International Journal of Botany Studies
ISSN: 2455-541X, Impact Factor: RJIF 5.12
www.botanyjournals.com
Volume 2; Issue 3; May 2017; Page No. 06-15

Stomatal behavior of trees in high and low floodplain in the Brazilian Amazon

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Abstract

The seasonal flood pulse characteristic of Amazonian floodplains (*várzeas*) has direct effects on vegetation, influencing the physiological aspects of the species, such as stomatal conductance (gs). This study aimed to analyze the ecophysiological behavior regarding the stomatal conductance (*gs*) aspect of seven native plant species of Amazonian floodplain ecosystem in two distinct seasons (rainy and dry season) and in two topographic environments (high and low floodplain). The gs readings performed on healthy leaves with the aid of an AP4 Porometer at three different times throughout the day. The results showed high physiological plasticity in the studied species, where the process of water regulation by the leaf stomata exhibits a distinct behavior between the dry and rainy periods. It was more homogeneous during the dry period, where there was a reduction in gas rates. *N. macrophylla* was the most tolerant species to water deficit of the dry period and *S. reticulata* the most sensitive. The most tolerant species to flooding was *C. tapia* and the most sensitive *G. brasiliensis.* These results suggest different ecophysiological behaviors of native Amazonian floodplain species, suggesting different management practices in the face of local and global climate change.

Keywords: plant physiology, seasonality, várzea, amazon

1. Introduction

In the Amazon, floodplains (várzeas) ecosystems covers an area of 200,000 km2 (Junk, 1993) [18]. They are river plains provided with forests periodically flooded by white water rivers (Prance, 1980) [38] that present extensive areas rich in natural resources, with an exuberant fauna and flora, whose peculiar characteristics are of great ecological, economic and social importance. White water rivers, such as the Amazon River, are rich in suspended sediments originating from parental material from Andean and pre-Andean soils, which began to settle in the Holocene some 10,000 years ago (Prance 1980, Sioli 1984) [38, 50]. Thus, floodplain soil presents a high nutrient content and constant renewal (Sioli and Soares, 2006) [51] caused by the annual rainfall cycle that allows a characteristic flood regime for these areas: flooding (rainy season) and drying (less rainy season), being designated as seasonal várzea (Almeida *et al*., 2004) [3].

Due to this, the Amazon River overflows among the lowland forests in a regular fluctuation cycle of its water level, a monomodal hydrological regime, that is, it has a unique annual flood pulse (Junk *et al*., 1989) [17, 19], whose maximum peak occurs between the months of March and July. On the other hand, we have the period of drought, between September and November (Barbosa *et al*., 2008) [4]. For years, the height of the water column has reached 10 m and can subject the forests to a flood or submersion that can last up to 210 days (Junk, 1989, Junol *et al*., 1989, Parolim, 2000) [17, 19].

Flooding is the main natural factor that limits the establishment of many plant species in floodplain areas due to water saturation and hypoxia (low concentrations of O2) of the soil, subjecting them to the development physiological or morphoanatomical mechanisms (Junk, 1989; Almeida *et al*., 2004; Silva *et al*., 2012) [17, 19, 3, 49, 52]. Among the main adaptations are: changes in the metabolic pathways for fermentative pathways and elimination of toxic volatile products, such as ethanol, ethylene and acetaldehyde accumulated during hypoxia (Ferreira *et al*, 2006) [11]; total or partial deciduous leaves (Almeida *et al*., 2004) [3] in order to avoid loss of water. Associated with growth reduction of some organs (Junk, 1993; Almeida *et al*., 2004; Carvalho *et al*., 2002) [18, 3] and also carbohydrate accumulation (Parolin *et al*., 2002) [42], lenticel hypertrophy, aerenchym formation and adventitious and superficial roots or tubular roots that guarantee greater sustentation of large trees (Silva *et al*., 2012) [49, 52]; (Almeida *et al*., 2004) [3]. The fruiting and dispersal observed by Junk (1993) [18], occurring for most species during the flood period by means of fish (Batista *et al*., 2008) [5, 15].

The stomatal conductance (gs), is of fundamental importance since it is an ecophysiological factor that controls the vital processes of plants, since it regulates gas exchanges (CO_2 and O_2) between the plant and the atmosphere, limiting water losses and acting as a potential water indicator (Landsberg, 2003; Nogueira *et al*, 2004) [24, 37]. Considering floodplains forests to being fundamental ecosystems in the contribution both to carbon sequestration and to the recycling air humidity, this research pretended diagnostic some stomatal behavior of floodplains trees. Studies by Kallarackal and Somen (1997) [20] have revealed that throughout the day there is a regular pattern in the physiological behavior performed by stomata. These authors observed that in the morning, the stomatal conductance rates are higher and during the afternoon, their values reduced, suffering direct influence of the global radiation balance and the vapor pressure deficit (DPV). In the times of greater demand evaporative of atmosphere, a reduction of *gs* observed as an evolutionary strategy to potentiate the efficiency in water use. According to Landsberg (2003) [24], the progressive reduction of the stomatal opening capacity constitutes the first line of defense of the plants under conditions of strong water stress, in order to avoid plant desiccation and death, but also directly affects the efficiency of water use and the conditions of gas exchange.

The water stress conditions caused by the excess water in the rainy season, and the lack of it, in the dry period, cause seasonal physiological adjustments in the *gs* rates of the floodplains (várzeas) species (Lopez and Cursar, 2003) [27]. The reductions in *gs* of certain species when subjected to dry stress water stress is a physiological strategy to avoid excessive loss of water and maintain its metabolic activities (Marenco and Lopes, 2005) [31]. In the rainy season, flooding of the soil causes a greater control of the *gs*, and the degree of stomatal opening ends up determining the difference between tolerant and non-tolerant species to flood stress (Mielke *et al*., 2003) [36]. Thus, the controls of the *gs* of the forest species are fundamental to guarantee their permanence in a heterogeneous environment such as the Amazonian floodplains (Nogueira *et al*., 2004) [37].

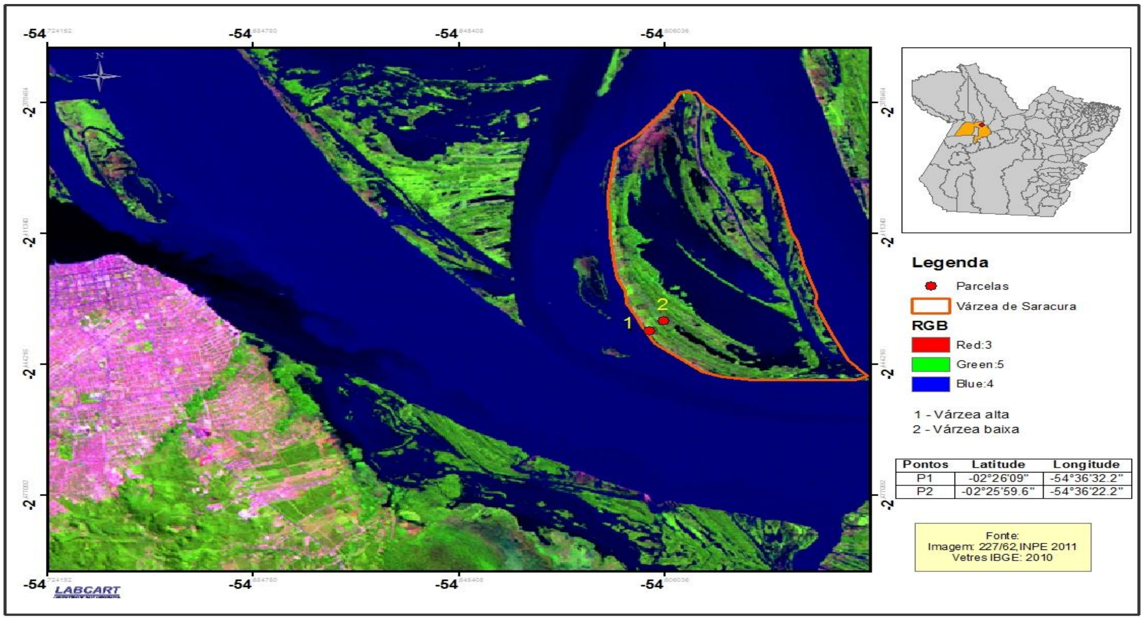
On the other hand, ecological differences caused by the topography of the Amazonian floodplains may influence the stomatal conductance rates of species found in this environment. According to the relief, Porro (1998) [44] classifies two types of floodplain: high (refers to the ecosystem closest to the river results from the largest deposition of sediments over time) and low (the portion of receding land with Igarapé, temporary and permanent lakes). Thus, individuals of the same species expected to exhibit different stomatal control depending on the environment in which they found. It is noteworthy that studies of this nature are non-existent for the Amazon.

Additionally, studies show that there will be an increase in atmospheric CO_2 and temperature, as well as changes in the availability of water in the Amazon, influencing the flood and dry period (Grandis *et al*., 2010) [13]. Thus, in the uncertainty of what will occur with floodplains plant species if the expected conditions for global climatic changes accelerate, the plant ecophysiological behavior could be a great bio indicator. The plant physiological responses are fundamental to help in understanding how the trees of tropical regions of natural flooding and drought will respond to possible future environmental variations. Based on the hypothesis that the plant species of floodplains present different ecophysiological responses of stomatal conductance (*gs*) as a function of the seasonality and topographic distribution, the present research aimed to characterize the stomatal behavior of seven native plant species of Amazonian floodplain ecosystem. This research will conducted in two distinct seasons (rainy and dry) and two different topographic environments (high and low floodplain).

2. Material and methods

Study area

The study area is located in Amazonian floodplain, in Afro descendent (quilombola) community, called Saracura, belonging to Santarém city, Western Pará, territory of Low Amazon, between coordinates 02 ° 22'01.5 "S and 54 ° 36 ' 40.3 "W (Figure 1).



Pontos	Latitude	Longitude
P1	-02°26'09"	-54°36'32.2"
P2	-02°25'59.6"	-54°36'22.2"

Fonte:
Imagem: 227/62,INPE 2011
Vetres IBGE: 2010

Fig 1: Location of study area, Saracura floodplain. Note the presence of two plots, one in the high floodplain (várzea) (1) and the other in the low floodplain (2). Santarém-Para, Territory of Low Amazon, Brazil.

The climate of region is Ami type, hot and humid equatorial (Köppen, 1948) [23]. The mean annual temperature varies between 25.4 ° C and 27.1 ° C and relative air humidity is around 86% all year round. Although it presents a greater variation in the rainfall pattern, it determines two very different periods: a rainy season (December to June) and a less rainy season or dry season (July to November), with annual average values around 1,920 mm (Rodrigues *et al*., 2001) [47]. Soil considered naturally fertile and rich in nutrients, as it renewed through annual floods that deposit sediments at its margins (Sioli and Soares, 2006) [51]. In this way, they undergo both sedimentary and topographic influences related to the level of flood, which gives rise to two distinct environments: the "low floodplain" with the Glei Little Humic soil remaining temporarily flooded and the "high floodplain" presenting Yellow Latosol more compacted with Low water influence (Jardim and Viera, 2001) [16].

Selection and identification of species

An area of native vegetation was selected where two plots of 50 x 50 m were demarcated, one in the high várzea strip at 0,40 m of the river and another in the low várzea at 180 m of the same. Seven native plant species considered useful for the Saracura community selected as a function of the relative frequency of citation (FRC) and value of use (VU) (Cavalcante and Oliveira, 2017) and that occurred in both environments (Table 1). The botanical samples collected georeferenced and dehydrated for later identification. The fertile exsiccates deposited in the Herbarium of the National Research Institute of the Amazon.

Table 1: Species studied in the floodplain of quilombola community of Saracura. FRC means Relative Frequency of Citation; VU means valour of specie use.

Common name	Specie	Family	Habit	FRC	VU
Catauarizeiro	*Crataeva tapia* L.	Capparidaceae	Arboreal	56	0.78
Bacurizeiro	*Garcinia brasiliensis* Mart.	Clusiaceae	Arboreal	44	0.65
Mungubeira	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	Bombacaceae	Arboreal	47	0.56
Meracoroeira	*Laetia corymbulosa Spruce ex Benth*	Salicaceaceae	Arboreal	38	0.43
Loro	*Nectandra cuspidata* Nees & Mart.	Lauraceae	Arboreal	9	0.15
Matapasto	*Senna reticulata* (Willd.) H.S.Irwin & Barneby	Leguminosae	Arboreal-shrub Arboreal	19	0.09
Parreira	*Neea macrophylla* Poepp. & Endl.	Nyctaginaceae	Arboreal	6	0.06

Analysis of stomatal conductance

For determination of stomatal conductance (*gs*-mmol H_2O / m^{-2} / s^{-1}), eight leaves were selected from the lower part of the canopy, not detached, full expanded). Measurements were made using an AP4 (ΔT Devices, Cambridge, England) and occurred on two consecutive days during the rainy season (June) and the dry period (October). A daily course from 8:00 a.m. to 9:30 p.m., at 12:30 p.m. and from 5:00 p.m. to 6:30 p.m., under natural conditions of photosynthetically active radiation (PAR) and atmospheric CO_2 (350 ppm). In the low floodplain, the height of the water slide varied from 1.26 - 3.88 cm and in the high floodplain of 0.69 - 2.71 cm.

Soil collection for Humidity characterization

The moisture content (U) of the soil in each topographic environment in low floodplain (U = 51%) and high floodplain (U = 28%) was determined by thermogravimetric method, according to Embrapa (1997) [10].

Statistical analyzes

The statistical program used was BioEstat, Version 5.0 (Ayres *et al*., 2007) [2], through Analysis of Descriptive Statistics, Analysis of Variance (ANOVA), Multivariate Analysis by the test of Hotelling and Bartlett, besides Regression Analysis with adjustment of Curves.

3. Results and Discussions

The ecophysiological responses of stomatal conductance of *G. brasiliensis, C. tapia, N. cuspidata, S. reticulata, L. corymbulosa, P. munguba, N. macrophylla* are homogeneous in the dry period and heterogeneous in the rainy season (Figure 2). In general, the species studied showed a reduction in *gs* during the dry period, with variation of $10.68 < gs < 423.88$ mmol H_2O / m^{-2} / s^{-1} in low floodplain and $22.48 < gs < 302.38$ mmol H_2O / m^{-2} / S^{-1} in high floodplain (Figure 2, C and D). This behavior possibly occurs because, as there is water restriction in the soil, the plants tend to restrict the opening of stomata in order to avoid the loss of water to the atmosphere and ensure the maintenance of their physiological activities dependent on water, such as photosynthesis (Marenco and Lopes, 2005) [31]. This type of stoma response is an evolutionary adaptation of the species to conserve water when there is high evaporative demand of the atmosphere, which usually occurs in the dry period (Machado *et al*., 2002) [30]. Water saving is a strategy used by most plants to withstand critical water stress situations (Santos and Carleso, 1998) [48]. Thus, it suggested that the species studied could adapt to possible future climate changes, such as extreme droughts. In the rainy season, *G. brasiliensis and N. macrophylla* were the species that showed the greatest control in the *gs* in both environments, low floodplain and high floodplain, suggesting that these species are less tolerant to flooding then others (Maurenza *et al*., 2009; Vartapetian and Jackson, 1997) [33, 56].

However, most of the plants studied did not present this reaction, since the highest *gs* values were found for the rainy season, varying in average of $61.31 < gs < 1799.75$ mmol H_2O / m^{-2} / s^{-1} in low floodplain and $31.75 < gs < 1459.88$ mmol H_2O / m^{-2} / s^{-1} in the high floodplain (Figure 2, A and B). The species *C. tapia* (1,799 mmol H_2O / m^{-2} / s^{-1}) and *L. corymbulosa* (1,650 mmol H_2O / m^{-2} / s^{-1}) in the low floodplain and *N. cuspidata* (545 mmol H_2O / m^{-2} / s^{-1}) and *P. munguba* (878 mmol H_2O / m^{-2} / s^{-1}) in the high floodplain indicate that they are the most tolerant to flooding, since they presented lower control in the *gs*. Similar results found by Parolin *et al*. (2001) [40-41], which found in *S. reticulata* and species belonging to the genera *Crataeva* and *Nectandra*, also found in this study, high stomatal conductance rates during hypoxia conditions caused by soil flooding. The maintenance of high values of stomatal conductance and consequently of the photosynthetic rate can guarantee the survival and growth of some species as a consequence of morphological changes even under soil hypoxia conditions, such as the biomass allocation to the root system in order to increase the absorb and transport water (Mielke *et al*., 2005) [35]. In addition, plants also be increase the formation of adventitious roots and lenticels that facilitate gas exchange, contributing to O_2 fixation and the release of potentially toxic compounds such as ethanol, ethylene and acetaldehyde, which often accumulate during Hypoxia (Batista *et al*., 2008) [5, 15].

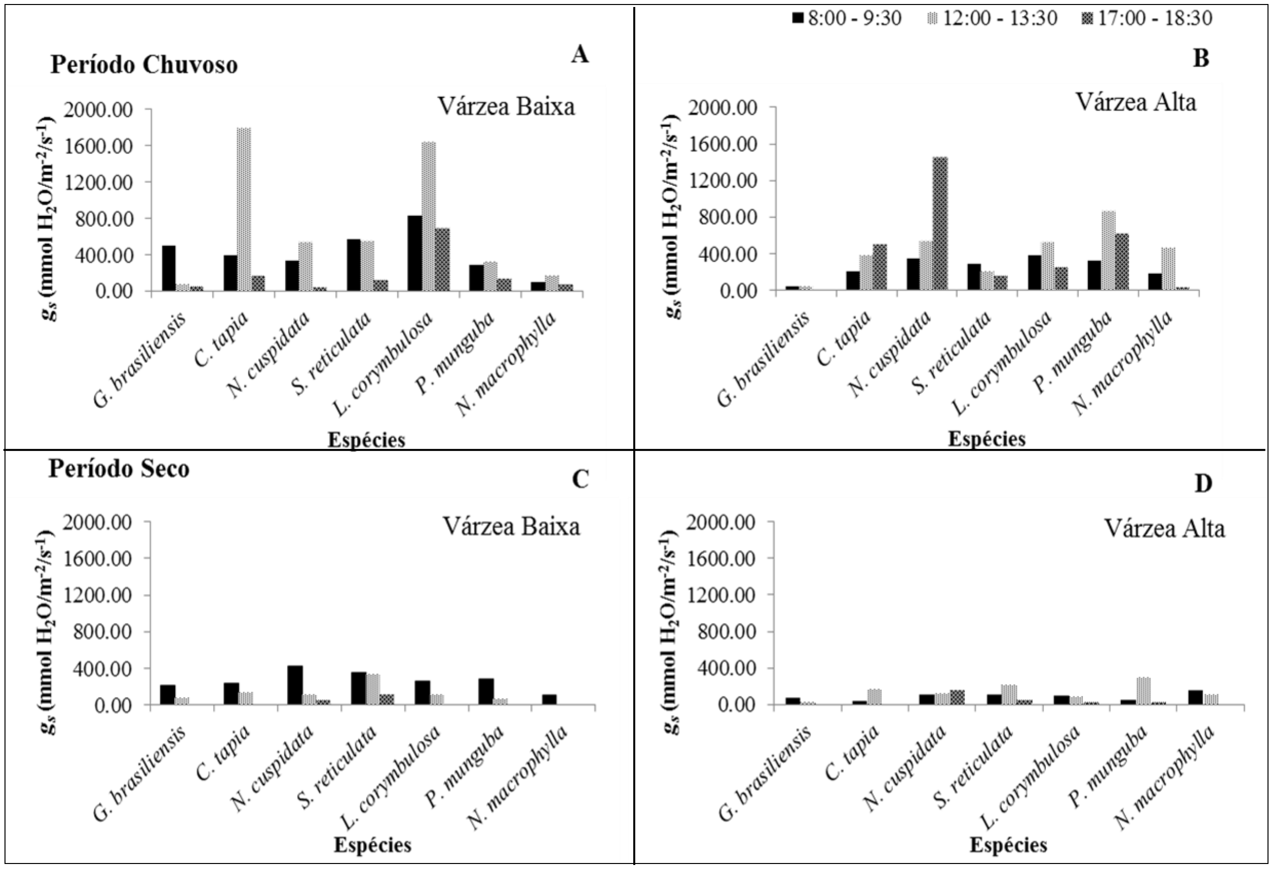


Fig 2: Stomatal conductance (*gs* H_2O / m^{-2} / s^{-1}) on leaves of seven species at three distinct times a day (8:00; 12:00 and 17:00h) in low floodplain (water column 1.26 - 3.88 cm, A and C) and high floodplain (water column 0.69 - 2, 71 cm, B and D), Santarém, Pará, Brazil.

However, the results of the Variance Analysis for two criteria revealed that the water regulation process carried out by the stomata differed between the species found in the low floodplain in both seasonal, rainy (p = 0.04) and dry (p = 0.01) periods and between the species found in the high floodplain, only during the dry period (p = 0.05) (Figure 1).

For the rainy period in the low floodplain, the flood influenced the rates of *gs* for the species *C. tapia* and *L. corymbulosa* at noon. At that time there is a higher evaporative demand for the atmosphere (Kitão, 2000), for this reason, species less resistant to water losses exert stomatal control, which was not the case for *C. tapia and L. corymbulosa*, thus they are more resistant to stress caused by the flood, since they did not exercise this control in the *gs*. In dry periods there was a rigid control in stomatal conductance (*gs)* of species that occurred in the low and high floodplain. This fact can attributed to the high DPV (vapour pressure deficit), which even in the Amazon during this period is high; since the humidity contained in the atmosphere is lower (Rodrigues *et al*, 2011) [46].

These results suggest that there is a variable physiological plasticity between species regarding the process of *gs* against environmental conditions, with a greater or lesser potential for stomatal aperture restriction which, although it is primarily related to environmental factors such as light, temperature and humidity (Rodrigues *et al*., 2011) [46], has a strong influence for flooding (Figure 2).

The flooding is a condition of water stress due to excess water in the soil leads to a decrease in water absorption by plant and consequently the reduction in *gs* as a strategy to avoid water loss (Kolb *et al*., 1998) [22]. Silva *et al*. (2012) [49, 52], report that even in flooded environments, plants also suffer from lack of water. However, it is noted that certain flood tolerant species show an initial drop in the *gs* followed by a recovery days later during the flooding period (Mielke *et al*., 2005) [35].

The Analysis of Variance (ANOVA) for one criterion allowed understand how in fact the schedules influence the *gs* rates of the floodplains species. In the early morning hours (8:00 am to 9:30 am), the mean values of *gs* differed significantly during the rainy season, low floodplain *(p* = 0.0002) and high floodplain (p = 0.001). Dry period, in both topographic environments (p <0.0001). This indicates that the differences of *gs* of the species in floodplain environments are punctual with intrinsic physiological responses of each one acquired during the evolution process, that associated to environmental factors potentiate their performance (Silvestrini *et al*., 2007) [54]. The *L. corymbulosa* species, in the dry period, in the low várzea and *N. macrophylla* in the dry period in both topographic environments presented the highest stomatal conductance. Thus, it suggested that *L. corymbulosa* and *N. macroplylla* are efficient in maintaining their metabolic activities in the early hours of the morning, as they may be carrying high photosynthetic rates as consequence of their high *gs* (Machado *et al*., 2002) [30]. The most uniform variation of solar radiation in both rainfall (PAR 86 - 95 μmol.m^{-2}.s^{-1}) and dry (254 - 262 μmol.m^{-2}.s^{-1}) (Cascardo *et al*., 1993) [7], which may have contributed to the high conductances in these species when water potentials are possibly high and not capable of inducing stomatal closure. This relationship also observed in several studies (Carvalho *et al*., 1998, Costa *et al*., 2007) [6, 8]. From 12:00 to 1:00 p.m., the mean of *gs* between species also differed significantly during the rainy and dry periods, in the low floodplain and in the high floodplain. In the rainy season, *C. tapia* in the low floodplain and *P. munguba* in the high floodplain had high conductances in response to high irradiance; suggest have a better ecophysiological performance. They can use in an efficient way the available abiotic resources of the most critical time of the day, such as photosynthetically active radiation (PAR), favoring the carboxylation of organic compounds, as well as the increase in electron transport and photochemical yield (Gonçalves *et al*, 2012) [14]. This physiological plasticity caused by acclimatization to the light environment is fundamental for the establishment, growth and survival of tree species (Santos *et al*., 2012) [49].

In the dry season, *S. reticulata*, in the low floodplain, and *P. munguba*, in the high floodplain, presented high conductances differing from other species in the time of 12:00 to 13:30. It suggested that these species will more sensitive in cases of extreme droughts because they do not regulate the stomatal pore opening. On the other hand, according to Lee *et al*. 2000 [26], morphophysiological adjustments or changes in leaf characteristics related to photosynthesis, such as stomatal density, can occur as a mechanism of acclimatization the stress situation at high irradiances, which depend either on genetic or environmental factors. Studies show absence of uniformity in the opening of the stomata on the leaf surface (Marenco *et al*., 2006) [32], this fact can guarantee the assimilation of carbon, influencing gas exchanges, such as photosynthesis and transpiration, as a way to maintain high energy levels and ensure rapid growth before flooding. Some species, such as *S. reticulata*, present a reduction in biomass, photosynthesis (A) and photochemical yield as a response to water stress that is accentuated at noon especially in the dry season (Parolin, 2001) [40-41]. However, they invest in the initial phase of life with a rapid sprouting growth increasing in height as a strategy to escape from submersion (Parolin *et al*., 2002) [42].

From 17:00 to 18:30, the studied species presented significant mean differences in their *gs* process in both topographic environments and seasonal periods analyzed (p <0.0001). In the rainy season *L. corymbulosa* and *N. cuspidata*, and dry period *S. reticulata and N. cuspidata*, differed from the other species with the highest *gs* rates. It suggested that these species are more efficient when presenting high rates of *gs* and possibly high photosynthetic rates, even with the reduction of solar radiation in the observed time, probably this fact related to the recovery in the state of hydration of the leaf in the late afternoon is fundamental for carbon assimilation (Costa and Marenco, 2007) [8].

The multivariate analysis by the Hotelling test allowed comparing the magnitude of this ecophysiological behavior between the seasonal (rainy and dry) periods, among the species studied (variables). In each topographic environment (lowland and highland) and in each time analyzed it was observed that there was a significant distinction in the *gs* of species between two seasonal periods, at 12:00 - 13:30 and 17:00 - 18:30 h in the low várzea *(p* <0.0001) (Table 2). These results suggesting that predisposing factors in the low floodplain, such as soil water saturation in the rainy season and the reduction of soil water potential in the dry period, probably contribute to water leaf status variation and their process of water regulation by stomata (Carvalho *et al*., 1998; Costa and Marenco, 2007) [6, 8]. Since these processes are also commonly associated with the DPV, which varies between the two seasonal periods and consequently influences the *gs* variations. The reduced water in atmosphere as it occurs in dry period, the vapor pressure deficit increases, and consequently, increases the stomatal conductance and the inverse usually occurs in the rainy season (Rodrigues *et al*., 2011) [46].

The species *N. macrophylla, P. munguba and G. brasiliensis*, in this order, demonstrated greater efficiency than the other species in the control of water losses from 12:00 to 13:30 h from the dry period in the low floodplain (Table 3). Therefore, in future scenarios of extreme droughts and high air temperatures, they are more efficient in critical environmental situations, since they can reduce water losses, reduce *gs*, conserve water and photo protection (Valladares and Pearcy 1997) [55]. Once the natural exposure to high photosynthetically active radiation (1.250 μmol.m^{-2}.s^{-1}), at this time, could saturate the photosynthesis in species acclimated to the sun and cause photo inhibition, that is, the reduction of photosynthesis when exposed to high radiation (Maruyama *et al*., 2005) [34]. On the other hand, *S. reticulata* proved to be more sensitive to water stress, since it presented the highest conductances. In the rainy season, *G. brasiliensis* seems to be the least tolerant species to the flooding of its roots since its conductance reduced considerably. On the other hand, *C. tapia* seems to be the most tolerant to present high conductances, especially in response to the high PAR (800 μmol.m^{-2}.s^{-1}) of the half-day time, even under flood stress. These two conditions, photosynthetically active radiation and water, contribute to the maintenance of metabolic processes dependent on these factors (Larcher, 2006) [25].

Table 2: Multivariate Analysis using the Hotelling Test to compare two seasonal periods (rainy and dry) from the *gs* (mmol H_2O / m^{-2} / s^{-1}) responses of seven species studied on low floodplain and high floodplain and for each time (8:00 - 9: 30 a.m. – 12:00-13:30 p.m. – 17:00-18:30 p.m.)

	Rainy x Dry		
	Low floodplains		
Horários =	8:00 - 9:30	12:00 - 13:30	17:00 - 18:30
T2 (Hotteling) =	130.8611	965.3657	1652.068
(p) =	0.9983	< 0.0001	< 0.0001
		High floodplains	
Horários =	8:00 - 9:30	12:00 - 13:30	17:00 - 18:30
T2 (Hotteling) =	220.1544	519.9941	358.2719
(*p*) =	0.9997	1	0.9998

Table 3: Multivariate analysis using Hotelling test for comparison the *gs* responses (mmol H_2O / m^{-2} / s^{-1}) of seven species (*G. brasiliensis, C tapia, N. cuspidata, S. reticulata; L. corymbulosa; P. munguba; N. macrophylla*) on two seasonal periods (rainy and dry) respectively with PAR= 800 - 980 µmol.m^{-2}.s^{-1} and dry season with PAR= 1.250 - 1.270 µmol.m^{-2}.s^{-1}) from 12:00 to 13:30 h.

Species	***G. brasiliensis***	***C. Tapia***	***N. cuspidata***	***S. reticulata***	***L. corymbulosa***	***P. munguba***	***N. macrophylla***
Mean Rainy season	86.43	1799.75	550.62	556.25	1650	334	178.25
Mean Dry season	82.43	140.5	124.875	339.5	118.25	73.8	32.07
(*p*) =	0.0001						

However, the ecophysiological behavior of floodplain species as a function of topographic distribution at each time and seasonal period analyzed, revealed from the multivariate analysis by the Hotelling test (Table 4) that the *gs* responses of individuals of same species were heterogeneous between low and high floodplain ($p = 0.0001$), only in the dry period from 8:00 a.m. to 9:30 p.m. It suggested that the differences in *gs* of individuals of each species in the dry period between topographic environments are due to variation in soil moisture content, which in low floodplain was 51% and in the high floodplain was 28%. Although these differences occurred only in the early hours of the morning, it suggested that this fact is due to the effects of solar radiation that in the early hours of the morning was high and varied between the environments of 254 µmol.$m^{-2.}$ S^{-1} and 462 µmol.m^{-2}.s^{-1}, respectively, in the low floodplain and the high floodplain. On the other hand, at other times (12:00 - 13:30 and 17:00 - 18:30 h) the behavior was homogeneous, that is, when the individuals of the same species were analyzed, there are no differences in the strategy of water losses in function of its topographic distribution in the dry period.

The survival and composition of species in extremely dynamic environments such as floodplains (flood periods followed by drought periods) depends on several factors, among which the regulation of stomatal conductance is one of the main ones (Lopez and Cursar, 2003) [27]. In this way, the difference in the *gs* rates between species can have a great impact on their performance in the colonization of heterogeneous environments (Nogueira *et al*., 2004) [37], besides emphasizing the difference between successional groups (Parolin *et al*., 2001, Lorenzi, 2009b, Lorenzi, 2009a) [40-41, 28, 29]. Stomatal conductance (*gs*), and growth rates are high in pioneer species compared to non-pioneer species, since the behavior of pioneer species is typically opportunistic using resources according to availability in the environment (Nogueira *et al*., 2004) [37].

Table 4: Multivariate Analysis using Hotelling Test to compare two topographic environments (low floodplain and high floodplain) from *gs* (mmol H_2O / m^{-2} / s^{-1}) of seven species (S. brasiliensis, C. tapia, N. cuspidata, S. reticulata, L. corymbulosa, P. munguba, N. macrophylla) for each seasonal period (dry and rainy) and for each time analyzed (8:00 - 9: 30 a.m. – 12:00-13:30 p.m. – 17:00-18:30 p.m.).

	low floodplain X high floodplain		
	Dry season		
Hours	8:00 - 9:30	12:00 - 13:30	17:00 - 18:30
T2 (Hotteling) =	1830.011	131.8854	65.9239
(p) =	< 0.0001	0.9984	0.9848
	Rainy season		
Horários =	8:00 - 9:30	12:00 - 13:30	17:00 - 18:30
T2 (Hotteling) =	101.9649	93.5585	191.1549
(p) =	0.9961	0.9949	0.9995

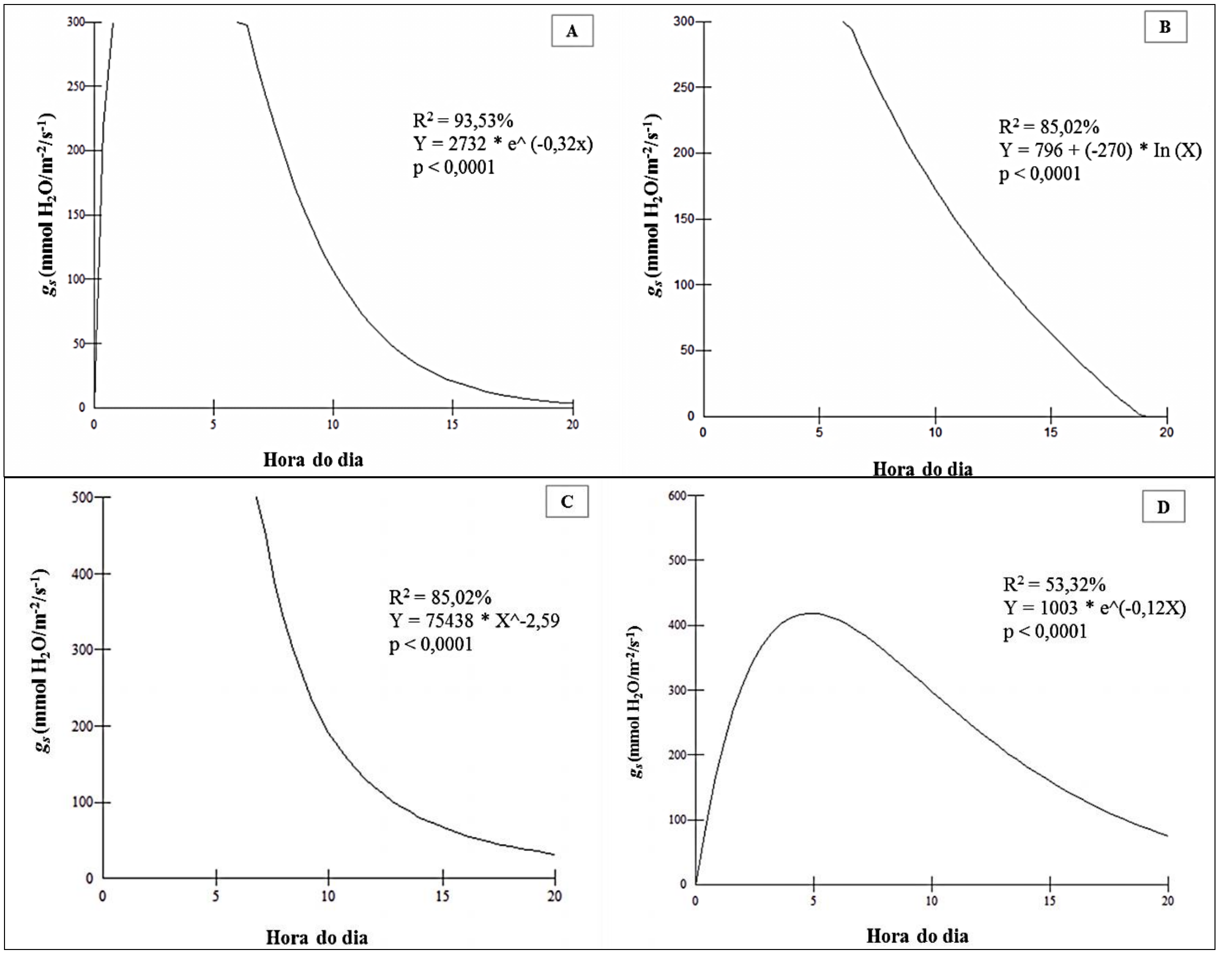
The Multivariate Analysis by Bartlett Test showed that when a systematic analysis between three schedules taken into account, there is a significant difference in the *gs* of species studied between the times analyzed in each topographic environment (low and high floodplain), rainy season and Dry period. The physiological process of *gs* between species throughout the day are similar to each other, since they presented high coefficients of maximum likelihood. The species have a maximum similarity (101%) in their ecophysiological behavior through the *gs* process in the low floodplain, in the dry period. This indicates that plants under water stress (water lack) situation have homogeneous day-to-day *gs* responses (Table 5).

Table 5: Multivariate Analysis by Bartlett Test for comparison of stomatal conductance (*gs* mmol H_2O / m^{-2} / s^{-1}) at three different times (8:00 - 9: 30 a.m. – 12:00-13:30 p.m. – 17:00-18:30 p.m.) of *C. brasiliensis, C. tapia, N. cuspidata, S. reticulata, L. corymbulosa, P. munguba, N. macrophylla.* The species are distributed in low floodplain (Water column= 1.26 - 3.88 cm) and in high floodplain (water column= 0.69 - 2.71 cm) during the rainy and dry season.

Seasons	Rainy		Dry	
	Low floodplains	**High floodplains**	**Low floodplains**	**High floodplains**
Phi (Maximum Similarity Coeficiente)	68.2347	93.6472	101.6222	88.9409
(p) =	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Number of Variable =	7			

In fact, the physiological behavior of *gs* throughout the day is homogeneous among species that occur in the low floodplain during the dry period. Since the regression analysis showed that species studied presented the same pattern of *gs* in the three times analyzed throughout the day, although the mathematical models that conformed to this behavior varied among them (Figure 3). The water regulation by stomata follows a pattern in a daily course, in which in the early hours of the morning the gas rates are high decreasing progressively throughout the day (Kallarackal and Somen, 1997) [20]. In this way, it observed that the timetable significantly influences the stomatal control of water losses. These variations in gs are found in several studies and follow a physiological pattern of the majority of the species that occur in floodplains (Carvalho *et al*., 1998; Costa and Marenco, 2007) [6, 8]. In the early hours of the day, Passos *et al*. (2005) [43] suggest higher gas rates found as result of the leaf water potential effect, which is high at this time. At midday and throughout the afternoon, this process of water regulation reduced as a strategy to avoid excessive water loss, during times of greater evaporative demand of the atmosphere (Rodrigues *et al*., 2011) [46].

Besides the ecophysiological strategy presented for the species under study, other adjustments at the molecular level may also be acting (Maurenza *et al*., 2009) [33], as the production of carbohydrates in the dry season before the rise of the waters (Simoni *et al*. (2003). Alternatively, the metabolic shift of the alcoholic fermentation pathways with the release of potentially toxic gases such as ethanol (Ferreira *et al*., 2009) [12]. In this way, it suggested that future studies carried out to understand the physiological plasticity of these species in a more comprehensive way to make it possible to infer if the effects of global climate change will have consequences on their distribution in the Amazonian floodplains.



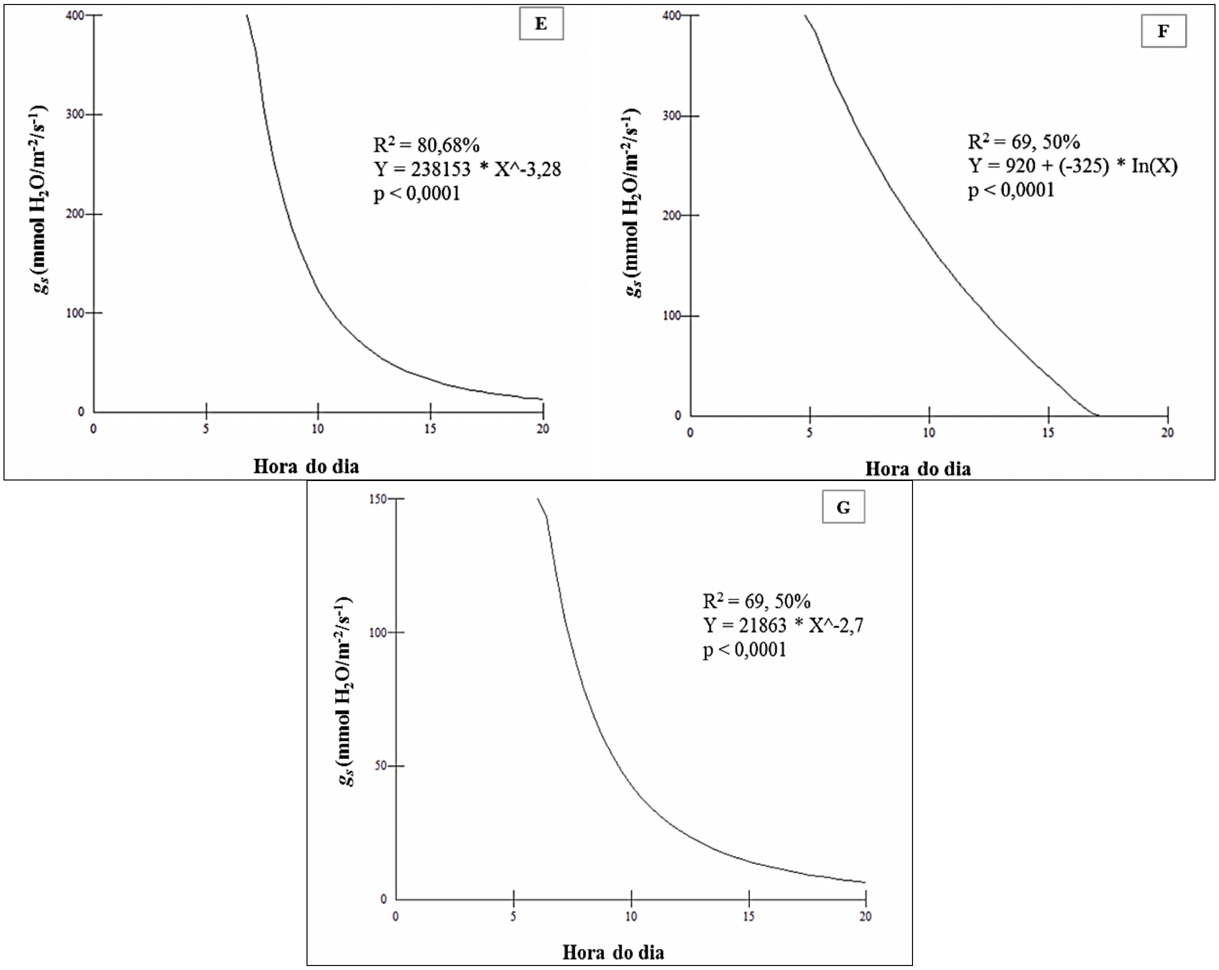


Fig 3: Regression Analysis of stomatal conductance (*gs* mmol H_2O / m^{-2} / s^{-1}) according to schedules (8:00 a.m. - 9:30 p.m. – 12:00-13:30 p.m.: 17:00-18:30 p.m.). Exponential model of *G. brasiliensis* (A); Logarithmic model of *C. tapia* (B); Geometric model of *N. cuspidata* (C), Exponential model of *S. reticulata* (D), Geometric model of *L. corymbulosa* (E), Logarithmic model of *P. munguba* (F); Geometric model of *N. macrophylla* (G) In the low várzea, in the dry period.

4. Conclusions

The Amazonian floodplain vegetation presents high physiological plasticity; there is a difference in stomatal behavior of trees between the dry period and the rainy season on floodplains. Associated, the rainy season confers heterogeneity of plant physiological response. The dry period confers homogeneity physiological responses. The stomatal conductance of species varied according to topographic distribution only in dry period, in the first hours of morning. The most tolerant species to water deficit on dry period was *N. macrophylla* and the most sensitive was *S. reticulata.* However, the most tolerant species to water stress in rainy season was *C. tapia* and the most sensitive species was *G. brasiliensis.* Therefore, attention should paid to these species when considering global climate change.

5. Acknowledgements

To Laboratory of Amazonian Ecosystems Studies (LEEA-IBEF-UFOPA) for logistic support, laboratory colleagues for field support and CAPES for grant assistance granted.

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