

Age-related and stand-wise estimates of carbon stocks and sequestration in the aboveground coarse wood biomass of wetland forests in the northern Pantanal, Brazil

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Abstract. In this study we use allometric models combined with tree ring analysis to estimate carbon stocks and sequestration in the aboveground coarse wood biomass (AGWB) of wetland forests in the Pantanal, located in central South America. In four 1-ha plots in stands characterized by the pioneer tree species *Vochysia divergens* Pohl (Vochysiaceae) forest inventories (trees ≥ 10 cm diameter at breast height, D) have been performed and converted to estimates of AGWB by two allometric models using three independent parameters (D , tree height H and wood density ρ). We perform a propagation of measurement errors to estimate uncertainties in the estimates of AGWB. Carbon stocks of AGWB vary from 7.8 ± 1.5 to 97.2 ± 14.4 Mg C ha⁻¹ between the four stands. From models relating tree ages determined by dendrochronological techniques to C-stocks in AGWB we derived estimates for C-sequestration which differs from 0.50 ± 0.03 to 3.34 ± 0.31 Mg C ha⁻¹ yr⁻¹. Maps based on geostatistic techniques indicate the heterogeneous spatial distribution of tree ages and C-stocks of the four studied stands. This distribution is the result of forest dynamics due to the colonizing and retreating of *V. divergens* and other species associated with pluriannual wet and dry episodes in the Pantanal, respectively. Such information is essential for the management of the cultural landscape of the Pantanal wetlands.

1 Introduction

The aboveground coarse wood biomass (AGWB) of tropical forests is a dynamic carbon pool and plays an important role in the global carbon cycle (Malhi et al., 2004). In areas undergoing deforestation AGWB is also a source of carbon emission to the atmosphere (Houghton et al., 2000). Deforestation, especially in tropical countries, contributes substantially to increasing greenhouse gas concentrations in the atmosphere (IPCC, 2007). In this context the United Nations collaborative initiative on reducing emissions from deforestation and forest degradation (REDD) in developing countries is an effort to mitigate global warming. The REDD+ goes beyond deforestation and forest degradation, and includes the role of conservation, sustainable management of intact forests and enhancement of forest carbon stocks to create a monetary value for carbon stored in forests. But uncertainties still remain in the absolute magnitude of AGWB and carbon sequestration in different tropical forest ecosystems. There is also controversial discussion over how the carbon pools will react to changing environmental factors such as increased CO₂ concentrations in the atmosphere and shifting patterns in precipitation (Ometto et al., 2005; Lloyd et al., 2007) driven by large-scale climate variations such as sea surface temperature (SST) anomalies in the tropical ocean sectors.

Generally C-sequestration in the AGWB of tropical forests is estimated by repeated diameter measurements from different censuses in permanent sample plots, as for instance, within the RAINFOR program (Amazon Forest Inventory



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Network) (Peacock et al., 2007). However, repeated diameter measurements often present problems of a different nature such as buttresses and other bole deformations which can cause errors in the determination of diameter increment rates (Chave et al., 2004). Other well-known problems are “negative” diameter increment rates between two censuses which by definition do not exist, save as the result of bark shedding or dehydration causing a shrinking of bark and sapwood. Tree ring analysis (dendrochronology) produces annual diameter increments by retrospective analysis over the whole lifespan of a tree. In this study we estimate the changes in AGWB using tree rings which are annually formed in the wood of Pantanal’s tree species as a consequence of seasonal rainfall (Ishii, 1998; Mattos, 1999; Arruda, 2006; Fortes, 2006) in combination with two allometric models.

The Pantanal is one of the largest wetlands in the world, but increases in deforestation for the establishment of cultivated pastures and agriculture lands endanger its ecosystems (Silva et al., 1999; Seidl et al., 2001). Rivers periodically flood the Pantanal as a result of the seasonal precipitation regime in their watersheds (Nunes da Cunha and Junk, 2004). Wetland forests in the Pantanal establish at elevations up to 3 m above the mean water level and consist of different species compositions depending on the flood and drought tolerance of the tree species and soil conditions (Nunes da Cunha and Junk, 2001, 2004; Arieira et al., 2011). The different forest types cover 30 % of the total area and have crucial functions in this unique wetland ecosystem as habitats for a large number of plant and animal species, and as biogeochemical sinks and sources (Silva et al., 1999; Nunes da Cunha et al., 2004). However, their function in the biogeochemical cycle as C-stockers and C-sequesters is unknown. Such data are fundamental to develop plans for conservation and sustainable management of natural resources and cultural landscapes. Estimations of AGWB for forests in the Pantanal so far are based on estimations for single tree species (Haase and Haase, 1995; Salis et al., 2006). Despite the fact that former studies in the Pantanal have contributed substantially in developing allometric equations for biomass estimations, they do not provide estimations for C-stocks in AGWB and the forest’s productivity in terms of C-sequestration.

In this study we analyze the structure of four stands with a high abundance of the pioneer species *Vochysia divergens* Pohl (Vochysiaceae) (Brazilian name: “cambará”) and other associated tree species in the understory. We estimate C-stocks of the AGWB using two allometric models with three independent predictors. We determine tree ages and diameter increment rates of *V. divergens* and other species by tree-ring analyses. Combining the changes in the C-stock of AGWB using the current diameter increment rates provides an estimate of the annual C-sequestration rates in AGWB. Using geostatistical techniques we illustrate the spatial distribution of tree ages and C-stocks and discuss forest dynamics related to the occurrence of wet and dry episodes.

2 Material and methods

2.1 Study area

The field study was carried out in the northern Pantanal of the Brazilian state Mato Grosso located in the center of South America (16–22° S; 55–58° W) (Fig. 1). The study site is the SESC Pantanal Ecological Station located in the vicinity of the northern limit of the Particular Reserve of Natural Patrimony (PRNP), close to the Cuiabá River (Arieira and Nunes da Cunha, 2006). Mean annual rainfall in the region varies between 1100–1200 mm and shows a distinct seasonality as a result of the rainy season from October to April and the dry season from May to September with mean temperatures of 23 and 26 °C in the rainy and dry seasons, respectively (Hasenack et al., 2003). The flood pattern in the northern Pantanal is strongly influenced by the local precipitation and maximum flood levels occur during January and February, synchronously with the rainy season (Nunes da Cunha and Junk, 2001, 2004).

About 32 % of the forest cover in the northern Pantanal is monodominant forest characterized by the tree species *V. divergens*, a light demanding, flood adapted pioneer tree species reaching up to 25 m in height and more than 80 cm in diameter (Nunes da Cunha and Junk, 2004; Lorenzi, 2002; Arieira et al., 2011). This species invades open areas of the Pantanal developing almost monospecific stands, locally called “cambarazal” (Pott, 1982; Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006) with preference for medium and long-term flooded sites with a flood duration between two to four months (Arieira et al., 2011). *Vochysia* is brevi-deciduous remaining leafless for a short period (Schöngart et al., 2002) after shedding its leaves between April and July at the beginning of the dry season (Nunes da Cunha and Junk, 2004), which results in the formation of annual tree rings (Ishii, 1998; Fortes, 2006). This allows the application of tree ring analysis to determine ages and diameter increment rates for this and also many other associated tree species in Pantanal’s wetland forests (Ishii, 1998; Mattos, 1999; Arruda, 2006; Fortes, 2006). Tree growth and colonization of *V. divergens* and other tree species is sensitive to interannual rainfall variability (Mattos, 1999; Fortes, 2006) and consequently this species responds to decadal rainfall variability by invading open areas during wet episodes and retreating during dry episodes such as in the beginning of the 1960s (Nunes da Cunha and Junk, 2004), thus creating a patchwork of different successional stages. The tree species has relatively high diameter increment rates of about 7 mm yr⁻¹ at stand ages of 25–66 yr in the southern Pantanal (Ishii, 1998). The *Vochysia* stands stock on gley soils characterized by a bluish-gray color resulting from iron reduction (Fortunatti and Couto, 2004).

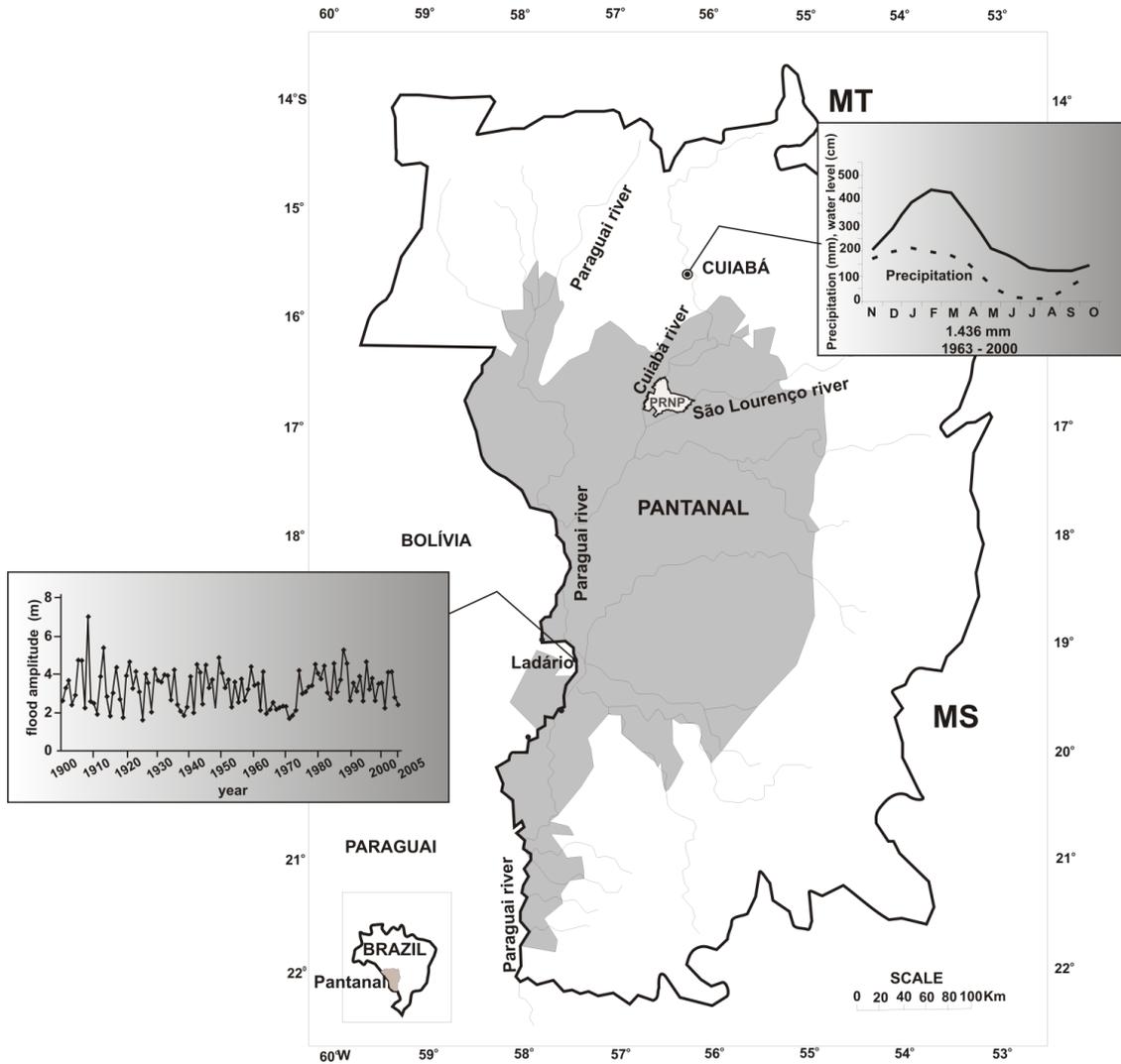


Fig. 1. Overview of the study site in N-Pantanal (SESC Pantanal Ecological Station) of Brazil. The inset figures indicate the seasonality in rainfall (city of Cuiabá) and water level fluctuations (Cuiabá River) as well as the interannual variation of the amplitude of the Paraguay River at the hydrological station in Ladário (data: ANA/GEF/PNUMA/OEA).

2.2 Field measurements

Four 1-ha plots were established in stands containing *V. divergens*, in different positions along the flood gradient (Arieira and Nunes da Cunha, 2006) which are annually inundated by an average water column of 0.72–1.79 m (Table 1). Each plot was divided into 100 quadratic units of 10 × 10 m. The stands represent different successional stages with different population structures of *V. divergens* as the result of the variability in hydro-geomorphologic conditions but also land use history (Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006). In all plots we measured diameter at breast height (*D*) 130 cm above the ground with a diameter tape. From 75–91 % of all individuals in the stands, total tree height (*H*) was measured with a Blume Leiss BL 6

(Zeiss, Jena). Sterile and fertile botanical material was collected from the tree species and identified in the Herbarium of the Federal University of Mato Grosso (UFMT).

2.3 Estimation of C-stocks in AGWB

The application of the appropriate allometric equation for biomass estimations is of crucial importance for reducing errors (Ketterings et al., 2001; Chave et al., 2004). Estimations of AGWB in the Pantanal have been performed by species-specific allometric models using *D* alone as the predictor (Haase and Haase, 1995; Salis et al., 2006). However, such models have error biases, if they are applied to estimate the AGWB of forest composed by other tree species, because they have considerably varying tree heights, wood densities,

Table 1. Stand parameters of trees ≥ 10 cm D in four 1-ha stands in the Pantanal (s.d.: standard deviation). Numbers in brackets indicate relative numbers for *V. divergens*.

Parameter	Unit	Stand 1	Stand 4	Stand 2	Stand 3
Mean flood height	m	0.72 \pm 0.28	1.13 \pm 0.16	1.46 \pm 0.27	1.79 \pm 0.15
Tree density	trees ha ⁻¹	126 (4.0 %)	446 (84.3 %)	251 (47.0 %)	256 (54.3 %)
Tree species	spp. ha ⁻¹	22	12	9	15
Mean $D \pm$ s.d.	cm	18.8 \pm 7.6	36.1 \pm 11.4	32.0 \pm 15.7	38.3 \pm 20.0
Range of D	cm	10.2–43.0	10.2–73.8	10.5–78.9	10.2–88.2
Mean $H \pm$ s.d.	m	8.0 \pm 3.1	15.8 \pm 6.7	16.6 \pm 6.5	17.0 \pm 6.5
Range of H	m	2.1–17.2	1.7–25.9	2.3–29.0	3.0–28.8
Basal area	m ² ha ⁻¹	4.1 (7.3 %)	28.3 (91.0 %)	25.1 (79.4 %)	37.5 (86.6 %)

Table 2. Wood density ρ and mean diameter increment (MDI) rates of characteristic tree species in the Pantanal (Arruda, 2006).

Tree species	N (ρ /MDI)	ρ (g cm ⁻³)	MDI (mm)
<i>Albizia polyantha</i> (Spreng. F.) Lewis (Fabaceae)	0/4	–	5.4 \pm 1.5
<i>Alchornea discolor</i> Poepp. (Euphorbiaceae)	2/3	0.34 \pm 0.04	7.7 \pm 6.5
<i>Byrsonima orbignyana</i> A. Juss. (Malpighiaceae)	2/3	0.47 \pm 0.01	5.0 \pm 1.7
<i>Cecropia pachystachya</i> Trécul (Urticaceae)	3/3	0.30 \pm 0.07	14.0 \pm 6.5
<i>Couepia uiti</i> (Mart. & Zucc.) Benth. ex Hook. f. (Chrysobalanaceae)	3/3	0.44 \pm 0.02	8.5 \pm 4.3
<i>Coccoloba ochreolata</i> Wedd. (Polygonaceae)	5/7	0.59 \pm 0.04	4.4 \pm 1.2
<i>Duroia duckei</i> Huber (Rubiaceae)	2/4	0.52 \pm 0.01	5.2 \pm 2.8
<i>Garcinia brasiliensis</i> (Mart.) Planch. & Triana (Clusiaceae)	2/0	0.64 \pm 0.05	–
<i>Mabea paniculata</i> Spruce ex Benth. (Euphorbiaceae)	1/3	0.56	6.1 \pm 0.8
<i>Mouriri guianensis</i> Aubl. (Melastomataceae)	4/5	0.60 \pm 0.06	4.5 \pm 2.0
<i>Ocotea longifolia</i> Kunth (Lauraceae)	6/5	0.47 \pm 0.05	5.8 \pm 1.9
<i>Sapium obovatum</i> Kl. (Euphorbiaceae)	5/5	0.29 \pm 0.09	7.2 \pm 3.2
<i>Vochysia divergens</i> Pohl (Vochysiaceae)	17/26	0.40 \pm 0.08	7.9 \pm 2.8
Other species	81/76	0.48 \pm 0.14	5.7 \pm 3.2
Mean	133/136	0.47 \pm 0.13	6.3 \pm 3.5

and crown architectures depending on the climatic, hydrologic and edaphic conditions and the stand age (successional stage) (Worbes et al., 1992; Chave et al., 2004, 2005). The species-specific allometric models of Salis et al. (2006) estimate AGWB by D for tree species which do not occur in our studied stands and are thus not useful for this study. Haase and Haase (1995) develop an allometric equation for *V. divergens* to estimate dry weight by D . This model was calibrated using 14 trees with diameters from 2 to 46 cm. However, the authors recommend not using the model for trees out of this diameter range.

An important parameter for the AGWB estimation is wood specific density (ρ , in g cm⁻³), which can vary considerably between tree species even in the same stand (Fearnside, 1997; Baker et al., 2004; Nogueira et al., 2005; Wittmann et al., 2006, 2008; Schöngart et al., 2010). From 48 characteristic tree species of the Pantanal comprising 130 samples (cores and stem disks), ρ was calculated by the dry/fresh volume ratio after measuring the fresh volume in the field and

drying the sample for 72 h at 105 °C (Schöngart et al., 2005). With this data set (Arruda, 2006) we estimated ρ for 67–98 % of the individuals in the four stands. For another 4–31 % of the individuals we used published data for the mean values and standard deviations of ρ (Loureiro et al., 1979; Worbes et al., 1992; Fearnside, 1997; Ter Steege, 2001; Schöngart, 2003; Baker et al., 2004; Wittmann et al., 2006, 2008; Chave et al., 2009). For the remaining trees (<1.6 % of all individuals) we estimated ρ by using the mean value of the analyzed tree species (Table 2).

Many estimates of AGWB in tropical forests are based on D alone as the independent parameter (e.g. Chambers et al., 2001) or at least a combination of D and ρ (e.g. Malhi et al., 2004). Some allometric models include H as an additional parameter (Brown et al., 1989; Chave et al., 2005). However, H is rarely used to estimate AGWB due to difficulties of measuring this parameter in the complex vertical structure of tropical forests (Feldpausch et al., 2011). Chave et al. (2005) indicate that the most reliable estimate of C-stocks

and consequently C-sequestration is achieved by allometric models which use, in decreasing order of importance, D , ρ and H as predictors. The authors suggest that the integration of H reduces the standard error of AGWB estimates by about 7%. For this reason we incorporate tree height for our estimates of AGWB. Tree height was measured for 75–91% of all individuals in a stand. This was possible since the studied wetland forests do not have a complex vertical structure. To avoid errors, height was not measured from strongly inclined trees or when the visibility of the tree crown was limited. From those remaining trees we estimated height by a non-linear regression model between D (in cm) and measured H (in m). One species-specific relationship was computed for *V. divergens*, the other species were pooled and a common second relationship was determined, both using a logarithmic equation:

$$H = a + b \ln(D) \quad (1)$$

To evaluate uncertainties due to the choice of the model (Chave et al., 2004), we selected two published allometric models which have been developed outside the biogeographic region using pan-tropical equations (Cannell, 1984; Chave et al., 2005). Both models transform D , ρ and H into estimates of AGWB. Cannell (1984) suggested that the AGWB of a tree corresponds to the product of the trunk basal area ($BA = \pi D^2/4$), ρ , total tree height (H) and a constant form factor ($F = 0.06$) assuming the taper does not change as the trees become larger:

$$AGWB_1 = F \cdot \rho \cdot H \cdot \pi \cdot (D/2)^2 \quad (2)$$

Chave et al. (2005) developed allometric models based on a large data set from the tropics to estimate AGWB for different forest types. For forests with a distinct dry season (rainfall below 1500 mm per year, and a 5 month dry season), they suggested transforming forest inventory data into estimates of AGWB by the equation:

$$AGWB_2 = a \cdot (\rho \cdot H \cdot D^2)^b \quad (3)$$

The coefficients of Eq. (3) are $a = 0.112$ and $b = 0.916$. The units of the parameters used in Eqs. (2) and (3) were: AGWB in kilogram, ρ in gram per cubic centimeter, H in meter and D in centimeter. Using Eqs. (2)–(3) we estimated AGWB for every tree in stands 1–4 and took the sum for the total AGWB of a stand (in Megagram $Mg \text{ ha}^{-1}$).

Estimates of AGWB based on inventory data contain uncertainties such as measurement errors of D , H , and ρ , and errors caused by the choice of an allometric model and plot size (Chave et al., 2004). In this study we perform a propagation of measurement errors (Drosg, 2009) which influences the estimates of AGWB. Although the tree species in the studied stands do not have buttresses, measurement errors of D frequently occur. We assume for the error propagation an uncertainty of 1% in the measured diameter and denote this error as σ_D . Height measurements normally are difficult to perform in the complex vertical structure of tropical

forests (Feldpausch et al., 2011), although the studied wetland forests present a quite simple vertical structure and tree heights are below 30 m. For the error propagation we assume a measurement error σ_H of 10% (Chave et al., 2004). To address uncertainties in the determination of ρ we use the standard deviation of species-specific ρ to estimate the related error σ_ρ (for those tree species without information for ρ we apply the standard deviation of the mean ρ from all analyzed species to estimate σ_ρ). As Eq. (2) uses a constant form factor F we address an error of 10% for this parameter ($\sigma_F = 0.006$). The propagation of measurement errors σ_F , σ_D , σ_H and σ_ρ to estimate AGWB is performed for every single tree using the following equation:

$$\sigma_{AGWB(1)}^2 = (\pi/4)^2 \cdot \left[(\sigma_F \cdot D^2 \cdot H \cdot \rho)^2 + (\sigma_D \cdot F \cdot 2D \cdot H \cdot \rho)^2 + (\sigma_H \cdot F \cdot D^2 \cdot \rho)^2 + (\sigma_\rho \cdot F \cdot D^2 \cdot H)^2 \right] \quad (4)$$

For Eq. (3) we apply the following equation to propagate measurement errors in the estimate for all trees:

$$\sigma_{AGWB(2)}^2 = (a \cdot b \cdot (D^2 \cdot \rho \cdot H)^{(b-1)})^2 \cdot \left[(\sigma_D \cdot H \cdot \rho \cdot 2D)^2 + (\sigma_H \cdot D^2 \cdot \rho)^2 + (\sigma_\rho \cdot D^2 \cdot H)^2 \right] \quad (5)$$

We calculated the relative contribution of each error in Eqs. (4) and (5) in form of percentages differentiating between trees of *V. divergens* and other species. We then calculate separately for each model, the sum of these errors which results by simple addition of variances:

$$\sigma_{AGWB(1)} = (\sum(\sigma_{AGWB(1)}^2))^{0.5} \text{ and } \sigma_{AGWB(2)} = (\sum(\sigma_{AGWB(2)}^2))^{0.5} \quad (6)$$

In the next step we calculate the mean AGWB and the new variance from Eqs. (2)–(3) to consider errors due to the choice of an allometric model:

$$\sigma_{AGWB(\text{mean})}^2 = (\sigma_{AGWB(1)}^2 + \sigma_{AGWB(2)}^2) \cdot 0.25 \quad (7)$$

Commonly carbon content is estimated as being 50% of the AGWB (Clark et al., 2001; Malhi et al., 2004). Elias and Potvin (2003) determined from 32 tropical tree species of Central Panama a lower wood carbon content ranging from 44.4 to 49.4%. They found a strong relationship between ρ and C-content from different tree species. We assume that C-content of AGWB from Pantanal's wetland forests also correlates with ρ and transform the linear regression model of Elias and Potvin (2003) to estimate C-content using ρ (g cm^{-3}) for the wetland tree species using the following equation:

$$C (\%) = (\rho + 16.21)/0.3732 \quad (8)$$

Multiplying the C-content with AGWB produces an estimate for its C-stock and takes into consideration the variances.

2.4 Tree ring analysis and estimation of C-sequestration in AGWB

In the surroundings of the PRNP stem disks were collected with a chainsaw at 130 cm height between August 2004 and September 2005. The samples included 26 trees of *V. divergens* (Fortes, 2006) and 108 trees of 57 other common wetland tree species (Arruda, 2006). The wood samples were analyzed in the dendroecological laboratory at the National Institute for Amazon Research (INPA) in Manaus, using standard dendrochronological procedures (Pilcher, 1990). Samples were progressively sanded to analyze the tree ring structure macroscopically by wood anatomical features characterized by density variations (e.g. Annonaceae, Lauraceae, Myrtaceae), marginal parenchyma bands (e.g. Fabaceae sensu lato), alternating fiber and parenchyma tissues (e.g. Sapotaceae, Moraceae, Lecythidaceae) or rarely, by variations in the vessel size and distribution (Worbes, 2002). Ring width was measured for trees from *V. divergens* to the nearest 0.01 mm using a digital measuring device (LINTAB, RINNTECH, Inc.) supported by the software TSAP (Time Series Analyses and Presentation).

Tree age, determined by ring counting, was related to D to produce one model for *V. divergens* and a second model for the other associated tree species fitting the age-diameter relationship to a non-linear (sigmoidal) regression (Schöngart et al., 2007, 2010):

$$D = a / (1 + b \cdot \text{age}^{-c}) \quad (9)$$

From these two models we derived the current (annual) diameter increment (CDI, in cm) for *V. divergens* and other tree species as being the difference in D from year to year (t) by the following equation:

$$\text{CDI} = D_{(t)} - D_{(t-1)} \quad (10)$$

We relate tree age from those trees analyzed by dendrochronological methods to their estimated C-stocks in AGWB (considering the propagation of measurement errors) using a sigmoidal regression model. One model is produced for *V. divergens*; the other tree species are pooled to produce a second model:

$$\text{C-stock} = a / (1 + b \cdot \text{age}^{-c}) \quad (11)$$

From these regression models we derive C-sequestration in AGWB (kg C yr^{-1}) for *V. divergens* and for other tree species calculating the difference of the C-stock between consecutive years (t) along the whole life span:

$$\text{C-sequestration} = \text{C-stock}_{(t)} - \text{C-stock}_{(t-1)} \quad (12)$$

Based on a total of 134 trees with determined ages, we develop a linear multiple regression model to predict age by D (cm) and ρ (g cm^{-3}):

$$\text{Age} = a + b \cdot D + c \cdot \rho \quad (13)$$

Using Eq. (13) we estimate for all individuals in stands 1–4 tree age. To estimate C-sequestration we calculate in the next step the differences in C-stock of AGWB for the year of stand inventory (t) and the year before ($t - 1$) using Eqs. (2) and (3). To do that, we subtracted the CDI from D and then reduced H by the specific diameter-height relationship of Eq. (1). The variance of C-sequestration of a tree is estimated by the difference of the variances from the C-stocks in AGWB calculated using Eqs. (4) and (5) as well as a mean value calculated using Eq. (7). The sum of the individual variances yields an estimate for the uncertainties in the C-sequestration of a stand.

Growth modeling was performed with the software program X-Act 7.0 (SciLab) and Statistica 6.0.

2.5 Mapping C-stocks and tree age

Maps for the spatial distribution of ages and carbon stocks from all trees in each stand were produced using two geostatistic techniques: (1) variogram analysis and (2) simple kriging (Arieira et al., 2011). Variogram analysis was applied to derive information on the spatial data structure (Wagner and Fortin, 2005). Kriging is a spatial interpolation technique for producing estimates at unobserved locations by a weighted average of nearby samples (Miller et al., 2007). Sample variograms were estimated and variogram models fitted to the 100 quadratic units of each 1-ha plot. Different variogram models (spherical, Gaussian, and exponential) were tested and the most reliable model was chosen based on the best adjustment between observed and predicted data evaluated by cross-validation. The ratio of nugget (Co) variance to total variance ($\text{Co} + \text{C}$) was calculated for each variogram to evaluate which proportion of the variance resulted from spatially structured variance and random factors. Considering the spatial correlation of data provided by the variograms, kriging was performed resulting in grid maps with cell size of 0.4×0.4 m. We applied variogram analysis and kriging using Gama Design Software, version 3.1.7. The resulting kriged maps were edited in Surfer Software, version 7.0.

3 Results

Tree density in the four studied stands varied between 126–446 individuals ha^{-1} comprising 9–22 tree species ha^{-1} (≥ 10 cm D) (Table 1). The relative abundance of *V. divergens* differed considerably between the studied stands ranging from 4 % (stand 1), 47 % (stand 2), 54 % (stand 3) to 84 % (stand 4). Mean D was 18.8 cm in stand 1, the other three stands had a much higher average D between 32.0 and 38.3 cm. The mean H (8.0 m) in stand 1 was two times lower than in the stands 2–4 (15.8–17.0 m). Basal area varied between $4.1 \text{ m}^2 \text{ ha}^{-1}$ in stand 1 and $37.5 \text{ m}^2 \text{ ha}^{-1}$ in stand 3. Due to the high relative abundance of *V. divergens* in stands 2–4, this species comprised 79–91 % of the stand's basal

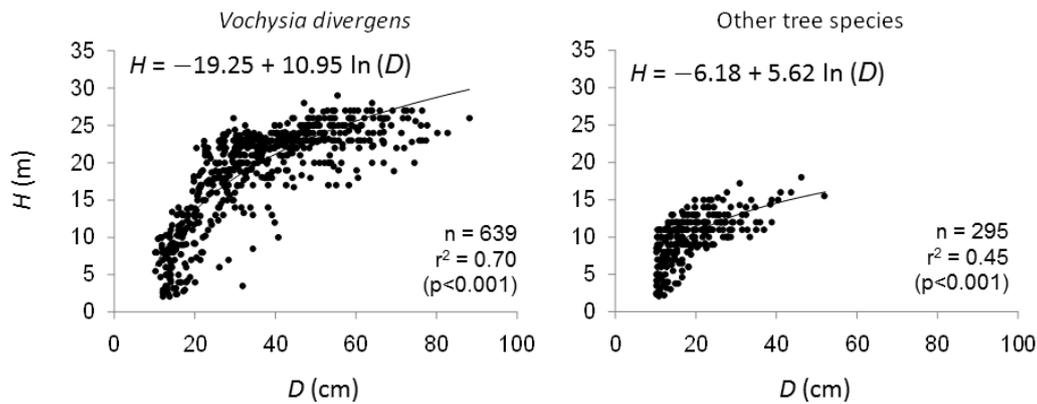


Fig. 2. Non-linear relationships between diameter at breast height, D , and tree height, H , from *Vochysia divergens* and other tree species from northern Pantanal wetland forests.

area, while in stand 1 *V. divergens* only achieved 7% of the total basal area. *V. divergens* had a relatively low ρ of $0.40 \pm 0.08 \text{ g cm}^{-3}$ (Table 2). Mean diameter increment rate (MDI), calculated by the ratio D and tree age determined by tree ring analysis (Arruda, 2006; Fortes, 2006), was $7.9 \pm 2.8 \text{ mm yr}^{-1}$ for *V. divergens*. The MDI of all species was $6.3 \pm 3.5 \text{ mm yr}^{-1}$ (Table 2). Wood density and MDIs were inversely correlated ($n = 105$; $r = -0.44$; $p < 0.001$).

To estimate the AGWB, we applied Eqs. (2)–(3) using D , ρ and H as independent variables (predictors). For those trees with missing tree heights we estimated H by the specific diameter-height relationship of Eq. (1), explaining between 70% (*V. divergens*) and 45% (other tree species) of the variability between the two parameters (Fig. 2). Equations (2)–(3) yielded for the same stand similar estimates for AGWB (Table 3). The mean value of AGWB calculated by Eqs. (2) and (3) indicated the lowest AGWB of $17.4 \pm 3.3 \text{ Mg ha}^{-1}$ for stand 1. For stands 4 and 2 estimated AGWB was similar with $137.3 \pm 19.7 \text{ Mg ha}^{-1}$ and $136.3 \pm 19.8 \text{ Mg ha}^{-1}$, respectively. The highest AGWB was predicted for stand 3 with $218.1 \pm 32.2 \text{ Mg ha}^{-1}$. Estimates for the C-content of AGWB by applying Eq. (7) varied from 44.6 to 44.9% and yielded C-stocks of $7.8 \pm 1.5 \text{ Mg C ha}^{-1}$ (stand 1), $63.3 \pm 8.8 \text{ Mg C ha}^{-1}$ (stand 4), $60.8 \pm 8.8 \text{ Mg C ha}^{-1}$ (stand 2) and $97.2 \pm 14.4 \text{ Mg C ha}^{-1}$ (stand 3).

The propagation of measurement errors in the prediction of AGWB was higher for the estimates calculated with Eq. (2) compared to Eq. (3) (Table 4). The uncertainties in the estimate of AGWB for *V. divergens* were 20.8% in Eq. (2) and 16.7% in Eq. (3). For the other species the calculated measurement errors were $19.2 \pm 6.2\%$ in Eq. (2) and $14.7 \pm 6.4\%$ in Eq. (3). Calculating the mean value of AGWB from Eqs. (2)–(3) reduced the uncertainties to $10.9 \pm 2.0\%$ for *V. divergens* and $10.6 \pm 5.1\%$ for other tree species. The uncertainties in the estimate of AGWB for *V. divergens* applying Eq. (2) was 52.8% from σ_ρ , while σ_F

and σ_H shared equally with 23.1% to the variance. The contribution of σ_H and σ_ρ to the variance of Eq. (3) was 30.1% and 68.7% for *V. divergens*, respectively (Table 4). For the estimate of AGWB for the other tree species, applying Eq. (2), σ_ρ contributed with $31.4 \pm 30.2\%$ (s.d.) to the variance, while $33.6 \pm 14.8\%$ was explained by σ_F and σ_H . The variance for the estimates of AGWB using Eq. (3) was shared by σ_H ($58.2 \pm 34.1\%$) and σ_ρ ($39.5 \pm 35.5\%$). If no information for ρ was available for a tree ($< 1.6\%$ of all individuals), σ_ρ became a major source of error contributing up to 90% to uncertainties in AGWB estimates. Uncertainties regarding the diameter measurements (assuming a measurement error of 1%) were negligible in Eqs. (2) and (3).

Tree age and D of *V. divergens* ($n = 26$; $r^2 = 0.94$; $p < 0.0001$) and other tree species ($n = 108$; $r^2 = 0.74$, $p < 0.0001$) correlated significantly (Fig. 3). We also found a close relationship between age and accumulated C-stock in AGWB of *V. divergens* and other tree species (Fig. 4). Maximum C-sequestration in AGWB of *V. divergens* occurred at an age of 80 yr, and for the other tree species at an age of 76 yr. The pioneer species *V. divergens* had higher productivity than the other associated tree species from the understory which can be traced back to lower irradiance in the sub-canopy. Based on the significant relationships between ρ and MDI as well as tree age and D we developed a multiple regression model that accurately predicted tree age by wood density and D as independent parameters ($n = 117$; $r^2 = 0.93$; $p < 0.0001$) (Fig. 5). Partial regression analysis indicated that D ($\beta = 0.921$; $t = 26.68$; $p < 0.0001$) contributed more than ρ ($\beta = 0.184$; $t = 5.33$; $p < 0.0001$) to explain the variability of tree age. By Eq. (13) we calculated tree ages in stands 1–4 and estimated (minimum) stand age by the maximum tree age of a stand (Worbes et al., 1992) which varied from 64 yr (stand 1) to 124 yr (stand 3). In the next step we calculated the difference between the C-stocks in AGWB for the year of forest inventory and the year before to estimate annual C-sequestration in AGWB (Table 3). Models (2)

Table 3. Estimated AGWB, Carbon stocks and C-sequestration projected by allometric Eqs. (2)–(3) in four stands of wetland forests in the Northern Pantanal. The propagation of measurement errors is indicated by standard errors.

	Stand 1	Stand 4	Stand 2	Stand 3
Stand age (years)	64	99	108	124
	(Mg ha ⁻¹)			
Eq. (2)				
AGWB ₁	15.9	131.0	133.6	218.1
σ_{AGWB_1}	4.1	25.5	26.1	42.9
Eq. (3)				
AGWB ₂	18.8	143.3	139.1	218.1
σ_{AGWB_2}	3.9	22.4	21.6	34.1
Mean of Eqs. (2)–(3)				
AGWB _{mean}	17.4	137.3	136.3	218.1
$\sigma_{AGWB_{mean}}$	3.3	19.7	19.8	32.2
	(Mg C ha ⁻¹)			
Eq. (2)				
C-stock (AGWB ₁)	7.2	58.3	59.6	97.2
$\sigma_{C-stock_1}$	1.9	11.4	11.7	19.1
Eq. (3)				
C-stock (AGWB ₂)	8.5	68.3	62.0	97.2
$\sigma_{C-stock_2}$	1.7	10.0	9.6	15.2
Mean of Eqs. (2)–(3)				
C-stock (AGWB _{mean})	7.8	63.3	60.8	97.2
$\sigma_{C-stock_{mean}}$	1.5	8.8	8.8	14.4
	(Mg C ha ⁻¹ yr ⁻¹)			
Eq. (2)				
C-sequestration (AGWB ₁)	0.47	3.27	2.31	2.96
$\sigma_{C-sequestration_1}$	0.01	0.67	0.46	0.63
Eq. (3)				
C-sequestration (AGWB ₂)	0.52	3.42	2.27	2.80
$\sigma_{C-sequestration_2}$	0.11	0.56	0.36	0.49
Mean of Eqs. (2)–(3)				
C-sequestration (AGWB _{mean})	0.50	3.34	2.29	2.88
$\sigma_{C-sequestration_{mean}}$	0.03	0.31	0.21	0.28

and (3) indicated almost the same C-sequestration in the four studied stands. The lowest estimated mean C-sequestration in AGWB is 0.50 ± 0.03 Mg C ha⁻¹ yr⁻¹ in the 64-yr old stand 1, while stand 4 (99 yr old) presented the highest C-sequestration with 3.34 ± 0.31 Mg C ha⁻¹ yr⁻¹. For stands 2 (108 yr old) and 3 (124 yr old) the models estimated a mean C-sequestration of 2.29 ± 0.21 Mg C ha⁻¹ yr⁻¹ and 2.88 ± 0.28 Mg C ha⁻¹ yr⁻¹, respectively.

Table 4. Propagation of assumed measurement errors for converting forest inventory data (D , H , ρ , F) into estimates of AGWB using Eqs. (2) and (3) differentiated for trees of *V. divergens* and other species.

<i>Vochysia divergens</i>	Eq. (2) (AGWB ₁)	Eq. (3) (AGWB ₂)
Total error in AGWB estimate	20.8 %	16.7 %
σ_{ρ}	52.8 %	30.1 %
σ_H	23.1 %	68.7 %
σ_D	1.0 %	1.2 %
σ_F	23.1 %	–
Other tree species	Eq. (2) (AGWB ₁)	Eq. (3) (AGWB ₂)
Total error in AGWB estimate	19.2 ± 6.2 %	14.7 ± 6.4 %
σ_{ρ}	31.4 ± 30.2 %	39.5 ± 35.5 %
σ_H	33.6 ± 14.8 %	58.2 ± 34.1 %
σ_D	1.3 ± 0.6 %	2.3 ± 1.4 %
σ_F	33.6 ± 14.8 %	–

Age structure of the stands indicated that the majority of trees ($D > 10$ cm) were between 20 and 40 yr old. In the chronosequence of stands, the number of *V. divergens* individuals increased towards higher age classes (Fig. 6a). The range of spatial dependence varied mainly between the youngest stand (stand 1, from 62.1 to 85.2 m) and the older ones (stand 2, 4, 3; from 26.8 to 59.1 m) (Table 5). Variogram analysis showed that the majority of the spatial heterogeneity of tree age and C-stock results from spatial dependent ecological processes, such as dispersion. Only a small portion of the variance of these two variables might be explained by random factors, as suggested by the ratio of nugget (Co) variance to total variance (Co + C) as seen in Table 5. Random factors might pose a greater influence on the spatial heterogeneity of tree age in the initial stages of succession, when *V. divergens* individuals were colonizing open areas. The maps in Fig. 6b show the patterns of establishment of *V. divergens* over the successional development of the forest. In all stands *V. divergens* distribution exhibited a clumpy pattern with variation of patch age. The stands presented islands of older trees and areas which had been colonized during the last 40 yr (Fig. 6b). The distribution of C-stocks (Fig. 6c) indicated low C-stocks in the recently colonized areas and higher C-stocks with increasing age.

4 Discussion

In this study we show a new approach in tropical forest research for estimating C-sequestration in AGWB by means of growth models based on tree ring analysis (Schöngart et al.,

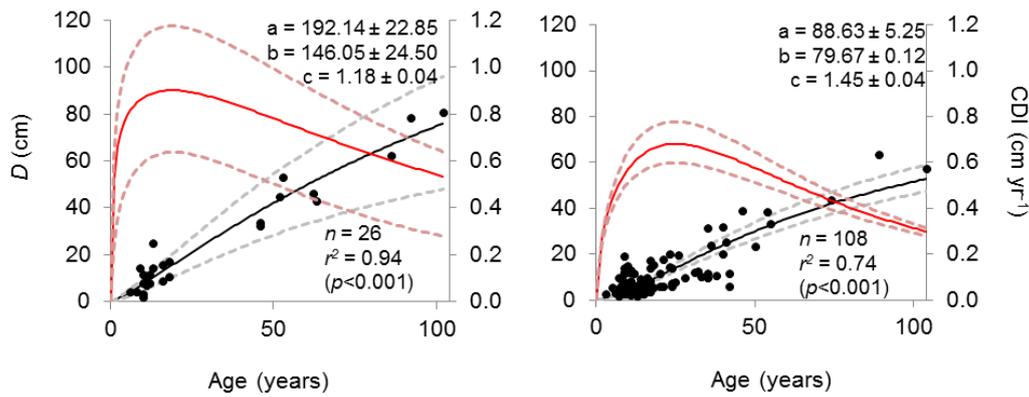


Fig. 3. Significant age-diameter relationships for *V. divergens* and other tree species. The red line indicates the annual current diameter increment (CDI). Indicated parameters are for the age-diameter relationship of Eq. (9). Standard deviation is indicated by the dotted lines.

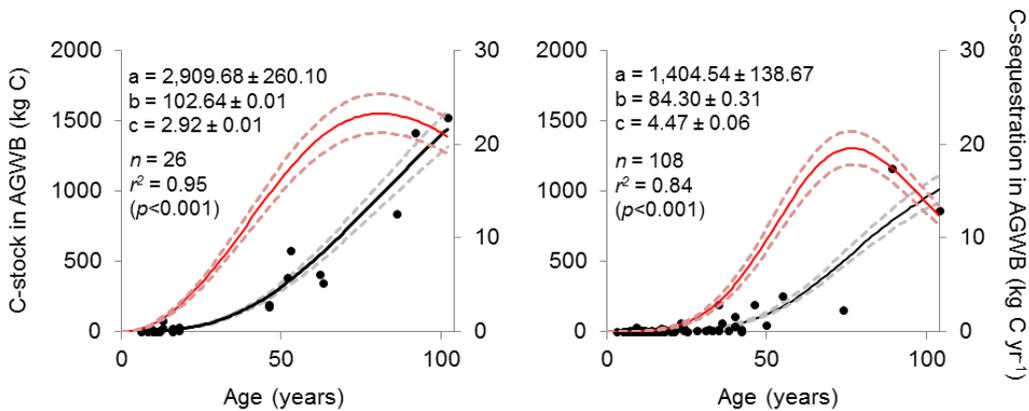


Fig. 4. C-stocks (black curve) and C-sequestration (red curve) of AGWB from *Vochysia divergens* and other tree species from northern Pantanal wetland forests related to tree ages. Indicated parameters are for Eq. (11). The dotted lines indicate the standard deviation.

2010). Ishii (1998) first indicated the occurrence of annual tree rings in the Pantanal using radiocarbon-dating and cambial wounding (windows of Mariaux). Mattos (1999) related ring width of *Tabebuia heptaphylla* successfully with precipitation patterns in the southern Pantanal. Ring width of *V. divergens* in the northern Pantanal is significantly correlated with the annual precipitation regime indicating the existence of annual tree rings for this species (Fortes, 2006). These results are congruent with many other dendrochronological studies performed in tropical regions with a seasonal precipitation regime (e.g. Jacoby and D’Arrigo, 1990; Stahle et al., 1999; Worbes, 1999; Enquist and Leffler, 2001; Fichtler et al., 2004; Brienen and Zuidema, 2005; Schöngart et al., 2006; Therrell et al., 2006; Brienen et al., 2010; Roozendaal and Zuidema, 2011). In comparison to repeated diameter measurements or permanently installed dendrometers, which yield reliable results only after several years of monitoring, dendrochronology allows an immediate estimation of C-sequestration (Schöngart et al., 2010) comprising the whole life span of a tree by retrospective analysis (Worbes, 2002).

Using a multiple regression model (Fig. 5) we predict tree age using *D* and ρ as independent parameters. Mean diameter increment correlates negatively with ρ , as is also known for tree species from the central Amazonian floodplain forests (Worbes et al., 1992; Schöngart, 2008; Schöngart et al., 2010). This can be explained by the percentage of wood anatomical features such as fiber length and fiber diameter, percentage of parenchyma and vessels as well as the incorporation of mineral salts and chemical substances in the heartwood such as terpenes, essential oils, tannins, flavonoids, aldehydes, alcohols, and colored pigments leading to different wood densities. Pioneer tree species generally have low fiber content and high vessel areas (Worbes, 1996) resulting in low wood densities, while climax tree species have high wood densities due to high fiber contents and thick cell walls with the incorporation of secondary substances and a relatively low vessel area. This relationship allows a reliable estimation of tree and stand ages for the monodominant forests formed by *V. divergens* covering a large proportion of Pantanal’s landscape (Ariera et al., 2011) and is a powerful tool for future research and also for applications in conservation,

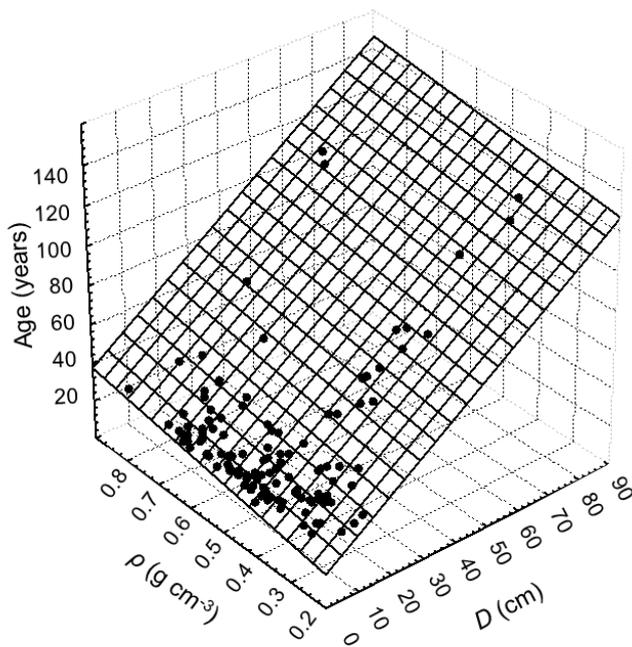


Fig. 5. Multiple regression model predicting tree age as a function of diameter, D , and wood density, ρ , developed by a data set of 117 trees of different successional stages of the wetland forests in the northern Pantanal ($\text{Age} = 8.274 + 1.2153 \cdot D + 28.405 \cdot \rho$).

forest and landscape management. Such models can also be calibrated for other forest types in the Pantanal and other tropical regions.

In this study we perform an estimate of AGWB by allometric models developed on a pan-tropical database (Cannell, 1984; Chave et al., 2005). The results of the predicted AGWB (Table 3) indicate similar values within a forest stand, since both models use three independent parameters (D , H , ρ). This suggests that allometric differences between models do play a less important role for the estimate of AGWB (Chave et al., 2005). Schöngart et al. (2010) compared seven different allometric equations using two and three independent parameters (D , H and ρ) in different combinations to transform inventory data into estimates of AGWB for different successional stages of central Amazonian floodplain forests. Equations (2) and (3) as well as another three-parameter model of Chave et al. (2005) also produced similar values of AGWB for the Amazonian floodplain forests. However, the tested models based on two parameters with different combinations (Brown et al., 1989; Malhi et al., 2004) yield considerably differing estimates of AGWB in comparison to those based on three parameters due to differences in the $H:D$ relationship and ρ between the Amazonian floodplain tree species and the species used to calibrate the allometric models. A much higher uncertainty in the prediction of AGWB comes from the assumed measurement errors, especially from σ_ρ and σ_H in Eqs. (2) and (3). Such measurement errors are rarely propagated in studies es-

timating AGWB (Chave et al., 2004). Tree height is rarely used to predict AGWB (Chave et al., 2004), but an important parameter as H and thus the $H:D$ ratio varies considerably between forest types (Schöngart et al., 2010; Feldpausch et al., 2011). If an allometric model developed outside the biogeographic region that does not consider H as predictor is applied to estimate AGWB, H can become a major source of error, when the $H:D$ relationship between the original dataset differs considerably from that of the performed inventory. The same holds for wood density which can vary more than fivefold between tropical tree species (Chave et al., 2004; Schöngart et al., 2010). Huge databases comprising wood densities for hundreds of tropical tree species exist (e.g. Chave et al., 2009), yet for many tree species in the Pantanal region ρ is still unknown.

In Table 6 we compare our estimates of C-stock and C-sequestration in AGWB with data from a riparian forest in the southern Pantanal region (Wittmann et al., 2008), different successional stages from central Amazonian floodplain forests (Worbes, 1997; Schöngart et al., 2010), and dry forests from Mexico (Vargas et al., 2008). The estimated C-stocks in AGWB of the four studied stands are lower when compared to the estimated C-stocks in a flooded riparian forest along the Miranda River in the southern Brazilian Pantanal. This riparian forest studied by Wittmann et al. (2008) has 443 individuals ($D > 10$ cm), a higher basal area of $47.8 \text{ m}^2 \text{ ha}^{-1}$ and the tree species present a higher mean ρ ($0.63 \pm 0.12 \text{ g cm}^{-3}$) which results in a higher C-stock in AGWB which the authors predicted by using Eq. (2). The floodplain forests of central Amazonia also present higher values in the C-stocks of AGWB which can be traced back to higher tree densities, tree heights, and wood densities in the floodplain forests with similar stand age. C-sequestration in AGWB is also higher in the Amazonian floodplain forests which is a result of the high nutrient status of their alluvial soils (Schöngart et al., 2010). Seasonally tropical dry forests of Mexico indicate for the 99-yr and 108-yr old stands similar C-stocks to the wetland forests of the Pantanal, however, estimated C-sequestration in AGWB is lower in the dry forests compared to the wetland forest.

The use of geostatistical techniques to map wetland vegetation is a promising tool for conservation assessment and long-term ecological monitoring in wetlands also, because detailed biological information acquired in fieldwork can be integrated in the mapping procedure (Arieira et al., 2011). The distribution of C-stocks and tree age at stand scales indicate for stands 1–4 a spatial heterogeneity with older forest islands associated with higher C-stocks and younger patches with lower C-stocks (Fig. 6). These younger areas were probably occupied by *V. divergens* after consecutive severe droughts in the 1960s (Fig. 1) (Nunes da Cunha and Junk, 2004). The understanding of such dynamical processes is essential for the development of management concepts for the cultural landscapes and natural resources of this large wetland (timber, non-wood forest products). Traditional

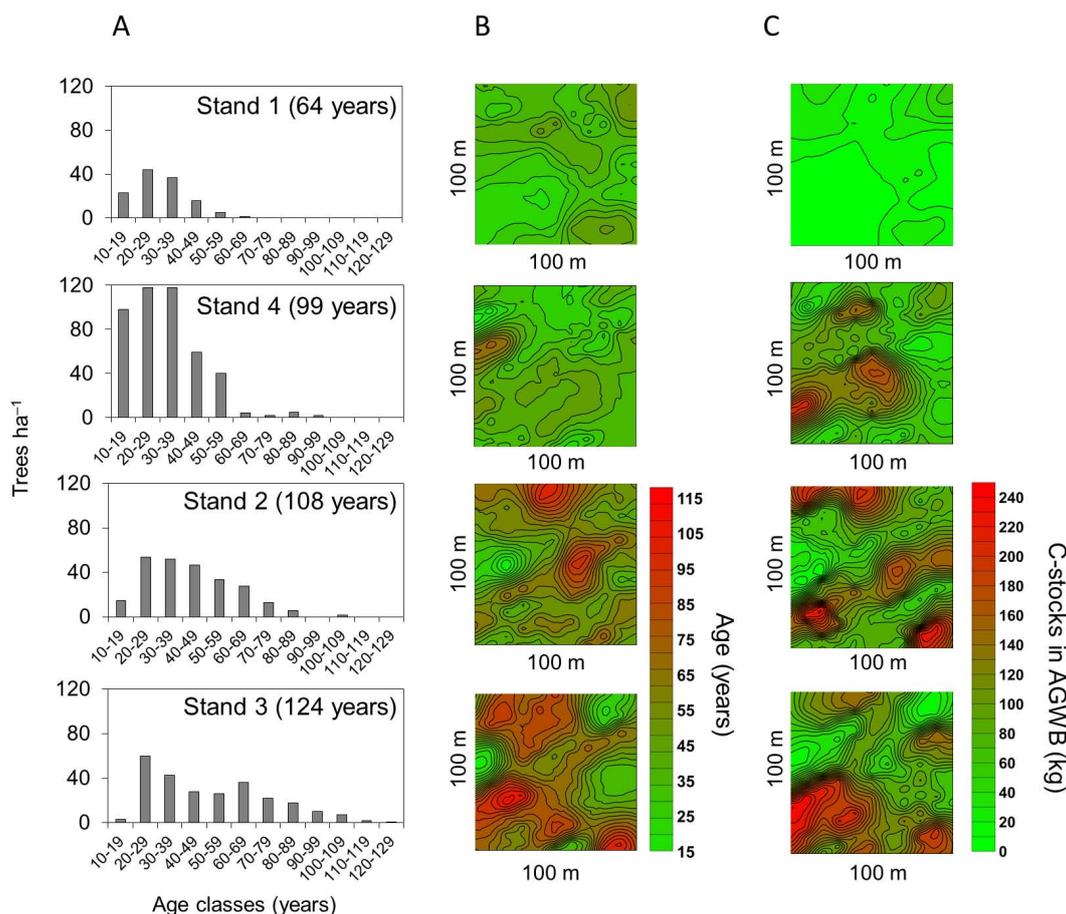


Fig. 6. (A) Age structure of the studied stands. Kriged maps indicate the spatial distribution of (B) tree age and (C) carbon stocks of the studied stands.

Table 5. Results of the variogram analysis: C_0 is the nugget effect, $C_0 + C$ is the sill representing the variance, A is range of spatial dependence, and $(C_0 \cdot 100) / C$ is the proportion of variance explained by random factors.

Plot	Variable	Model	Nugget	Sill	Range (m)	R^2	$(C_0 \cdot 100) / C$
			C_0	$C_0 + C$	A		
Stand 1	Age	Spherical	1.595	3.468	85.2	0.98	45.99
	C-Stocks	Spherical	840	15130	62.1	1	5.55
Stand 2	Age	Spherical	12.5	233.2	32.8	1	5.36
	C-Stocks	Spherical	100	265 100	28.4	0.92	0.04
Stand 3	Age	Spherical	64	458	32.5	0.99	13.97
	C-Stocks	Exponential	77 000	430 000	59.1	0.99	17.91
Stand 4	Age	Spherical	0.01	99.6	26.8	0.86	0.01
	C-Stocks	Spherical	100	188 600	37.3	0.97	0.05

conflicts in the Pantanal between private stakeholders such as farmers and environmentalists require management plans. Extensive cattle ranching is the principle economic activity in the Pantanal. Farmers consider *V. divergens* and other tree

species such as *Byrsonima orbignyana* (Malpighiaceae) and *Curatella americana* (Dilleneaceae) as invaders of their pastures (Santos et al., 2006). The dominating wet conditions during the last decades favored the progress of secondary

Table 6. Comparison of C-storage, C-sequestration and C-turnover in AGWB of successional stages in wetland forests of the northern Pantanal and floodplain forests in the central Amazonia.

Trees ($D \geq 10$ cm)	C-stock (Mg C ha ⁻¹)	C-sequestration (Mg C ha ⁻¹ yr ⁻¹)
Pantanal (This study)		
Stand 1 (stand age 64 yr)	7.8 ± 1.5	0.5
Stand 4 (stand age 99 yr)	63.3 ± 8.8	3.3 ± 0.3
Stand 2 (stand age 108 yr)	60.8 ± 8.8	2.3 ± 0.2
Stand 3 (stand age 124 yr)	97.2 ± 14.4	2.9 ± 0.3
Flooded riparian forest, Miranda River, southern Brazilian Pantanal		
Wittmann et al. (2008) (unknown age)	124.7 ¹	–
Central Amazonian floodplain forests		
Worbes (1997) (stand age 80 yr)	140.0 ¹	–
Schöngart et al. (2010) (stand age 52 yr)	117.4 ¹	7.2
Schöngart et al. (2010) (stand age 125 yr)	115.0 ¹	3.7
Seasonal dry forests, Mexico		
Vargas et al. (2008) (stand age 64 yr)	58.6 ²	1.2 ³
Vargas et al. (2008) (stand age 99 yr)	65.1 ²	1.0 ³
Vargas et al. (2008) (stand age 108 yr)	65.9 ²	1.0 ³
Vargas et al. (2008) (stand age 124 yr)	67.1 ²	0.9 ³

¹ AGWB estimated by Eq. (1), C-content estimated by 50% of AGWB.

² Calculated by a non-linear regression model (Richards Function) (C-stock = $69.1 \cdot (1 - \exp(-0.027 \cdot \text{age}))^{0.84}$) (Vargas et al., 2008).

³ Calculated by a non-linear regression model (C-sequestration = $-0.4414 \cdot \ln(\text{age}) + 3.0449$) (Vargas et al., 2008).

succession invading pastures (Junk et al., 2006) and reduced considerably the area available for cattle, which is already limited by flooding. On the other hand, the secondary succession is of ecological value since these developing forests provide environmental services such as enhancing carbon stocks, habitat for a diverse fauna and flora, regulation of microclimate and hydrological cycles (Hasenack et al., 2003; Junk et al., 2006, 2011).

Dendroclimatological studies indicate for many tropical regions such as Indonesia (Jacoby and D'Arrigo, 1990), Namibia (Fichtler et al., 2004), Central Amazonia (Schöngart et al., 2004, 2005), West Africa (Schöngart et al., 2006), Zimbabwe (Therrell et al., 2006), and Mexico (Brienen et al., 2010) significant correlations between tree growth and ocean's SSTs, which trigger regional precipitation patterns and hydrological cycles in many areas of the tropics. Growth of *V. divergens* in the N-Pantanal responds to rainfall variability (Fortes, 2006). Positive SST anomalies in the El Niño 1 + 2 region of the tropical Pacific basin (0–10° S, 80–90° W) cause significant lower rainfall in the Pantanal during the period October–December ($r = -0.39$; $p < 0.01$) resulting in reduced diameter increment rates (Fortes, 2006). If these drought episodes last for several years, as occurred during the 1960s (Fig. 1), forests of *V. divergens* die back (Nunes da Cunha and Junk, 2004), emitting large amounts of

carbon from the AGWB to the atmosphere due to the high mortality rates. On the other hand, consecutive years of wet conditions favor the invasion of *V. divergens* into open areas and due to the higher increment rates (Fortes, 2006) more carbon is sequestered in the AGWB. However, future climate scenarios (IPCC, 2007) indicate increasing SSTs in the tropical oceans, which possibly will affect C-stocks in the AGWB of the wetland forests in the Pantanal, lowering C-sequestration rates in the *V. divergens* dominated forests and increasing C-emission from the AGWB to the atmosphere. To what extent more drought resistant species will substitute *V. divergens* stands and compensate for the lower sequestration rates remains an open question.

5 Conclusions

Annual tree rings are widely distributed in the tropics and dendrochronology is a powerful methodology for a fast assessment of forest productivity at different stand ages and can be applied in different tropical forest ecosystems. Such information is of importance in the actual discussion of the function of tropical forests as C-sinks in view of the ongoing global and regional climate change. The Pantanal wetland consists of different forest types as a consequence of varying

edaphic, hydrologic and climatic conditions as well as land-use change (Ariera et al., 2011). More information on C-stocks, C-sequestration and climate growth relationships of the different forest types composed of drought resistant and flood tolerant tree species are necessary to give a better picture of the role of wetland forests in the carbon cycle of the Pantanal. To estimate the carbon balance in AGWB, it is also necessary to initiate the monitoring of wetland forests in permanent observation plots to obtain data on mortality and recruitment rates of important tree species and different forest types.

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