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Growth rhythm of *Vochysia divergens* Pohl (Vochysiaceae) in the Northern Pantanal

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ABSTRACT. The Pantanal is the largest wetland in the world, characterized by high biodiversity, but large areas have been invaded by *Vochysia divergens*, a flood-adapted pioneer and native tree of the riparian forest and Brazilian Savanna. Seasonality in rainfall causes annual rhythms in the tree's physiology, in which climatic stress factors induce a cambial dormancy in trees and, in consequence, growth zones in the trunk. Current analysis evaluates the seasonal variation of the diameter increase of *V. divergens* specimens in a seasonal floodable forest of the Northern Brazilian Pantanal. Field sampling was conducted between January and December 2012. Air temperature, relative humidity and precipitation were measured at a micrometeorological station, water level was measured by graded tape, and soil water content was measured by a portable TDR sensor. Diameter growth was monitored by dendrometric bands and aboveground litter production was sampled by litter traps. The annual diameter increase was 4.0 mm. There was correlation between diameter increment and climate and phenology, with the highest increase during the flooding period and the lowest during the dry season and reproductive period. Climate and phenology affected the growth rhythm of *V. divergens*.

Keywords: diametric increment, dendrometric bands, climate-growth relation, phenology, Cambará.

Ritmo de crescimento de *Vochysia divergens* Pohl (Vochysiaceae) no Pantanal Norte

RESUMO. O Pantanal é a maior area úmida do mundo, com alta diversidade de plantas e animais, mas vastas áreas são invadidas por *Vochysia divergens* Pohl (Vochysiaceae), que é uma árvore pioneira bem adaptada à inundação e nativa de matas ripárias e cerrado. A sazonalidade da chuva leva a ritmos anuais na fisiologia das árvores em que fatores de estresse climático induzem à dormência cambial e, consequentemente às zonas de crescimento no caule. Assim, o objetivo deste estudo foi avaliar a variação sazonal do incremento diamétrico de indivíduos de *V. divergens* em uma floresta sazonalmente inundável no pantanal norte. As coletas ocorreram de janeiro a dezembro/2012. A temperatura do ar, umidade relativa e precipitação foram obtidas por estação micrometeorológica, o nível de água no solo por trena graduada e o conteúdo de água no solo por sensor TDR. O incremento diamétrico foi monitorado por bandas dendrométricas e a produção de liteira por coletores. O incremento diamétrico anual foi 4,0 mm. Houve correlação do incremento diamétrico com clima e fenologia, com maior incremento na inundação e menor na estação seca e no período reprodutivo da espécie. Portanto, o ritmo de crescimento de *V. divergens* foi afetado pelo clima e fenologia.

Palavras-chave: incremento diamétrico, bandas dendométricas, relação clima-incremento, fenologia, Cambará.

Introduction

The Pantanal, located in South America, is the largest seasonal flooded plain in the world (JUNK et al., 2006), occupying a surface area of approximately 150,000 km^2 that spans over Brazil, Paraguay and Bolivia (HAASE, 1999). Its main attribute is the flood pulse which causes several cycles of alternating aerobic and anaerobic conditions and interferes in the availability of nutrients, in the production of toxic substances (PONNAMPERUMA, 1972; KIRK, 2004) and in water availability for plants. The topographical variations and differences in local flooding (intensity and duration) model the landscape and the distribution of vegetation types (NEIFF, 1990; NUNES DA CUNHA et al., 2007) since they are engaged in the distribution and abundance of plants (ZEILHOFER; SCHESSL, 2000; NUNES DA CUNHA; JUNK, 2001; REBELLATO; NUNES DA CUNHA, 2005; DAMASCENO-JÚNIOR et al., 2005; ARIEIRA; NUNES DA CUNHA, 2006).

The Pantanal is an extremely diverse place, with approximately 144 families of higher plants and more than 1,000 plant species (JUNK; NUNES DA CUNHA, 2005). Only 5% of tree species live exclusively in prolonged flooding areas; 30% are restricted to rarely flooded areas; and 65% are widely distributed within the flooding gradient of the Pantanal (NUNES DA CUNHA; JUNK, 2001). However, such biodiversity is highly vulnerable because of practices in land use, changes in hydrology and climate, and invasive species (JUNK et al., 2006). In terms of invasive species, the spread of *Vochysia divergens* Pohl (locally known as *cambará*) is a well-documented example in the Pantanal (VOURLITIS et al., 2011).

Vochisia divergens is a native tree of the Brazilian savannah (cerrado) and riparian forest (LORENZI, 2002). It is a flood-adapted pioneer species that has been vigorously spreading into seasonally flooded native grassland for more than four decades (NUNES DA CUNHA; JUNK, 2004). The species may grow to heights between 28 and 30 m and has a dense leafy canopy that effectively shades out grasses, forbs and trees, forming dense, species-poor stands known as *cambarazal* (NUNES DA CUNHA; JUNK, 2004). During high rainfall years, prolonged flooding allows seedling recruitment to occur prior to the dry season when the probability of tree mortality increases. On the other hand, during dry years, forest fire is an important agent for limiting the distribution of *cambará* outside the riparian zone (NUNES DA CUNHA; JUNK, 2004). Although the reason for the invasion of the *cambará* is still poorly understood, the interactions between flooding, soil properties and forest fire appear to be critical for invasion success (ZEILHOFER; SCHESSL, 2000; NUNES DA CUNHA; JUNK, 2004).

In fact, several factors may contribute towards invasion success, including seed production, germination, seedling recruitment, susceptibility to disease and/or herbivores, carbon allocation, life history and high relative growth rate (REJMÁNEK; RICHARDSON, 1996; MACK et al., 2000; GROTKOPP; REJMÁNEK, 2007). The ability to tolerate flooding is a highly relevant factor for the invasion success of plants in the Pantanal since modifications in soil properties may affect negatively the physiological functioning of several tree species (DALMAGRO et al., 2013). On the other hand, many species have developed a wide range of adaptive strategies which make them tolerate periodic flooding (IWANAGA; YAMAMOTO, 2008; PEZESHKI; DELAUNE, 2012), and allow them to maintain a high photosynthetic activity during most of the year. Such tolerance may allow these species to dominate over natural competitors that may be more efficient under non-flooding conditions but unable to compete in flooding situations (PAROLIN et al., 2010).

Further, most tropical rainforests not only experience some seasonality during the rainfall period but they also have a distinct dry season (WORBES, 1995) which also provides annual rhythms in tree physiology (BORCHERT, 1994a) and often causes leaf-abscission (WORBES, 1999). These climatic stress factors induce a cambial dormancy in trees and, consequently, growth zones in the wood (WORBES, 1995). Some results indicate complete cambial dormancy or reduced diameter growth in many species due to a dry season of at least two months of arid conditions (WORBES, 1995, 1999). Thereby, a distinct growth boundary is formed in many tree species (WORBES, 1995; DÜNISCH et al., 2003; FICHTLER et al., 2003) in spite of the traditional belief that tropical rainforest trees do not produce growth rings (LIEBERMAN et al., 1985; WHITMORE, 1998). Tree rings in woody plants are generally induced by seasonally alternating favorable and unfavorable growth conditions (WORBES, 1995).

Furthermore, responses of trees to favorable and unfavorable growth conditions vary between sites for the same species (BREITSPRECHER; BETHEL, 1990), as they differ between the species, often with regard to leaf-fall behavior (BORCHERT et al., 2002). Due to the above, the relationships between rainfall, leaf-fall behavior and growth of tropical rainforest trees should be better understood. Information on age of trees and their growth rates is crucial to understand the dynamics of tree populations (ENRIGHT; HARTSHORN, 1981) and to develop sustainable management systems for tropical timber species (STAHLE et al., 1999; WORBES et al., 2003). Owing to the urgent need for the preservation of tropical rainforests, their sustainable timber production and the rapidly expansion of *V. divergens* in the natural grasslands of the Pantanal, more in-depth information is required on the periodicity of growth of tropical timber trees. Current analysis assesses the seasonality of diameter increase of specimens of *V. divergens* in a flooded forest in the Northern Brazilian Pantanal.

Material and methods

Study site: The study was conducted in the northern Pantanal (16°29'04" S and 56°25'25" W), approximately 160 km southwest from Cuiabá, Mato Grosso State, Brazil (Figure 1). According to Köppen classification, the regional climate is Aw, or rather, a hot and wet climate with rainfall in the summer and drought in the winter.

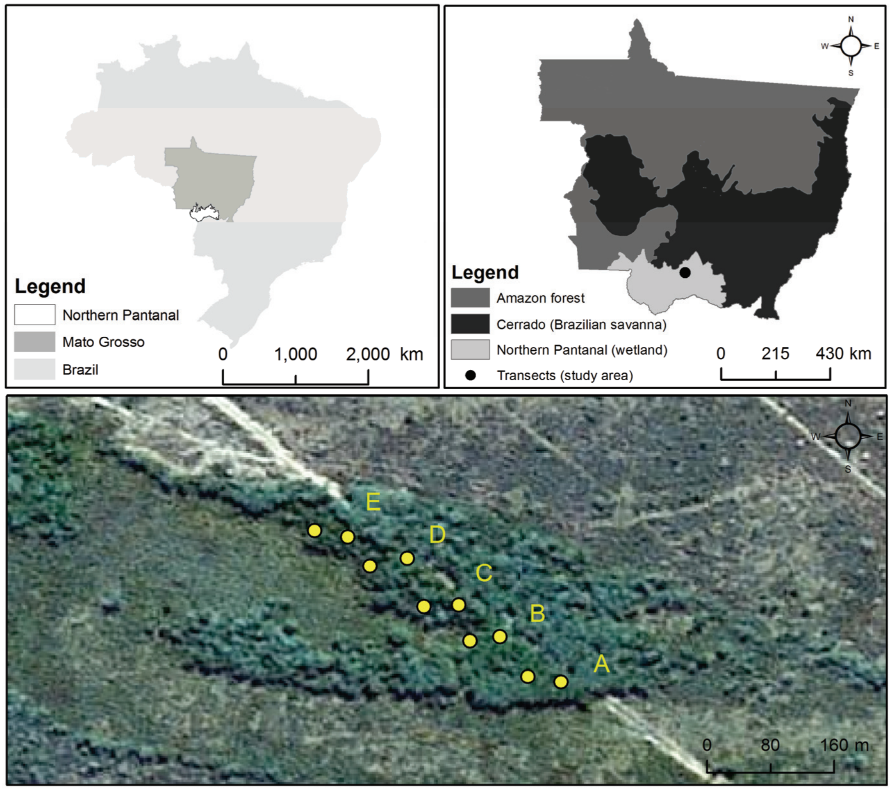

Figure 1. Location of the seasonally flooded forest in the Northern Brazilian Pantanal.

Annual rainfall averaged 1400 mm with a dry season from May through September (NUNES DA CUNHA; JUNK, 2001).

The annual average of air temperature ranged between 29 and 32°C (maximum) and between 17 and 20°C (minimum) (BIUDES et al., 2014). The topography is virtually flat, with extensive flooding during the wet season (FANTIN-CRUZ et al., 2010). Soils are of sedimentary origin, occurring in clayey and sandy phases alternately and discontinuously, with a dominance of hydromorphic soils (CORINGA et al., 2012).

Vegetation was characterized by dense canopy; tree height between 10 and 20 m; mean diameter 28.36 cm; tree density 839.98 specimens/ha, basal area 66.16 m^2 ha^{-1}, 14 species distributed into 13 families, of which the species with the highest abundance was *V. divergens*, followed by *Licania parvifolia* Huber and *Mouriri elliptica* Mart. (MACHADO et al., 2015).

Field Measurements: Five 50 m transects (A,B,C,D,E) were established in the study area, with sampling points at 5 m intervals. The distance between transects was 80 m. Field sampling was conducted over one year (January-December 2012). The water level was measured by a graded tape, at 55 sampling points, once a month during the flooding period.

The soil water content was measured at the 0-12 cm layer using a portable TDR sensor (Hidrossense II Mod CS620, Campbell Sci., USA). Species were sampled every 5 m on each 50 m transect with the point-quarter method (GOLDSMITH; HARRISON, 1976).

Briefly, each measurement point was divided into four quadrants, and within each quadrant, the distance to the nearest tree and its circumference greater than 20 cm at breast height (1.3 m aboveground) were measured. All sampled trees were identified and marked with plastic numbered plates for long-term monitoring.

Micrometeorological variables, soil water content and water level: A micrometeorological station (WXT520, Vaisala Inc., Helsinki, Finland) was installed 2 km south of the study area. The air temperature (°C), relative humidity (%) and rainfall (mm) were measured every 10 seconds and data stored at intervals of 30 minutes in a datalogger (CR1000, Campbell Scientific, Logan, Utah, USA), connected to a solar panel battery.

Vapor pressure deficit (VPD; kPa) was calculated by Equation (1).

$$\mathrm{VPD} = es - ea \tag{1}$$

where: *es* (Equation 2) is the saturation vapor pressure (kPa) estimated by the air temperature (*Ta*; °C); and *ea* (Equation 3) is the actual vapor pressure (kPa) estimated by *es* and relative humidity (RH; %).

$$es = 0.611 * 10^{\left[\frac{(7.5*Ta)}{237.3+Ta}\right]} \tag{2}$$

$$ea = \frac{(RH * es)}{100} \tag{3}$$

The soil water content (SWC) was measured at the 0-12 cm layer using a portable TDR sensor (Hidrossense II Mod CS620, Campbell Sci, USA). The water level was measured once a month by a graded tape at 55 sampling points.

Diameter increase of *Vochysia divergens* Pohl: Specimens *V. divergens* were chosen from the species sampled using the point-quarter method. The growth of *V. divergens* specimens was monitored by dendrometric bands that provided measurement of changes in the circumference of the tree trunk. Diameter increase was monitored in 34 specimens once a month during one year. The diameter growth rate was established by the difference between the subsequent time and the previous time. Circumference increase was measured by a digital caliper and converted into diametric increment by dividing the obtained value in millimeter (mm) by π.

Litterfall production: Aboveground litter production (>1 mm diameter) was sampled by 1 m^2 collector. Litter traps were constructed with 1 mm-mesh nylon fabric attached to an iron frame and elevated elevated above the ground to avoid contamination by soil and water (SALA; AUSTIN, 2000). Litter was retrieved monthly, separated into leaves and flowers fractions of *V. divergens*, dried at 70°C for 72h and weighed on a digital balance (AD 500, Marte, Santa Rita do Sapucaí, Brazil). Litterfall was expressed as seasonal percentage (%) of the dry mass per unit of ground area over a period of one month (mg ha^{-1} month^{-1}).

Statistical analysis: Differences between means were determined by assessing whether 95% confidence intervals overlapped (SOKAL; ROHLF, 1995). Cross-correlation was used to evaluate whether there was time lag between diameter increase and some variables (hydroclimate and litterfall). It is a measure of similarity of two waveforms as a function of a time-lag applied to one of them (WEI, 2006). All statistical analyzes were performed with R program 3.1.0 (R CORE TEAM, 2014).

Results

Hydrometeorological patterns: The dry season had low rainfall rates, with no precipitation in July and August (Figure 2a). Annual precipitation was 1637.91 mm with 84% of total amount during the wet season. Annual air temperature was 24.4°C, with a minimum in July (19.9°C) and a maximum in December (26.7°C). The flooding period occurred from January to June and in December (Figure 2b). SWC followed the seasonal trend in rainfall with the lowest rates in September and highest rates near the flooding period. Seasonal variation in VPD followed the inverse of seasonal trend in rainfall and relative humidity (Figure 2c). The peak of VPD was in September with low rates in relative humidity and soil water content.

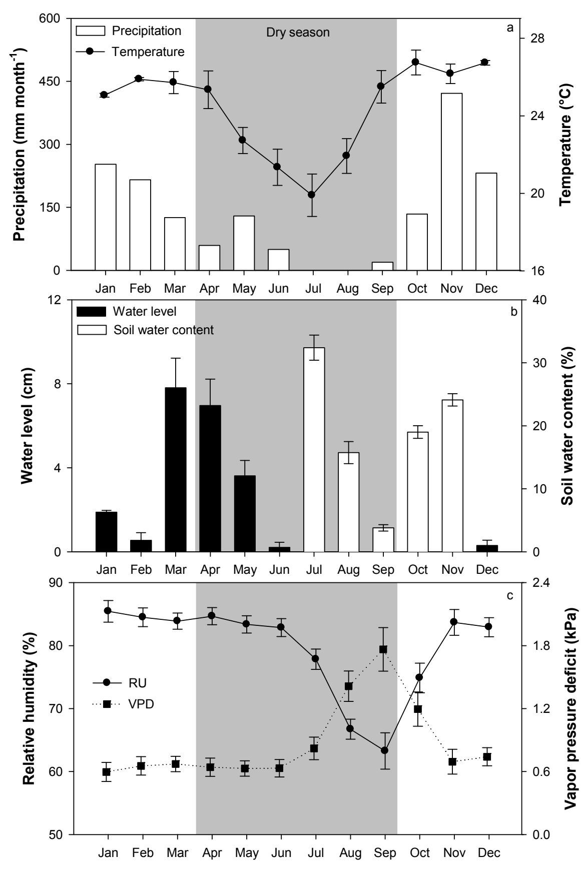

Figure 2. Monthly mean rainfall and air temperature (a); water level and water soil content (b); relative humidity and vapor pressure deficit (c) in a seasonally flooded forest with dominance of *Vochysia divergens* in the Northern Brazilian Pantanal. Bars represent ±95% confidence interval.

Tree growth: The monthly mean rate of diametric increment of *V. divergens* decreased from January to August, and increased from September to December (Figure 3a). The highest diameter increase rate occurred in January (0.86 mm) with no increase in August (-0.1 mm). The highest increase occurred in the period January-March followed by the period October-December whereas the lowest occurred between July and September followed by April-June (Figure 3b). Negative growth in July-September was probably due to measurement errors during manual data collection using a caliper. The annual mean diameter increment of V. divergens was 4.0 mm for the study area.

Seasonal litterfall dynamics: The peak of flower litter fall occurred in July and leaves litter fall in September (Figure 4a). The highest production of leaves and flowers of *V. divergens* occurred between July and September whilst the lowest occurred between January and March (Figure 4b).

Effects of climate and phenology on tree growth: There was a positive correlation, at no delay, between diameter growth and relative humidity (R^2 = 0.72), and a negative correlation, at no delay, between diameter growth and DPV (R^2 = -0.65), diameter growth and leaf production (R^2 = -0.64) and diameter growth and flowerproduction (R^2 = -0.64). On the other hand, there was a positive correlation at a delay of one month between diameter growth and SWC (R^2 = 0.70), and a delay of two months between diameter growth and flooding (R^2 = 0.86). There was a positive correlation at a delay of one month between diameter growth and rainfall (R^2 = 0.73), and diameter growth and temperature (R^2 = 0.61).

Discussion

The trend of seasonal rainfall was consistent with the region's climatology. The wet season occurred between October and March and may represent more than 80% of the amount of total annual precipitation. Meanwhile, low rainfall was recorded between June and September, which is consistent with the 4-5-month duration of the dry season (VOURLITIS et al., 2008; BIUDES et al., 2012, 2014). The seasonal variation in soil water content followed the rainfall trend with saturated soil from January to June, with a peak in March.

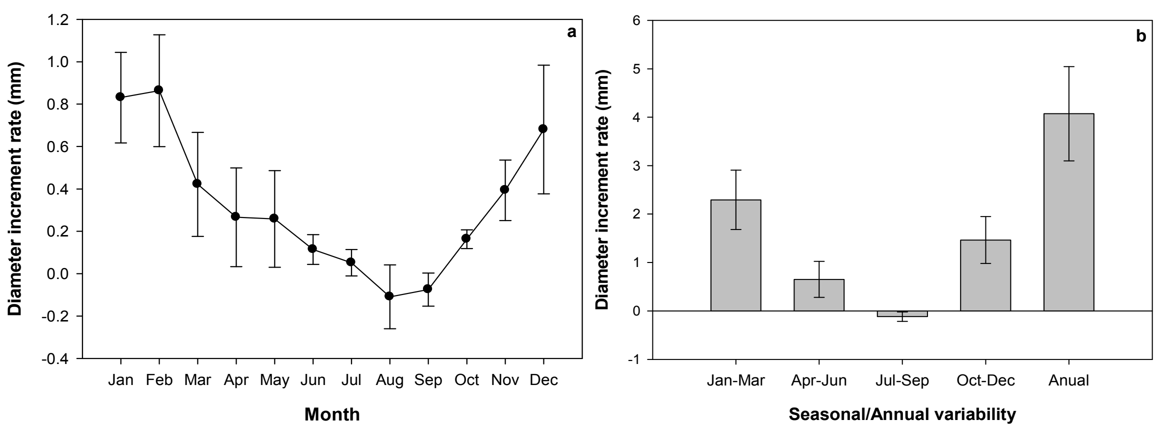

Figure 3. Annual diameter increase rate of *Vochysia divergens* and its monthly and seasonal variability in a seasonally flooded forest in the northern Brazilian Pantanal, 2012. Bars represent ±95% confidence interval.

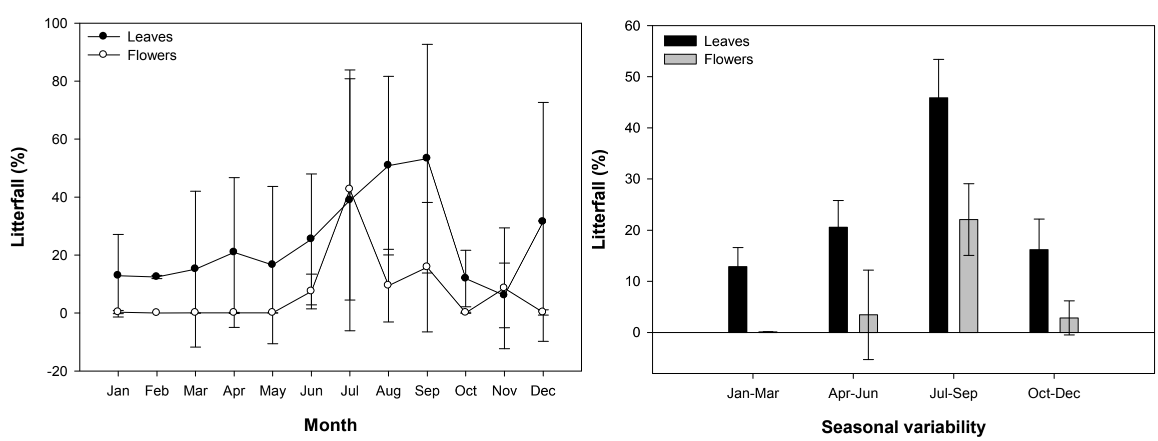

Figure 4. Monthly and seasonal variability of litterfall leaves and flowers of *Vochysia divergens* in a seasonally flooded forest in the northern Brazilian Pantanal, 2012. Bars represent ±95% confidence interval.

Flooding is caused by local rainfall due to the predominant clay texture of the soil and to slight topographic variation (PENHA et al. 1999; ARIEIRA; NUNES DA CUNHA, 2006). Thus, the flooding in the Pantanal is a function of rainfall intensity, with 2 – 8 month duration (BIUDES et al., 2009, 2014; ARIEIRA et al., 2011). In general, the flooding presents a monomodal pattern with small amplitude (HAMILTON et al., 1996).

Air temperature showed consistent seasonal trends with lowest rates in the dry season when waves of cold air from the southern regions of the continent may persist for several days (GRACE et al., 1996; ROCHA et al., 2009; BIUDES et al., 2012). Seasonal variation in VPD followed the inverse of seasonal trends in rainfall and relative air humidity, with higher rates in the dry season, consistent with a variety of tropical forest in the Amazon Basin (ROCHA et al., 2004) and Pantanal (BIUDES et al., 2014).

Current study demonstrates that the annual diameter increment rate of *V. divergens* was higher than rates reported by Dong et al. (2012), Vieira et al. (2004) and Clark and Clark (1995), but lower than those reported by Arieita and Nunes da Cunha (2012) and Silva et al. (2002) (Table 1). Arieita and Nunes da Cunha (2012) used dendrochronology techniques to provide a model relating age and diameter of *V. divergens* with mean growth rate estimated at 7.9 mm $year^{-1}$. Although there was a high growth rate in earlier lifetime of individuals of *V. divergens*, it decreased over the years until it becomes low at maturity (ARIEIRA; NUNES DA CUNHA, 2012).

Table 1. Comparison of diametric increment rate (DIR - mm) of *Vochysia divergens* with other species in different studies.

Studies	DIR (mm)	Sites
Current research (2012)	4.89	Pantanal Mato-grossense
Dong et al. (2012)	0.65-2.1	Tropical forests
Silva et al. (2002)	1.64	Amazon forest (Manaus, Brazil)
Vieira et al. (2004)	1.7-3.9	Amazon forest (Brazil)
Clark and Clark (1995)	1.9-5.2	05 species from rainforests in Costa Rica
Arieira et al. (2012)	7.9	Pantanal Mato-grossense (*V. divergens*)
Silva et al. (2002)	5.28-11.41	Commercial tree species of Amazon forest

The annual increase rate of *V. divergens* showed consistent seasonal trends, with its highest rates between January and March; negative increase or no diameter increase between July and September; intermediate rates between April and June and between October and December. The trend from January to March is characterized by high relative air humidity, low vapor pressure deficit, high temperature and rainfall in which soil becomes saturated due to its clayey texture. While the seasonal trend between April and June is characterized by decreasing temperature, emergence of new leaves (DALMOLIN et al., 2013), decreasing solar radiation (BIUDES et al., 2012, 2014) and low rainfall rates, the soil still remained saturated (MACHADO et al., 2015).

The seasonal trend from July to September is characterized by increasing temperature, low or no rainfall rates, low soil water content and relative air humidity with increasing vapor pressure deficit, increasing leaf abscission of older leaves and the production of reproductive structures of *V. divergens*. Pott and Pott (1994) pointed out that the flower production of *V. divergens* occurs from July to September. Some tropical species produce flowers or leaves during the dry season after shedding their leaves. This apparent violation of physiological theories may be explained by rehydration caused by the osmotic adjustment of stem tissues and improved water availability due to roots extension into moist subsoil layers (BORCHERT, 1994b). The water supply is significant for the turgor of differentiating xylem cells (LARSON, 1969; DÜNISCH; BAUCH, 1994), the biosynthesis of carbohydrates (LANGENFELD-HEYSER, 1987) and the transport of mineral elements (KRAMER, 1985; KOZLOWSKI et al., 1991).

The trend between October and December is characterized by increasing temperature, rainfall, relative air humidity and soil water content, and a decrease in vapor pressure deficit. Thus, the seasonal pattern of *V. divergens*´s diameter increase followed the patterns of regional climate and phonologic changes in the species.

Callado et al. (2004) observed higher diameter increase in *Handroanthus umbellatus* (Sond.) Mattos during the flooding and rain periods, and no growth or negative growth in the dry season which coincided with leaf abscission of older leaves and production of reproductive structures in a flooded forest in the Atlantic Rainforest in Rio de Janeiro, Brazil. *Handroanthus umbellata* and *V. divergens* are flood-tolerant plants because they keep increasing diameter increase during flooding.

Moreover, Schöngart et al. (2002) pointed out that the growth of the tree´s diameter in the Amazon basin is higher in the dry season than in the flood period, since flooding causes the drop of leaves that leads to numbness exchange. Trees develop a variety of mechanisms to compensate for the limitation of stomata conductance in the flooding, such as reduction in the supply of adenosine triphosphate (EPSTEIN; BLOOM, 2005), the accumulation of lactic acid and acidification of the cytoplasm (CRAWFORD, 1992; DREW, 1997;

OLIVEIRA; JOLY 2010), a decrease in permeability and hydraulic conductivity of the root, and an increase in the synthesis of abscisic acid (WILKINSON; DAVIES, 2002).

Schöngart et al. (2004) also highlighted that reduced water availability for vegetation due to low rainfall caused by El Niño makes growth rings of *Piranhea trifoliata* Baill. wider in the Venezuelan Amazon forest. Therefore, the interannual variation of diameter increment is higher in tropical forests than in temperate forests because of rainfall variations in the tropics (WORBES et al., 2003) which require long-term studies.

Dalmolin et al. (2013) conducted an experiment with seedlings of *V. divergens*. Results indicated a decrease in the production rate of leaves, plant height and gas exchange. Since these seedlings showed positive growth and carbon gain, they indicated tolerance to flooding. Dalmagro et al. (2013) pointed out that *V. divergens* showed no significant differences in net photosynthetic rate, stomata conductance, maximum rate of carboxylation of Rubisco, electron transport at saturating light and compensation point of carbon dioxide between the dry season and the flood period. The authors explained that their result is due to the sufficiency of water coming from the access to deep water sources by *V. divergens* during the dry season, despite the low water content on the soil surface (HAASE, 1999; BIUDES et al., 2009, 2014; VOURLITIS et al., 2011). However, there was no special dry season during the period studied by Dalmagro et al. (2013) since it rained every month.

The diameter increase of *V. divergens* was more affected by the dry season than by flooding due to low soil water content, leaf abscission and flower production. The dry season caused decrease in the soil´s water contents which reduced photosynthesis, increased respiration rate and reduction of primary productivity (TIAN et al., 1998). Growth rhythm is consequently related to climate seasonality. This is probably due to variations of the cambial activity and is connected with phenological periods. Long-term research should be developed to better understand the seasonal dynamics of diameter increase of *V. divergens*.

Conclusion

The seasonal variation of the diameter increase of *V. divergens* was evaluated in a seasonal floodable forest in the Northern Pantanal. The annual mean diameter increment of *V. divergens* was 4.0 mm for the study area. The highest increase occurred during the flooding period and lowest during the dry season and reproductive period. Thus, climate and phenology affected the growth rhythm of *V. divergens* in the study area.

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References

ARIEIRA, J.; KARSSENBERG, D.; DE JONG, S. M.; ADDINK, E. A.; COUTO, E. G.; NUNES DA CUNHA, C.; SKØIEN, J. O. Integrating field sampling, geostatistics and remote sensing to map wetland vegetation in the Pantanal, Brazil. **Biogeosciences**, v. 8, n. 1, p. 667-686, 2011.

ARIEIRA, J.; NUNES DA CUNHA, C. Estrutura populacional do cambará (*Vochysia divergens* Pohl, Vochysiaceae), espécie monodominante em floresta inundável no Pantanal Mato-grossense. **Oecologia Australis**, v. 16, n. 4, p. 819-831, 2012.

ARIEIRA, J.; NUNES DA CUNHA, C. Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. **Acta Botanica Brasilica**, v. 20, n. 3, p. 569-580, 2006.

BIUDES, M. S.; CAMPELO JÚNIOR, J. H.; NOGUEIRA, J. S.; SANCHES, L. Estimativa do balanço de energia em cambarazal e pastagem no norte do Pantanal pelo método da razão de Bowen. **Revista Brasileira de Meteorologia**, v. 24, n. 2, p. 135-143, 2009.

BIUDES, M. S.; MACHADO, N. G.; DANELICHEN, V. H. M.; SOUZA, M. C.; VOURLITIS, G. L.; NOGUEIRA, J. S. Ground and Remote Sensing-Based Measurements of Leaf Area Index in a Transitional Forest and Seasonal Flooded Forest in Brazil. **International Journal of Biometeorology**, v. 58, n. 1, p. 1181-1193, 2014.

BIUDES, M. S.; NOGUEIRA, J. S.; DALMAGRO, H. J.; MACHADO, N. G.; DANELICHEN, V. H. M.; SOUZA, M. C. Mudança no microclima provocada pela conversão de uma floresta de cambará em pastagem no norte do Pantanal. **Revista de Ciências Agro-Ambientais**, v. 10, n. 1, p. 61-68, 2012.

BORCHERT, R. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. **Ecology**, v. 75, n. 1, p. 1437-1449, 1994a.

BORCHERT, R. Water status and development of tropical trees during seasonal drought. **Trees - Structure and Function**, v. 8, n. 1, p. 115-125, 1994b.

BORCHERT, R.; RIVERA, G.; HAGNAUER, W. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. **Biotropica**, v. 34, n. 1, p. 27-39, 2002.

BREITSPRECHER, A.; BETHEL, J. S. Stem-periodicity of trees in a tropical wet forest of Costa Rica. **Ecology**, v. 7, n. 1, p. 1156-1164, 1990.

CALLADO, C. K.; SILVA NETO, S. J.; SCARANO, F. B.; COSTA, C. G. Radial growth dynamics of *Tabebuia umbellata* (Bignoniaceae), a flood-tolerant tree from the Atlantic Forest swamps in Brazil. **IAWA Journal**, v. 25, n. 2, p. 175-183, 2004.

CLARK, D. A.; CLARK, D. B. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. **Forest Ecology and Management**, v. 80, n. 1-3, p. 235-244, 1995.

CORINGA, E. A. O.; COUTO, E. G.; PEREZ, X. L. O.; TORRADO, P. V. Atributos de solos hidromórficos no Pantanal Norte Matogrossense. **Acta Amazonica**, v. 42, n. 1, p. 465-472, 2012.

CRAWFORD, R. M. M. Oxygen availability as an ecological limit to plant distribution. In: BEGON, M.; FITTER, A. H. (Ed.). **Advances in ecological research**. New York: Academic Press, 1992. v. 23, p. 93-185.

DALMAGRO, H. J.; LOBO, F. A.; VOURLITIS, G. L.; DALMOLIN, A. C.; ANTUNES, M. Z.; ORTÍZ, C. E. R.; NOGUEIRA, J. S. Photosynthetic parameters of two invasive tree species of the Brazilian Pantanal in response to seasonal flooding. **Photosynthetica**, v. 51, n. 2, p. 281-294, 2013.

DALMOLIN, A. C.; DALMAGRO, H. J.; LOBO, F.; ANTUNES, M. Z.; ORTÍZ, C. E. R.; VOURLITIS, G. L. Photosynthetic light and carbon dioxide response of the invasive tree, *Vochysia divergens* Pohl, to experimental flooding and shading. **Photosynthetica**, v. 51, n. 1, p. 379-386, 2013.

DAMASCENO-JÚNIOR, G. A.; SEMIR, J.; SANTOS, F. A. M.; LEITÃO-FILHO, H. F. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. **Flora**, v. 200, n. 2, p. 119-135, 2005.

DONG, S. X.; DAVIES, S. J.; ASHTON, P. S.; BUNYAVEJCHEWIN, S.; SUPARDI, M. N.; KASSIM, A. R, TAN, S.; MOORCROFT, P. R. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across 4 tropical forests. **Proceeding of the Royal Society Biological Science**, v. 279, n. 1, p. 3923-3931, 2012.

DREW, M. C. Oxygen deficiency and root metabolism: injury and acclimation under under hypoxia and anoxia. **Annual Review of Plant Physiology**, v. 48, n. 1, p. 223-250, 1997.

DÜNISCH, O.; BAUCH, J. Influence of soil substrate and drought on wood formation of spruce (*Picea abies* [L.] Karst.) under controlled conditions. **Holzforschung**, v. 48, n. 1, p. 447-457, 1994.

DÜNISCH, O.; MONTOIA, V. R.; BAUCH J. Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. **Trees-Structure and Function**, v. 17, n. 1, p. 244-250, 2003.

ENRIGHT, N. J.; HARTSHORN, G. S. The demography of tree species in undisturbed tropical rainforest. In: BORMANN, F. H.; BERLYN, G. (Ed.). **Age and growth rate of tropical trees**: new directions for research. Yale: School of Forestry and Environmental Studies, Yale University, 1981. p. 107-119. (Bulletin no. 94).

EPSTEIN, E.; BLOOM, A. J. **Mineral nutrition of plants**: principles and perspectives. 2nd ed. Sunderland: Sinauer Associates, Inc., 2005.

FANTIN-CRUZ, I.; GIRARD, P.; ZEILHOFER, P.; COLLISCHONN, W.; NUNES DA CUNHA, C. Unidades fitofisionômicas em mesoescala no Pantanal Norte e suas relações com a geomorfologia. **Biota Neotropica**, v. 10, n. 2, p. 31-38, 2010.

FICHTLER, E.; CLARK, D. A.; WORBES, M. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and C-14. **Biotropica**, v. 35, p. 306-317, 2003.

GOLDSMITH, F. B.; HARRISON, C. M. Description and analysis of vegetation. In: CHAPMAN, S. B. (Ed.). **Methods in plant ecology**. New York: Halsted Press, 1976. p. 85-156.

GRACE, J.; MALHI, Y.; LLOYD, J.; MCINTYRE, J.; MIRANDA, A. C.; MEIR, P.; MIRANDA, H. S. The use of Eddy Covariance to infer the net carbon dioxide uptake of Brazilian Rain Forest. **Global Change Biology**, v. 2, n. 1, p. 209-217, 1996.

GROTKOPP, E.; REJMÁNEK, M. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. **American Journal of Botany**, v. 94, n. 1, p. 526-532, 2007.

HAASE, R. Literfall and nutrient return in seasonally flooded and non-flooded forest of the Pantanal, Mato Grosso, Brazil. **Forest Ecology and Management**, v. 117, n. 1, p. 129-147, 1999.

HAMILTON, S. K.; SIPPEL, S. J.; MELACK, J. M. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. **Archiv für Hydrobiologie**, v. 137, n. 1, p. 1-23, 1996.

IWANAGA, F.; YAMAMOTO, F. Effects of flooding depth on growth, morphology and photosynthesis in *Alnus japonica* species. **New Forest**, v. 35, n. 1, p. 1-14, 2008.

JUNK, W. J.; BROWN, M.; CAMPBELL, I. C.; FINLAYSON, M.; GOPAL, B.; RAMBERG, L.; WARNER, B. G. The comparative biodiversity of seven globally important wetlands: A synthesis. **Aquatic Sciences**, v. 68, n. 3, p. 400-414, 2006.

JUNK, W. J.; NUNES DA CUNHA, C. Pantanal: a large South American wetland at a crossroads. **Ecological Engineering**, v. 24, n. 1, p. 391-401, 2005.

KIRK, G. **The biogeochemistry of submerged soils**. Chichester: John Wiley and Sons, 2004.

KOZLOWSKI, T. I.; KRAMER, P. J.; PALLARDY, S. G. **The physiological ecology of woody plants**. San Diego: Academic Press, 1991.

KRAMER, P. J. **Water relations of plants**. Orlando: Academic Press, 1985.

LANGENFELD-HEYSER, R. Distribution of leaf assimilates in the stem of *Picea abies* L. **Trees**, v. 1, n. 1, p. 102-109, 1987.

LARSON, P. R. **Wood formation and the concept of wood quality**. New Haven: Yale University, 1969.

LIEBERMAN, D.; LIEBERMAN, M.; HARTSHORN, G. S.; PERALTA, R. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. **Journal of Tropical Ecology**, v. 1, n. 1, p. 97-109, 1985.

LORENZI, H. **Árvores brasileiras**. São Paulo: Inst. Plantarum de Estudos da Flora, Ltd., 2002. v. 2.

MACHADO, N. G.; SANCHES, L.; SILVA, L. B.; NOVAIS, J. W. Z.; AQUINO, A. M.; BIUDES, M. S.; PINTO-JUNIOR, O. B.; NOGUEIRA, J. S. Soil nutrients and vegetation structure in a neotropical seasonal wetland. **Applied Ecology and Environmental Research**, v. 13, n. 1, p. 289-305, 2015.

MACK, R. N.; SIMBERLOFF, D.; LONSDALE, W. M.; EVANS, H.; CLOUT, M.; BAZZA, F. A. Biotic invasions: causes, epidemiology, global consequences, and control. **Ecological Applications**, v. 10, n. 1, p. 689-710, 2000.

NEIFF, J. J. Ideas for an ecological interpretation of the Paraná river. **Interciencia**, v. 15, n. 6, p. 424-441, 1990.

NUNES DA CUNHA, C.; JUNK, W. J. Distribution of wood plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. International Journal of **Ecology and Environmental Sciences**, v. 27, n. 1, p. 63-70, 2001.

NUNES DA CUNHA, C.; JUNK, W. J. Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. **Applied Vegetation Science**, v. 7, n. 1, p. 103-110, 2004.

NUNES DA CUNHA, C.; JUNK, W. J.; LEITÃO-FILHO, H. F. Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. **Amazoniana**, v. 19, n. 3-4, p. 159-184, 2007.

OLIVEIRA, V. C.; JOLY, C. A. Flooding tolerance of *Calophyllum brasiliense* Camb. (Clusiaceae): morphological, physiological and growth response. **Trees**, v. 24, n. 1, p. 185-193, 2010.

PAROLIN, P.; LUCAS, C.; PIEDADE, M. T. F.; WITTMANN, F. Drought responses of flood-tolerant trees in Amazonian floodplains. **Annals of Botany**, v. 105, n. 1, p. 129-139, 2010.

PENHA, J. M.; DA SILVA, C. J.; BIANCHINI, I. Productivity of the aquatic macrophytes *Pontederia lanceolata* Nutt. (Pontederiaceae) on the floodplains of the Pantanal Mato-grossense, Brazil. **Wetland Ecology and Management**, v. 7, n. 1, p. 155-163, 1999.

PEZESHKI, S. R.; DELAUNE, R. D. Soil oxidation-reduction in wetlands and its impact on plant functioning. **Biology**, v. 1, n. 2, p. 196-221, 2012.

PONNAMPERUMA, F. N. The chemistry of submerged soil. **Advances in Agronomy**, v. 24, n. 1, p. 29-96, 1972.

POTT, A.; POTT, V. J. **Plantas do pantanal**. Corumbá: Embrapa; CPAP, 1994.

R CORE TEAM. **R**: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, 2014.

REBELLATO, L.; NUNES DA CUNHA, C. Efeito do 'fluxo sazonal mínimo da inundação' sobre a composição e estrutura de um campo inundável no Pantanal de Poconé MT, Brasil. **Acta Botanica Brasilica**, v. 19, n. 4, p. 789-799, 2005.

REJMÁNEK, M.; RICHARDSON, D. M. What attributes make some plant species more invasive? **Ecology**, v. 77, n. 1, p. 1655-1661, 1996.

ROCHA, H. R.; GOULDEN, M. L.; MILLER, S. D.; MENTON, M. C.; PINTO, L. D. V. O.; FREITAS, H. C.; FIGUERA, A. M. S. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. **Ecological Applications**, v. 14, n. 1, p. 22-32, 2004.

ROCHA, H. R.; MANZI, A. O.; CABRAL, O. M.; MILLER, S. D.; GOULDEN, M. L.; SALESKA, S. R.; COUPE, N. R.; WOFSY, S. C.; BORMA, L. S.; ARTAXO, P.; VOURLITIS, G.; NOGUEIRA, J. S.; CARDOSO, F. L.; NOBRE, A. D.; KRUIJT, B.; FREITAS, H. C.; VON RANDOW, C.; AGUIAR, R. G.; MAIA, J. F. Patterns of water and heat flux across a biome gradient from tropical forest to savanna in Brazil. **Journal of Geophysical Research**, v. 114, n. 1, p. 1-8, 2009.

SALA, O. E.; AUSTIN, A. T. Methods of estimating aboveground net primary production. In: SALA, O. E.; JACKSON, R. B.; MOONEY, H. A.; HOWARTH, R. H. (Ed.). **Methods in ecosystem Science**. New York: Springer, 2000. p. 31-43.

SCHÖNGART, J.; JUNK, W. J.; PIEDADE, M. T. F.; AYRES, J. M.; HUTTERMANN, A.; WORBES, M. Teleconnection between tree growth in the Amazonian floodplains and the El Niño – Southern Oscillation effect. **Global Change Biology**, v. 10, n. 1, p. 683-692, 2004.

SCHÖNGART, J.; PIEDADE, M. T. F.; LUDWIGSHAUSEN, S.; HORNA, V.; WORBES, M. Phenology and stem-growth periodicity of tree spp in amazonian floodplain trees. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. **Journal of Tropical Ecology**, v. 18, n. 1, p. 581-597, 2002.

SILVA, R. P.; SANTOS, J.; TRIBUZY, E. S.; CHAMBERS, J. Q.; NAKAMURA, S.; HIGUCHI, N. Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. **Forest Ecology and Management**, v. 166, n. 1, p. 295-301, 2002.

SOKAL, R. R.; ROHLF, F. J. **Biometry**: the principles and practice of statistics in biological research. 3rd ed. New York: W.H. Freeman and Co., 1995.

STAHLE, D. W.; MUSHOVE, P. T.; CLEAVELAND, M. K.; ROIG, F. A.; HAYNES, G. A. Management implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. **Forest Ecology and Management**, v. 124, n. 1, p. 217-229, 1999.

TIAN, H.; MELILLO, J. M.; KICKLIGHTER, D. W.; McGUIRE, A. D.; HELFRICH III, J. V. K.; MOORE III, B.; VOROSMARTY, C. J. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. **Nature**, v. 396, n. 1, p. 664-667, 1998.

VIEIRA, S.; CAMARGO, P. B.; SELHORST, D.; SILVA, R.; HUTYRA, L.; CHAMBERS, J. Q.; BROWN, I. F.; HIGUCHI, N.; SANTOS, J.; WOFSY, S. C.; TRUMBORE, S. E.; MARTINELLI, L. A. Forest structure and carbon dynamics in Amazonian tropical rain forests. **Oecologia**, v. 140, n. 3, p. 468-479, 2004.

VOURLITIS, G. L.; LOBO, F. A.; BIUDES, M. S.; ORTÍZ, C. E. R.; NOGUEIRA, J. S. Spatial variations in soil chemistry and organic matter content across a *Vochysia divergens* invasion front in the Brazilian Pantanal. **Soil Science Society of American Journal**, v. 75, n. 1, p. 1554-1560, 2011.

VOURLITIS, G. L.; NOGUEIRA, J. S.; LOBO, F. A.; SENDALL, K. M.; DE FARIA, J. L. B.; DIAS, C. A. A.; ANDRADE, N. L. R. Energy balance and canopy conductance of a tropical semi-deciduous forest of the Southern Amazon Basin. **Water Resources Research**, v. 44, n. 3, p. 1-14, 2008.

WEI, W. W. S. **Time series analysis**: univariate and multivariate methods. 2nd ed. Boston: Pearson Addison Wesley, 2006.

WHITMORE, T. C. **An introduction to tropical rain forests**. New York: Oxford University Press, 1998.

WILKINSON, S.; DAVIES, W. J. ABA-based chemical signaling: the coordination of responses to stress in plants. **Plant, Cell and Environment**, v. 25, n. 1, p. 195-210, 2002.

WORBES, M. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. **Jounal of Ecology**, v. 87, n. 1, p. 391-403, 1999.

WORBES, M. How to measure growth dynamics in tropical trees - a review. **IAWA Journal**, v. 16, n. 1, p. 337-351, 1995.

WORBES, M.; STASCHEL, R.; ROLOFF, A.; JUNK, W. J. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. **Forest Ecology and Management**, v. 173, n. 1, p. 105-123, 2003.

ZEILHOFER, P.; SCHESSL, M. Relationship between vegetation and environmental conditions In the Northern Pantanal of Mato Grosso, Brazil. **Journal of Biogeography**, v. 27, n. 1, p. 159-168, 2000.

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