C stock to 100 cm depth. Yet, we found that if only the top 30 cm is considered for assessing the SOC stock, the regional C stock is underestimated by 28 to 45%. This can make an important difference in the regional C stocks assessment, since low hills contributed with more than a half and limestone mountains with almost a third to the regional C stock, because they cover larger portions of the land surface, compared to the fluvial terraces, which only contribute 5% of the regional C stock. Geopedologic mapping is therefore a low-cost strategy to improve regional C stocks assessments.

5. Conclusions

In the Lacandon tropical rainforest, ABG-C and SOC stocks are the biggest C stocks compared to litter and BGB-C stocks. Although we did not consider the wood density of tree species, which is an important predictive variable to assess the AGB (Chave et al., 2005), delineating geopedologic land units allowed us to identify significant relationships between AGB-C stocks and tree community attributes as well as soil properties. The assessment of AGB-C stocks by structural attributes of tropical forest has the advantage that the latter can easily be measured in the field by local communities or evaluated using remote sensing techniques (Poorter et al., 2015), but if the tree diameter or the number of trees are the only attributes used to assess C stocks, the forest C stock will be underestimated by 22 to 46%.

AGB of large trees ($>$ 50 cm dbh) contributed 37 to 75% to AGB-C stocks. However, in limestone mountains trees with dbh of 20–50 cm contributed 41% to AGB, and in low hills the same dbh size trees, contributed 50% to AGB. Therefore, if resources are scarce, sampling efforts to assess AGB-C stocks should concentrate on trees with dbh $\geq$ 20 cm to record ~90% of the AGB.

At the landscape scale, C stock assessment can be further improved if ABG determinations are performed considering differences in site quality. Fluvial terraces had a much larger AGB-C stock than the other two land units, but covered a much smaller area. The forest C stock of the region can easily be overestimated since fluvial terraces are much more accessible than the other land units. A stratified sampling scheme based on geopedologic mapping taking into account the area and the soil constraints for tree growth within each major map unit is recommended, with consideration of SOC stock to maximum profile depth.

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Appendix A

Loadings of the soil properties that determine the first two axes of the PCA. Significance levels are based on a Pearson's correlation between soil properties and PCA axes: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Soil properties	All units	
	Axis1	Axis2
Rooting depth (dm)	0.884**	-0.27^{ns}
SOC (Mg ha^{-1})	0.309^{ns}	0.332^{ns}
TN (Mg ha^{-1})	0.788*	-0.453^{ns}
Extractable P (mg kg^{-1})	0.029^{ns}	-0.485^{ns}
CEC ($cmol_c$ kg^{-1})	-0.442^{ns}	−0.857**
Ca (mol m^2)	0.814**	-0.473^{ns}
Mg (mol m^2)	0.841**	-0.314^{ns}
K (mol m^2)	0.967**	0.000^{ns}
Field Capacity (L m^{-2})	0.958**	-0.168^{ns}
Available water holding capacity (L m^{-2})	0.978**	-0.106^{ns}
Stoniness (vol%)	-0.579^{ns}	−0.705*
Al saturation (%)	-0.278^{ns}	0.885**
pH (water)	0.108^{ns}	−0.975**
Aeration capacity (vol%)	-0.387^{ns}	−0.826**
Bulk density (kg dm^{-3})	0.777*	0.475^{ns}
Sand (%)	0.596^{ns}	0.519^{ns}
Silt (%)	0.496^{ns}	-0.318^{ns}
Clay (%)	−0.766*	-0.194^{ns}
Cumulative percentage of explained variance (%)	45.76	75.03

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2017.10.023.

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