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Carbon dynamics in aboveground coarse wood biomass of wetland forests in the northern Pantanal, Brazil

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Abstract

This is the first estimation on carbon dynamics in the aboveground coarse wood biomass (AGWB) of wetland forests in the Pantanal, located in Central Southern America. In four 1-ha plots in stands characterized by the pioneer species *Vochysia divergens* Pohl (Vochysiaceae) forest inventories (trees ≥ 10 cm diameter at breast height, DBH) have been performed and converted to predictions of AGWB by five different allometric models using two or three predicting parameters (DBH, tree height, wood density). Best prediction has been achieved using allometric equations with three independent variables. Carbon stocks (50% of AGWB) vary from 7.4 to 100.9 Mg C ha⁻¹ between the four stands. Carbon sequestration differs 0.50–4.24 Mg C ha⁻¹ yr⁻¹ estimated by two growth models derived from tree-ring analysis describing the relationships between age and DBH for *V. divergens* and other tree species. We find a close correlation between estimated tree age and C-stock, C-sequestration and C-turnover (mean residence of C in AGWB).

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. In areas undergoing deforestation AGWB is also a source of carbon emission to the atmosphere (Houghton et al., 2000). However, uncertainties remain in the absolute magnitude of AGWB in different tropical forest ecosystems and there is a controversial discussion 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). The Pantanal is one of the largest wetlands in the world, but increases in deforestation for the implantation 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

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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 (Nunes da Cunha and Junk, 2001). The forests cover 30% of the total area and have crucial functions in this unique wetland ecosystem as habitats for a large number of partial endemic flora and fauna, and as biogeochemical sinks and sources (Silva et al., 1999; Nunes da Cunha et al., 2004). However, their function in the biogeochemical cycle as dynamic C-pool is unknown, but fundamental to understand forest dynamics to develop plans for conservation and sustainable managements. Estimations of AGWB for forests in the Pantanal so far have been performed for single tree species (Haase and Haase, 1995; Salis et al., 2006), but no estimations for C-stocks in AGWB and the forest's productivity in terms of C-sequestration are available.

Large areas in the Pantanal are covered by forests dominated by *Vochysia divergens* Pohl (Vochysiaceae) (Brazilian name: "cambará"), a light demanding, flood-adapted pioneer tree species reaching up to 25 m height and more than 80 cm in diameter (Nunes da Cunha and Junk, 2004; Lorenzi, 2002). This species invades open areas developing almost monospecific stands with preference to medium and long-term flooded sites locally called "cambarazal" (Pott, 1982; Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006). *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 (dendrochronology) to determine ages and diameter increment rates for tree species of the Pantanal (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

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species has relatively high diameter increment rates of about 7 mm a⁻¹ at stand ages of 25–66 years in the southern Pantanal (Ishii, 1998).

In this study we analyze stand structure of four *V. divergens*-dominated stands. We estimate C-stocks of the AGWB using different allometric models and discuss their suitability. We determine tree ages and diameter increment rates of *V. divergens* and other tree species by tree-ring analyses to estimate annual C-sequestration rates in AGWB.

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 centre 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 of 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 between 23°C and 26°C in the rainy and dry season, 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, synchronous with the rainy season (Nunes da Cunha and Junk, 2001, 2004). The *Vochysia*-stands stock on gley soils characterized by a bluish-gray color resulting from the iron reduction (Fortunatti and Couto, 2004).

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2.2 Field measurements

Four 1-ha plots were established in stands with presence of *V. divergens*, in different positions along the flood gradient (Arieira and Nunes da Cunha, 2006) annually inundated by a water column of 0.72–1.79 m (Table 1). Each plot was divided in 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 (DBH) with a diameter tape 130 cm above the ground (in case of buttresses the diameter was recorded directly above them). From 75–91% of all individuals in the stands total tree height 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 and sequestration in AGWB

The application of the appropriate allometric equation for biomass estimations is of crucial importance to reduce errors (Ketterings et al., 2001; Chave et al., 2004). Estimations of AGWB in the Pantanal have been performed by species-specific allometric models using only DBH as predictor (Haase and Haase, 1995; Salis et al., 2006). However, allometric models developed for single species, which only use DBH as predicting parameter, have biases to errors, if they are applied to estimate AGWB of forest composed by other tree species, because they have considerably varying tree heights, wood densities, 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). Therefore, we test in this study regression models using two or three independent parameters to convert the forest inventory data into estimations of the AGWB. These allometric models are derived from several harvested tree species of one or more stands (Chambers et al., 2001) or many forest types of different tropical

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regions (Brown et al., 1989; Chave et al., 2005).

An important parameter for 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; Schöngart, 2003; Baker et al., 2004; Nogueira et al., 2005). From 48 characteristic tree species of the Pantanal comprising 133 samples (cores and stem disks) ρ was calculated by the dry mass/fresh volume ratio after measuring the fresh volume in the filed 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 ρ published values (Loureiro et al., 1979; Worbes et al., 1992; Fearnside, 1997; Ter Steege, 2000; Schöngart, 2003; Baker et al., 2004; Wittmann et al., 2006). For the remaining trees (<1.6% of all individuals) we estimated ρ by the mean value of the stand (Table 1).

Aboveground coarse wood biomass (AGWB, in kg) was estimated for every tree using different allometric models. Cannell (1984) suggested that the AGWB of a tree corresponds to the product of the trunk basal area ($BA = \pi \text{ DBH}^2/4$), ρ , total tree height (H , in m) and a constant form factor ($F = 0.6$) (Nebel et al., 2001):

$$\text{AGWB} = F \times \rho \times H \times \pi \times (\text{DBH}/2)^2 \quad (1)$$

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, over 5 month dry season), they suggested two models:

$$\text{AGWB} = 0.112 \times (\rho \times H \times \text{DBH}^2)^{0.916} \quad (2)$$

$$\text{AGWB} = \rho \times \exp[-0.667 + 1.784 \ln(\text{DBH}) + 0.207 \ln(\text{DBH})^2 - 0.0208 \ln(\text{DBH})^3] \quad (3)$$

Malhi et al. (2004) estimated AGWB for 104 1-ha plots in non-flooded and floodplain forests of the Amazon basin using an allometric model from the Central Amazonian

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upland forests (Chambers et al., 2001) corrected by a factor considering the ρ of the tree:

$$AGWB = \rho / 0.67 \times \exp[0.33(\ln(DBH)) + 0.933(\ln(DBH^2)) - 0.122(\ln(DBH))^3] - 0.37 \quad (4)$$

Many studies use the allometric model established by Brown et al. (1989) based on 168 harvested trees in five humid tropical forests estimating AGWB by the following equation:

$$AGWB = 0.044 \times (DBH^2 \times H)^{0.9719} \quad (5)$$

By Eqs. (1–5) we estimate AGWB for every tree in stands 1–4. For formula using H as an independent parameter we fitted the relationship between DBH and tree height for every stand using a non-linear regression model to calculate the height for the remaining trees by their DBH:

$$H = a + b \ln(DBH) \quad (6)$$

2.4 Tree ring analysis

In the surroundings of the PRPN stem disks were collected at 130 cm height between August 2004 and September 2005 with a chainsaw comprising 26 trees of *V. divergens* (Fortes, 2006) and 110 trees of 57 other common wetland tree species (Arruda, 2006). The wood samples were analyzed in the dendrochronological 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, Meliaceae), 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 to the nearest 0.01 mm using

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a digital measuring device (LINTAB) supported by the software TSAP (Time Series Analyses and Presentation).

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

$$DBH = a/(1 + (b/age)^c) \quad (7)$$

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

$$CDI = DBH_t - DBH_{t-1} \quad (8)$$

To estimate the annual aboveground wood biomass production of a tree (AGWBP, $kg\ yr^{-1}$) we built the difference in the AGWB estimated by the Eqs. (1–5) in the year of the stand inventory (t) and the year before ($t-1$). Therefore we subtracted the CDI of Eq. (8) from the DBH in the models (1)–(5) and reduced tree height by the stand specific diameter-height relationship of Eq. (6):

$$AGWBP = AGWB_t - AGWB_{t-1} \quad (9)$$

Carbon content was estimated 50% of AGWB (C-stock) and AGWBP (C-sequestration) (Clark et al., 2001). The mean residence time of carbon in the living AGWB of a stand (C-turnover rates) results from the ratio of its C-stock and C-sequestration rate (Malhi et al., 2004). Growth modeling was performed with the software program X-Act 7.0 (SciLab) and Statistica 6.0.

3 Results

Trees per area in the four studied stands vary between 126–446 individuals ha^{-1} comprising 9–22 tree species ha^{-1} (≥ 10 cm DBH) (Table 1). The relative abundance of *V.*

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divergens differs considerably between the studied stands ranging from 4% (stand 1), 47% (stand 3), 54% (stand 4) to 84% (stand 2). Mean DBH is 18.8 cm in stand 1, the other three stands have much higher average DBHs between 32.0 and 38.3 cm. The mean tree height (8.0 m) in stand 1 is two times lower than in the stands 2–4 (15.8–17.0 m). Basal area varies between 4.1 m² ha⁻¹ in stand 1 and 37.5 m² ha⁻¹ in stand 4. Due to the high relative abundance of *V. divergens* in stands 2–4, this species comprises 79–91% of the stand's basal area, while in stand 1 *V. divergens* only achieves 7% of the total basal area. *Vochysia* has over 90% of the total volume in stands 2–4, in stand 1 only about 10%. The wood density and standard deviation between the stands varies between 0.55±0.15 g cm⁻³ (stand 1) and 0.42±0.07 g cm⁻³ (stand 2). Average ρ of the characteristic tree species of stand 1–4 is 0.47±0.13 g cm⁻³ (Table 2); *V. divergens* has a ρ of 0.40±0.08 g cm⁻³. Mean diameter increment rate (MDI), calculated by the ratio DBH and tree age determined by tree-ring analysis (Arruda, 2006; Fortes, 2006), indicates 7.9±2.8 mm yr⁻¹ for *V. divergens*, the MDI of all species is 6.3±2.8 mm yr⁻¹ (Table 2). Wood density and MDIs are significantly correlated ($n=106$; $r=0.44$; $P<0.001$).

To estimate the C-stocks, we apply Eqs. (1–5) using DBH, ρ and tree height as independent variables (predictors). For every individual, tree height is calculated by the stand-specific diameter-height relationship (Fig. 2), explaining between 35% and 68% of the variability between the two parameters. Carbon stocks in the AGWB differ considerably between the four stands, but also between the allometric models for the same stand (Table 3). The differences of C-stocks in AGWB estimated by Eqs. (1) and (2) indicate only little variation within a stand, while Eq. (3) produces low C-stocks and Eqs. (4) and (5) tend towards high values. The estimate varies more than the twofold between different equations. Stand 1 has the lowest C-stocks in AGWB varying between 6.8 Mg C ha⁻¹ and 18.3 Mg C ha⁻¹. Estimations of C-stocks in stand 2 differ from 56.9 to 116.1 Mg C ha⁻¹ and in stand 3 from 54.5 to 108.8 Mg C ha⁻¹. The highest C-stocks are indicated for stand 4 varying between 80.8 Mg C ha⁻¹ and 164.9 Mg C ha⁻¹.

Tree age and DBH of *V. divergens* ($n=26$; $r^2=0.94$; $P<0.0001$) and other tree species

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($n=108$; $r^2=0.70$, $P<0.0001$) correlate significantly (Fig. 3). Based on the relationship between ρ and MDIs as well as tree age and DBH we develop a quadratic multiple regression model that accurately predicts tree age by wood density and DBH as independent parameters ($n=117$; $r^2=0.86$; $P<0.0001$) by the following equation (Fig. 4):

$$\text{Age} = -8.1332 + 0.8809 \times \text{DBH} + 39.6445 \times \rho + 0.0005 \times \text{DBH}^2 + 0.6305 \times \rho \times \text{DBH} - 21.19 \times \rho^2 \quad (10)$$

Partial regression analysis indicates that the DBH (Beta=0.921; $t=26.68$; $P<0.0001$) contributes more than wood density (Beta=-0.263; $t=5.33$; $P<0.0001$) to explain the variability of the tree age. By Eq. (10) we estimated for every tree its age, and by the models in Fig. 3 the CDI at the given age. Height increment was estimated by the stand-specific DBH-height relationship (Fig. 2) calculating the difference of the height at DBH and the height at DBH-CDI. Applying Eqs. (1)–(5) this produces the difference between the C-stocks in ABGW for the year of the forest inventory and the year before and gives an estimate of the annual C-sequestration rate shown in Table 3. Models (1) and (2) indicate almost the same C-sequestration in the four studied stands, while model (3) tends to yield lower values and models (4) and (5) predict much higher values. The five allometric models indicate C-sequestration in the AGWB of stand 1 between $0.47 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $1.23 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. For stand 2 the models indicate C-sequestration in AGWB varying between $3.00 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $6.97 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. For the stands 3 and 4 the models predict estimations of C-sequestration varying between $2.00\text{--}4.89 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $2.29\text{--}4.28 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively.

4 Discussion

In this study we show a new approach in tropical forest research of estimating C-sequestration in AGWB by means of growth models based on tree-ring analyses. Ishii (1998) first indicated the occurrence of annual tree rings in the Pantanal using radiocarbon-dating and cambial wounding (windows of Mariaux). Mattos (1999)

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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). In comparison to repeated diameter measurements or permanently installed dendrometers, which yield confidential results only after several years of monitoring, dendrochronology allows an immediate estimation of C-sequestration comprising the whole life span of a tree by retrospective analysis (Worbes, 2002).

By a multiple regression model we predict tree age using DBH and ρ as independent parameters. Mean radial increment correlates negatively with ρ , as it is also known for tree species from the Central Amazonian floodplain forests (Worbes et al., 1992; Schöngart, 2003). 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 contents and high vessel areas (Worbes, 1996) resulting in low wood densities, while climax tree species have high wood densities due to high contents of fiber with thick cell walls with incorporations of secondary substances and a relatively low vessel area. This relationship allows a reliable estimation of tree age by measuring DBH and ρ , which can be easily determined by a wooden core of the trunk (Chave et al., 2004).

Our results indicate that the C-stocks and C-sequestration of the AGWB differ considerably depending on the applied allometric model (Table 3). The most accurate estimation of C-stocks and consequently C-sequestration is achieved by the allometric models (1) and (2) using DBH, ρ and tree height as predictors, as also indicated by

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Chave et al. (2005). Equation (3) uses only DBH and ρ to estimate AGWB in dry forests and produces much lower values than allometric model (2). Since the models (2) and (3) are derived from the same data set, these differences can be traced back to variation among the tree height between the Pantanal forests and the dry forests analyzed by Chave et al. (2005). Model (4) applied by Malhi et al. (2004) overestimates C-stocks in the AGWB of the studied stands, because this allometric equation has been established by harvested trees from the Central Amazonian terra firme forest (Chambers et al., 2001), where trees are much higher than in the Pantanal. Equation (5) developed by Brown et al. (1989) produces the highest predictions of AGWB, because this model does not consider ρ , which is lower in the successional stages of *V. divergens*-dominated wetland forests ($0.42\text{--}0.55\text{ g cm}^{-3}$, Tables 1 and 2) than the mean value of the data set ($0.60\text{--}0.65\text{ g cm}^{-3}$) (Brown, 1997). The majority of AGWB estimations in tropical forests performed so far applies allometric models, which use only DBH as a predictor, since this parameter is easily to measure in tropical forests. But the conversion of these field measurements to biomass estimations can produce large errors due to the variation in height and ρ between forest types and tree species. Realistic estimations of C-stocks and sequestration in AGWB can be only achieved applying allometric models using DBH, ρ and tree height as predictors, especially when these estimations are performed in new forest types.

We estimate (minimum) stand age by the maximum tree age produced by the multiple regression model (Fig. 4) (Worbes et al., 1992), which results between 64 years (stand 1) and 124 years (stand 4). We calculate the mean value of the estimations based on Eqs. (1) and (2) considering DBH, tree height and ρ as predictors. The 64 year-old stand 1 indicates C-stocks in the AGWB of 7.4 Mg C ha^{-1} , sequestering about $0.5\text{ Mg C ha}^{-1}\text{ yr}^{-1}$, which results in a mean residence time of C of 14.7 years. With increasing stand age C-stock accumulates to 70.9 Mg C ha^{-1} (stand 2; 99 years old), 68.8 Mg C ha^{-1} (stand 3; 108 years old), and $100.9\text{ Mg C ha}^{-1}$ (stand 4; 124 years old). Carbon sequestration reaches its maximum in stand 2 with $4.24\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ and declines with increasing stand age to $2.75\text{ Mg C ha}^{-1}\text{ yr}^{-1}$

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(stand 3) and $3.04 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (stand 4). The mean residence time of C in AGWB growths with increasing stand age to 16.7 years (stand 2), 25.0 years (stand 3) and 33.2 years (stand 4). Carbon stocks and C-sequestration of the AGWB in the wetland forests of the Pantanal are lower than those of Central Amazonian floodplain forests undated by nutrient-rich white-water rivers (várzea) (Worbes, 1997; Schöngart, 2003) estimated by model (1) (Table 4). The mean residence time of carbon in the AGWB (C-turnover) of the successional stages in the Pantanal is in the same range as in the Amazonian floodplain forests. Tropical dry forests in Mexico indicate higher C-stocks in the AGWB than the studied wetland forests (Vargas et al., 2008).

In Fig. 5 we relate C-stock, C-sequestration and mean residence time of carbon with tree age of 1079 individuals estimated by Eq. (10). A sigmoidal regression model explains 97% of the variability between tree age and C-stock in the AGWB of a tree. From this model we derive the annual C-sequestration calculating the difference in C-stocks from year to year. The model indicates a maximum C-sequestration at a tree age of about 80 years, when trees approximately accumulated almost 1 Mg C in the AGWB. The mean residence time of carbon in the AGWB at this tree age is 41 years. After this tree age the mean residence time of carbon in the AGWB increases considerably indicating that *V. divergens*-forests achieved maturity at stand ages of more than 80 yrs. After this age the forests have the potential to keep sequestered carbon from the atmosphere over several decades accumulated in the AGWB.

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) and Zimbabwe (Therrell et al., 2006) significant correlations between tree growth and ocean's sea surface temperatures (SSTs). Tree growth of *V. divergens* in the N-Pantanal responds to rainfall variability and it is significantly lower during positive SST anomalies in the El Niño 1+2 region of the tropical Pacific basin ($0\text{--}10^\circ \text{ S}$, $80\text{--}90^\circ \text{ W}$) causing significantly lower rainfall in the Pantanal during the period October-December ($r = -0.39$; $P < 0.01$) (Fortes, 2006). If these drought episodes last for several years, as it occurred during

the 1960s, 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 more carbon is accumulated in the AGWB. However, future climate scenarios (IPCC, 2007) indicate increasing SSTs in the tropical oceans, which will affect C-stock in 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

Total C-stocks and C-sequestration in the AGWB of Pantanal's wetland forests of 64 to 124 years stand age vary considerably between $7.4\text{--}100.9\text{ Mg C ha}^{-1}$ and $0.50\text{--}4.24\text{ Mg C ha}^{-1}\text{ yr}^{-1}$, respectively. In this study we apply dendrochronology to estimate changes in C-stocks of AGWB, which, for our knowledge, is the first time in tropical forest research. 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 the background of the rapid 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. 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.

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

Parameter	Unit	Stand 1	Stand 2	Stand 3	Stand 4
Mean flood height	m	0.72±0.28	1.13±0.16	1.46±0.27	1.79±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 DBH±std	cm	18.8±7.6	36.1±11.4	32.0±15.7	38.3±20.0
Mean tree height±std	m	8.0±3.1	15.8±6.7	16.6±6.5	17.0±6.5
Basal area	m ² ha ⁻¹	4.1 (7.3%)	28.3 (91.0%)	25.1 (79.4%)	37.5 (86.6%)
Volume*	m ³ ha ⁻¹	23 (9.5%)	337 (99.3%)	320 (90.9%)	483 (91.5%)
Mean wood density±std	g cm ⁻³	0.55±0.15	0.42±0.07	0.47±0.10	0.47±0.09

*Estimated by basal area×tree height×0.6 (form factor) (Cannell, 1984).

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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±1.5
<i>Alchornea discolor</i> Poepp. (Euphorbiaceae)	2/3	0.34±0.04	7.7±6.5
<i>Byrsonima orbignyana</i> A. Juss. (Malpigiaceae)	2/3	0.47±0.01	5.0±1.7
<i>Cecropia pachystachya</i> Trécul (Cecropiaceae)	3/3	0.30±0.07	14.0±6.5
<i>Couepia uiti</i> (Mart. & Zucc.) Benth. ex Hook. f. (Chrysobalanaceae)	3/3	0.44±0.02	8.5±4.3
<i>Coccoloba ochreolata</i> Wedd. (Polygonaceae)	5/7	0.59±0.04	4.4±1.2
<i>Duroia duckei</i> Huber (Rubiaceae)	2/4	0.52±0.01	5.2±2.8
<i>Garcinia brasiliensis</i> (Mart.) Planch. & Triana (Guttiferae)	2/0	0.64±0.05	–
<i>Mabea paniculata</i> Spruce ex Benth. (Euphorbiaceae)	1/3	0.56	6.1±0.8
<i>Mouriri guianensis</i> Aubl. (Melastomataceae)	4/5	0.60±0.06	4.5±2.0
<i>Ocotea longifolia</i> Kunth (Lauraceae)	6/5	0.47±0.05	5.8±1.9
<i>Sapium obovatum</i> Kl. (Euphorbiaceae)	5/5	0.31±0.07	7.2±3.2
<i>Vochysia divergens</i> Pohl (Vochysiaceae)	17/26	0.40±0.08	7.9±2.8
Other species	81/65	0.48±0.14	5.7±3.2
Mean	133/136	0.47±0.13	6.3±3.5

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Table 3. Carbon stocks and C-sequestration in AGWB estimated allometric Eqs. (1–5) in four stands of wetland forests in the Pantanal.

C-stocks (Mg C ha ⁻¹)	Stand 1	Stand 2	Stand 4	Stand 3
Equation (1)	6.8	67.9	67.3	100.4
Equation (2)	8.1	73.9	70.3	101.4
Equation (3)	10.9	56.9	54.5	80.8
Equation (4)	8.6	116.1	108.8	164.9
Equation (5)	18.3	105.0	103.5	151.6
C-sequestration (Mg C ha ⁻¹ yr ⁻¹)	Stand 1	Stand 2	Stand 4	Stand 3
Equation (1)	0.47	4.14	2.76	3.09
Equation (2)	0.54	4.33	2.74	2.98
Equation (3)	0.65	3.00	2.00	2.29
Equation (4)	0.59	6.97	4.89	4.28
Equation (5)	1.23	5.97	3.88	4.14

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Table 4. 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 (DBH \geq 10 cm)	C-stock (Mg C ha $^{-1}$)	C-sequestration (Mg C ha $^{-1}$ year $^{-1}$)	C-turnover (years)
Pantanal (this study)			
Stand 1 (stand age 64 years)	7.4	0.5	14.7
Stand 2 (stand age 99 years)	70.9	4.2	16.7
Stand 3 (stand age 108 years)	68.8	2.8	25.0
Stand 4 (stand age 124 years)	100.9	3.0	33.2
Central Amazonian floodplain forests			
Worbes (1997) (stand age 80 yrs)	140.0	–	–
Schöngart (2003) (stand age 52 years)	117.4	7.2	16.4
Schöngart (2003) (stand age 125 years)	115.0	3.7	30.7
Seasonal dry forests*			
Vargas et al. (2008) (stand age 64 years)	64.4	–	–
Vargas et al. (2008) (stand age 99 years)	103.9	–	–
Vargas et al. (2008) (stand age 108 years)	114.1	–	–
Vargas et al. (2008) (stand age 124 years)	132.1	–	–

* calculated by a linear regression model considering trees \geq 10 cm DBH (Vargas et al., 2008).

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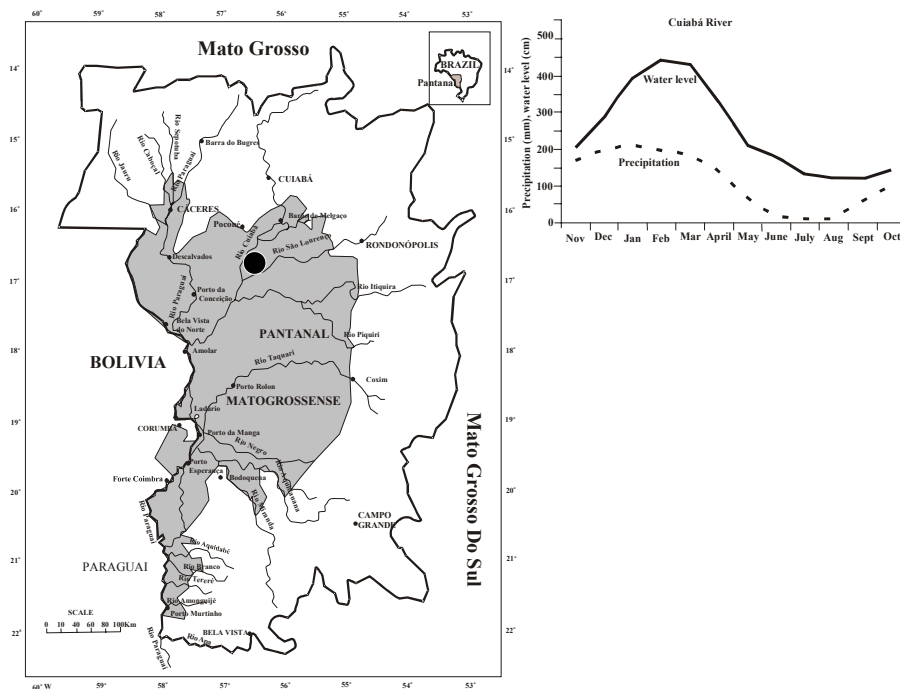


Fig. 1. Overview of study site in N-Pantanal (SESC Pantanal Ecological Station) of Brazil.

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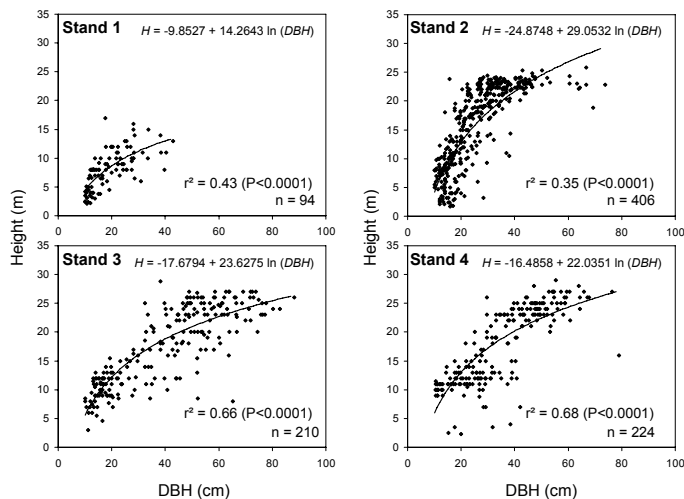


Fig. 2. Non-linear relationships between DBH and tree height of stands 1–4.

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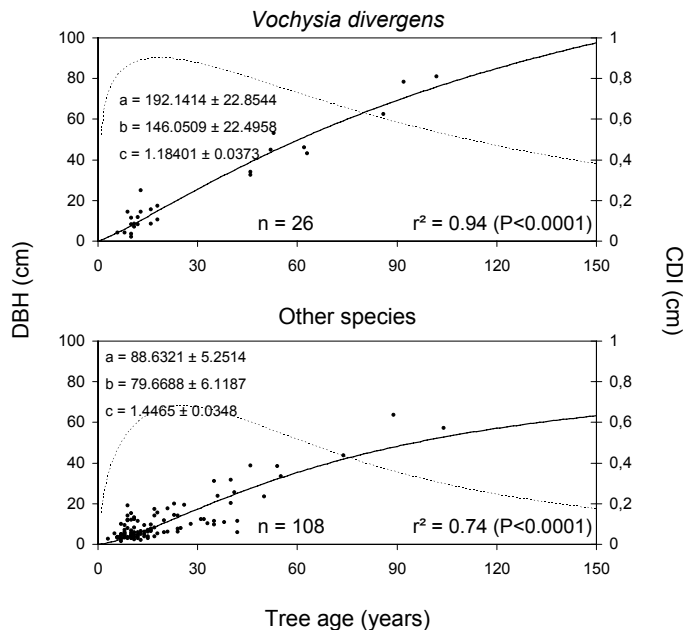


Fig. 3. Significant age-diameter relationships for *V. divergens* and other tree species. The dotted lines indicate the annual current diameter increment (CDI). Indicated parameters are for the age-DBH relationship of Eq. (7).

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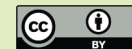
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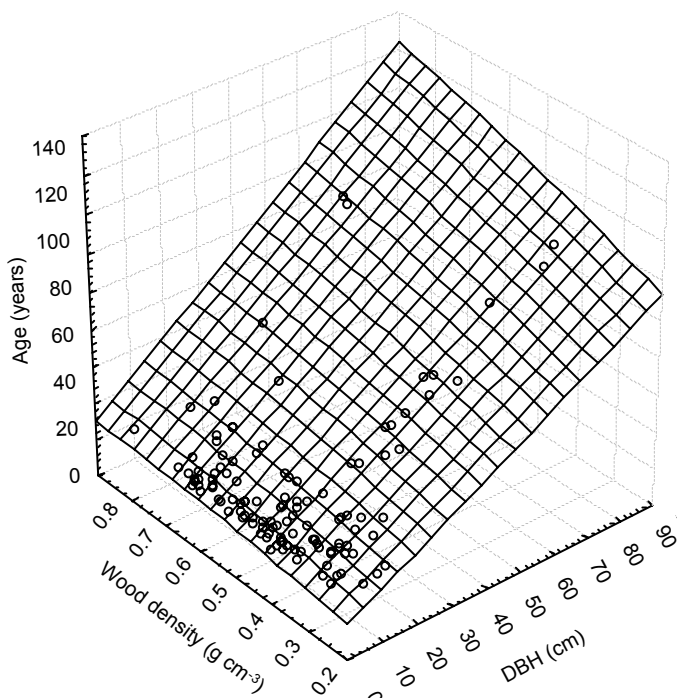


Fig. 4. Quadratic multiple regression model predicting tree age as a function of DBH and wood density developed by a data set of 117 trees of different successional stages of the wetland forests in the northern Pantanal.

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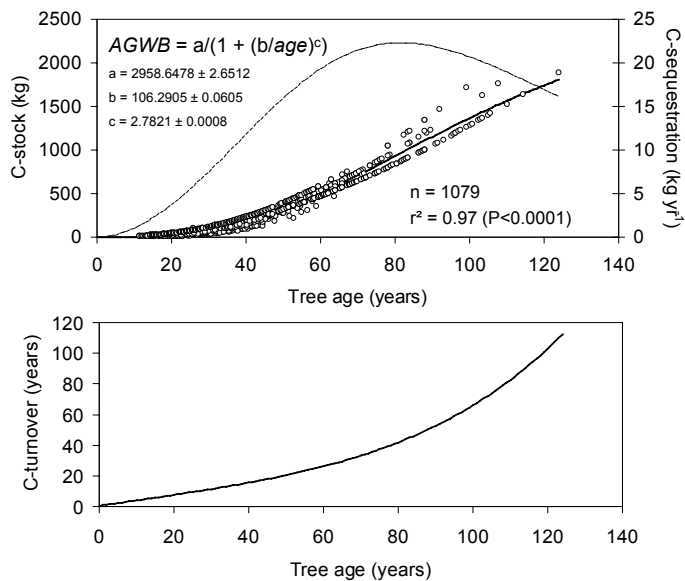


Fig. 5. C-stocks and C-sequestration of AGWB from 1079 trees of Pantanal wetland forests related to estimated tree ages (above). Carbon turnover (mean residence time of carbon in AGWB) related to estimated tree age (below).

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