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ORIGINAL ARTICLE

Influence of soil characteristics on physiological and growth responses of *Cytharexyllum myrianthum* Cham. (Verbenaceae) to flooding

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Abstract

The success of watershed riparian forest restoration programs can be affected by the selection of plant species tolerant to flooding and soil types that occur along water courses. We evaluated physiological and growth responses of *Cytharexyllum myrianthum* seedlings to flooding in three different soil types representative of the Almada River Watershed (ARW), southern Bahia, Brazil. The soils selected, based on the relative abundance and importance in the ARW, were: Luvisol, Argisol, and Spodosol. After 35 days of flooding, the Argisol had the lowest and the Spodosol had the highest reduction–oxidation (redox) potential (E_h). After 35 days of flooding, the Luvisol had higher pH and electrical conductivity (E_c) than the other soils. Stomatal conductance (g_s) and net photosynthesis (A) significantly declined in all soil types after 7 days of flooding. After that period, morphological changes characteristic of flood-tolerant plants, such as lenticel hypertrophy and adventitious root formation, were observed in all flooded plants. Following the morphological changes, g_s and A in flooded plants increased to values close to those of the non-flooded plants. The highest relative growth rates based on mass (RGRm) and net assimilation rates (NAR) for the non-flooded plants were observed in the Argisol. After 35 days of flooding, no significant differences in RGRm or NAR were observed between non-flooded and flooded plants in the Luvisol, but large significant decreases in RGRm and NAR were observed for the flooded plants in the Spodosol. Our results demonstrated that the ability of seedlings of the same species to acclimate to flooded soil conditions differs among soil types. Therefore, the characteristics of soils present in a watershed should be considered when selecting tree species for the reforestation of riparian forests.

Keywords Brazilian atlantic rainforest · Net photosynthesis · Riparian forest restoration · Soil redox potential · Stomatal conductance · Almada river watershed

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Introduction

The riparian ecosystems of the Brazilian Atlantic Forest have been subjected to fragmentation and loss of forest cover, which is directly associated with the expansion of agriculture and extensive cattle raising, as well as with commercial timber exploitation (Rodrigues and Gandolfi 2000; Tabarelli et al. 2005). Anthropogenic pressures threaten riparian ecosystems and may compromise the hydrological and ecological processes of river watersheds (Uieda and Paleari 2004). Restoration of degraded riparian forests is crucial to ensure the persistence of ecosystem services and the maintenance of biodiversity (Tabarelli et al. 2005). However, the success of forest restoration programs in areas near waterways requires species adapted to eventual periods of soil flooding (Faria et al. 2001; Junglos et al. 2018). In addition, the success of riparian forest restoration programs can be affected by the different soils that occur along a watershed (Jacomine 2000). This occurs, because the soil plays a fundamental role in the structure of landscapes (Rossi et al. 2005; Kotchetkoff-Henriques et al. 2005), providing mechanical support and the essential nutrients for plant establishment and growth (Rossi et al. 2005). The soil characteristics that most influence the distribution pattern of plant species are texture, drainage, and fertility (Tuomisto and Ruokolainen 1993; Jacomine 2000; Dubuis et al. 2013).

Flooding changes the availability of oxygen in the soil (Ponnamperuma 1984; Kozlowski 1997; Pezeshki 2001; Mielke and Schaffer 2010; Sasidharan et al. 2018) and consequently creates a hypoxic or anoxic environment for roots (Lobo and Joly 2000; Sasidharan et al. 2018). Under hypoxic and anoxic conditions, aerobic organisms are replaced by anaerobic organisms that use nitrate, manganese, iron, and sulfate as electron acceptors to maintain their respiration. Anaerobic respiration induces denitrification and the reduction of soil chemical constituents, contributing to the accumulation of phytotoxic compounds (Ponnamperuma 1984; Kozlowski 1997; Camargo et al. 1999; Pezeshki and DeLaune 2012). These processes lead to a progressive decrease of the reduction–oxidation (redox) potential (E_h) of the soil (Ponnamperuma 1984; Pezeshki and DeLaune 1998; Pezeshki 2001). However, the relationship between soil E_h and the physiological processes in plants is still poorly understood (Pezeshki and DeLaune 2012). Flooding also changes soil pH and electrical conductivity (E_c). Flooding increases pH in acidic soils, whereas pH decreases in alkaline soils (Ponnamperuma 1972, 1984; Camargo et al. 1999). These pH changes lead to changes in soil fertility by exerting effects on nutrient uptake and the concentration of phytotoxic nutrients (Ponnamperuma 1984). Soil E_c tends to increase immediately after flooding and then decreases and stabilizes at values close to those of non-flooded soils, these changes being controlled by the ions present in the soil (Ponnamperuma 1984; Camargo et al. 1999).

Reduced soil, coupled with oxygen deficiency, interferes with a plant's aerobic respiration (Kozlowski 2002), nutrient uptake (Kozlowski 2002; Alaoui-Sossé et al. 2005; Bidala et al. 2018), and photosynthesis (Kozlowski and Pallardy 2002; Mielke and Schaffer 2010; Li et al. 2015; Duarte et al. 2020). Normally, flood-tolerant species have morphological and anatomical modifications in response to flooding such as hypertrophy (swelling) of stem lenticels, formation of adventitious roots, and aerenchyma development (Larson et al. 1993; Nuñez-Elisea et al. 2000; Pires et al. 2018), which allow the physiological adjustment to flooded soil conditions (Kozlowski 1997; Pezeshki and DeLaune 1998; Pires et al. 2018; Duarte et al. 2020; Zhai et al. 2020). Ecophysiological studies with native plant species at the early stages of plant growth and development make it possible to understand the strategies for occupation and survival of different species in watersheds (Lobo and Joly 2000), contributing to the practice of planting seedlings in forest restoration programs (Paquette et al. 2009; Yeong et al. 2016; Junglos et al. 2018). In addition, knowledge of the relationships between plant species and the soils of a watershed can contribute to decision making for forest restoration actions.

Cytharexyllum myrianthum Cham. is a tree species in the Verbenaceae family, popularly known as 'pau-de-viola' (violawood) and found in humid areas (Bueno and Leonhardt 2011). This species occurs throughout the northeast, southeast and south of Brazil in phytogeographical domains of the Caatinga, Cerrado and Atlantic Forest (Thode and França 2015). *C. myrianthum* is considered tolerant to soil flooding and indicated for restoration of riparian forests (Andrade et al. 1999). In addition, *C. myrianthum* is a pioneer species, with rapid growth, producing a large number of fruit (Lorenzi 2002) with potential to attract avifauna (Bueno and Leonhardt 2011; Amaral et al. 2013).

The objective of this study was to evaluate the physiological responses of young *C. myrianthum* plants to flooding (root submergence) in three different soils representative of a small watershed located in southern Bahia, Brazil (Franco et al. 2011). Our hypotheses were: (a) different soil types may have different physicochemical characteristics, resulting in differences in E_h, pH and E_c among the different soil types when flooded; and (b) soil physicochemical characteristics induce different physiological and growth responses of young *C. myrianthum* plants to flooding.

Materials and methods

The Almada River Watershed (ARW) and soil characteristics

The ARW in the southern region of Bahia, Brazil, covers an area of 1,575 km^2 (Franco et al. 2011; Gomes et al. 2013; Santana et al. 2016). According to Köppen's classification, the region's climate is classified as Afi. Rainfall is well distributed throughout the year with a total annual average of approximately 2200 m (Lopes et al. 2019). The ARW follows the course of the Almada River, with an extension of about 138 km, in a west/east direction, from the source to the mouth in the Atlantic Ocean (Santana et al. 2016). Currently, much of ARW's original forest is fragmented by timber logging and livestock farming (Franco et al. 2011; Gomes et al. 2013; Viana and Moraes 2016). According to Lopes et al. (2019) the land use of the ARW is distributed in wetlands (0.3%), restingas (0.12%), urban areas (0.15%), remaining forest (0.65%), farming/pasture (22.9%) and cocoa cultivation (75.88%).

Despite its small size, the ARW has a complex geological structure and is composed of a variety of soil types (Gomes et al. 2013). According to Franco et al. (2011), about 66% of the total area of the ARW has a low declivity with areas receiving coastal discharge and valley bottoms. The ARW consists of distinct soil types (Franco et al. 2011). The Luvisol, Argisol and Spodosol, were selected for this study because of their representativeness and/or importance in the ARW (Fig. 1). The Luvisol and the Spodosol are in environmentally fragile areas and are representative soils of the upper course (west of the basin) and lower course of the Almada river (east of the basin), respectively (Franco et al. 2011; Gomes et al. 2013). The Luvisol is present in the valley bottoms that occur in the west part of the basin associated with the mountain relief. The Argisol is the most abundant soil type in the ARW (Franco et al. 2011). Argisols are associated with half slopes and valley bottoms that are prone to flooding and deposition of soil particles removed by the erosion process of the higher altitude areas, which favors their natural fertility. The Spodosol is present in coastal littoral areas of the Almada River Sedimentary Basin (Franco et al. 2011). The Spodosols are very poor in fertility, occurring in sandy beach vegetation environments (Embrapa Centro Nacional de Pesquisa de Solos 2006).

Soil samples were collected following the procedures defined by EMBRAPA (1995). After cleaning the surface vegetation, about 10 kg of soil per sample were collected in horizons A and B, at depths ranging from 0 to 1 m. The sample points were chosen as described by Franco et al. (2011). For this, the best field exposures of the studied soil profiles were considered, which were associated with cut slopes for Argisol and Luvisol, and eroded valley bottom profiles for Spodosol. After collection, the soil samples were taken to the Universidade Estadual de Santa Cruz (UESC). Samples from each soil were then separately homogenized

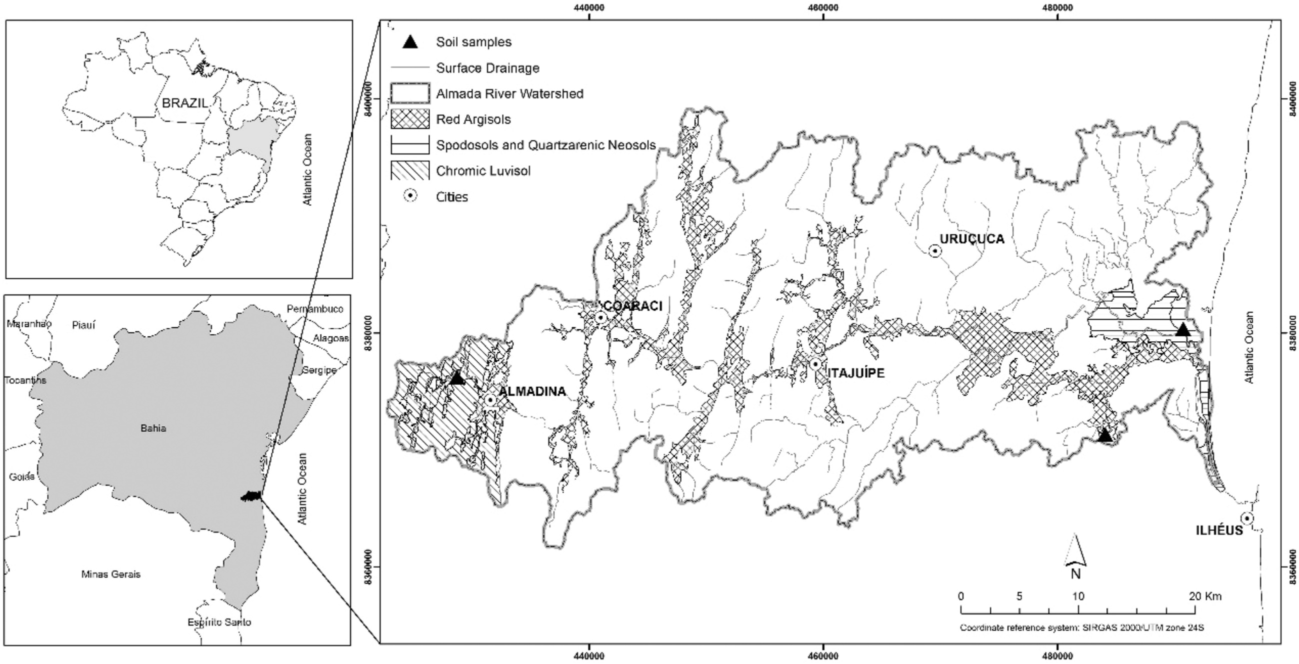

Fig. 1 Soil map of the Almada River Basin, southern Bahia, Brazil, showing collection points for the three soils

and placed in 1-L bags. Before filling the bags, a composite subsample of each soil was collected and sent to the to the Soil, Plant Tissue, and Fertilizers Analyses Laboratory of the Universidade Federal de Viçosa (UFV), Viçosa, MG, Brazil for analyses of the physicochemical characteristics of the soils. The complete physicochemical characteristics of the three soils is shown in Table 1. All three soils are sandy loams. Luvisol and Argisol have eutrophic characteristics with basis saturation indexes of about 91% and 58%, respectively. In contrast, Spodosol has a dystrophic characteristic with a basis saturation index of about 34%. Clay, organic matter and iron oxides are mainly responsible for the cation exchange capacity in soils of tropical regions (Ronquim 2010). Although Spodosol has the highest amount of organic matter, there is a low concentration of clay and iron. Thus, besides the small capacity of this soil to retain exchangeable cations, there is also a low basis saturation index, which means that the amount of cations such as Ca^{2+}, Mg^{2+} and K^+ is also small.

Plant material and experimental design

Seedlings of *C. myrianthum* were produced in the nursery of the Instituto Floresta Viva in Serra Grande, Uruçuca, Bahia through direct sowing in a container containing 100% HSFlorestal® commercial substrate. Five-month-old seedlings were transplanted into 1-L plastic bags, each containing one of the three different soils collected along the ARW. The plants were cultivated inside a structure of galvanized steel pipes approximately 12 m long, 6 m wide and 3 m high, covered with a shade cloth that allows the passage of 60% of solar radiation in full sun, at the UESC's campus. At transplanting, some substrate adhered to the roots, corresponding to about 20% of the total capacity of the plastic bag. After transplanting, the seedlings underwent a 30-day acclimation period during which time they were fertilized twice at 7-day intervals using 0.10 g dm^{-3} of mono-ammonium phosphate, 0.03 g dm^{-3} of red KCl and 0.07 g dm^{-3} of urea, diluted in 50 mL of water, as sources of phosphorus, potassium and nitrogen, respectively. After the acclimation period, the plants were divided into two flooding treatments: flooded or non-flooded for each of the three soil types, with 10 replicates per flooding treatment per soil type, totaling 60 seedlings. All seedlings were placed in PVC tubes (25 cm height and 50 mm diameter). The PVC tubes had two small holes in the base for drainage of irrigation water. For the flooding treatment, water was prevented from flowing out of the bottom of the PVC pipe by sealing the small holes at the base and keeping the water line 20 mm above the soil surface. Considering the climate and rainfall distribution in the region, and that eventual flooding periods of no more than 2 weeks can occur, the plants were flooded for 35 days. Non-flooded plants were irrigated daily during the 35-day experiment.

Table 1 Physicochemical characteristics of three different soil of the Almada River Watershed, south of Bahia, Brazil

Variable	Luvisol	Argisol	Spodosol
Coarse sand (kg kg^{-1})	0.466	0.391	0.723
Thin sand (kg kg^{-1})	0.179	0.152	0.242
Silt (kg kg^{-1})	0.183	0.091	0.006
Clay (kg kg^{-1})	0.172	0.365	0.028
Organic matter (dag Kg^{-1})	1.88	2.13	2.51
T (cmol$_c$ dm^{-3})	20.21	6.21	5.31
t (cmol$_c$ dm^{-3})	18.41	3.61	1.91
V (%)	91.1	58.1	34.1
P (mg dm^{-3})	80.2	1.5	0
K (mg dm^{-3})	41	27	15
Ca^{2+} (cmol$_c$ dm^{-3})	7.4	2.5	1.5
Mg^{2+} (cmol$_c$ dm^{-3})	10.87	1.04	0.31
S (mg dm^{-3})	14.1	21.1	21.8
Cu (mg dm^{-3})	1.43	0.79	0.31
Mn (mg dm^{-3})	62.8	10.4	4.5
Fe (mg dm^{-3})	58.1	66	13.4
Zn (mg dm^{-3})	3.81	4.34	1.30
pH H_2O	6.4	4.8	4.5

Microclimate

Throughout the experiment, photosynthetic photon flux (PPF) was measured with a quantum sensor (model S-LIA-M003) connected to a HOBO weather station (Onset Computer, Bourne, Mass., USA). Air temperature (Ta) and relative humidity (RH) were recorded with a Hobo H8 Pro Series datalogger (Onset Computer, Bourne, Mass., USA), and the vapor pressure deficit (VPD) was calculated as described by Dilley (1968). The average day, average night and maximum daily air temperatures were 27.8, 20.4, and 32.2 °C, respectively. The mean, maximum, and minimum total daily PPF during the experiment were 21.4, 26.5, and 10.3 mol photons m^{-2} day^{-1}, respectively. The mean, maximum, and minimum of average daily VPD during the experiment were 1.1, 1.6 and 0.3 kPa, respectively.

Soil physicochemical characteristics

During the flooding period, soil E_h, E_c, and pH were recorded in all flooded soils with a pH/ORP Meter 8651 (AZ Instrument Corp., Taiwan, China) and a portable conductivity meter TEC-4P-MP (Tecnal Scientific Equipment, São Paulo, Brazil). The E_h was measured at 6, 16 and 35 days after flooding, and E_c and pH were measured at 6, 14, 21 and 35 days after flooding.

Leaf gas exchange

Net photosynthesis (A) and stomatal conductance of water vapor (g_s) were measured at 7, 14 and 28 days after flooding, always between 6 and 10 h, in a mature, fully expanded leaf of 5 seedlings per treatment. A and g_s were measured with a portable photosynthesis system (model LI-6400, Li-Cor, Lincoln, Nebraska, USA) at a PPF of 1000 µmol photons m^{-2} s^{-1}. Air temperature, relative humidity, and reference CO_2 concentration in the leaf cuvette were 28 ºC, 65%, and 390 µmol CO_2 mol^{-1} air, respectively.

Plant growth

Leaf area (LA), stem diameter (D), dry mass of leaves (LDM), stems (SDM), roots (RDM), and total plant dry mass (TDM) were measured at the beginning and at the end of the experiment. The LA was measured with an automatic leaf area meter (model LI-3000, Li-Cor, Lincoln, Nebraska, USA). To determine plant dry mass, plants were separated into roots, stems, and leaves and dried in a forced ventilation oven at 60 °C to a constant weight. Plant dry mass was used to calculate the root [RMR = RDM/TDM], stem [SMR = SDM/TDM] and leaf [LMR = LDM/TDM] dry mass to total plant dry mass ratios. The relative growth rate expressed as diameter (RGRd) and mass (RGRm) and the net assimilation rate (NAR) were calculated according Hunt (2017).

Data analyses

The experiment was arranged in a completely randomized design with three soil types and two levels of flooding (3 × 2 factorial design). The physicochemical characteristics of the flooded soils (E_h, E_c and pH) were evaluated by a repeated measures two-way ANOVA (factors: time, soil type, and their interactions). Leaf gas exchange variables were evaluated by three-way ANOVA (factors: time, flooded, soil type, and their main interactions). Seedling growth variables were evaluated by two-way ANOVA (factors: flooded, soil type, and their interactions). All of the comparisons between means were made using a posteriori Tukey's Honestly Significant Difference (HSD) test ($\alpha = 0.05$). All of the statistical analyses were performed with R programming language, version 3.6.3 (R Core Team 2020).

Results

Throughout the sampling period (DAF: days after flooding), there was a significant reduction E_h and E_c (Table 2). The lowest E_h was at 35 DAF and the highest E_c was at 6 DAF. There were no significant differences between 6 and 14 DAF

Table 2 Effects of time (T, days after flooding), soil type (S), and interactions between time (T) and soil type (TxS) on reduction–oxidation (redox) potential (E_h), electrical conductivity (E_c), and soil pH of flooded seedlings of *C. myrianthum*

Variable	Time (T: days after flooding)				Soil (S)			T	S	TxS	R^2_m	R^2_c	P_{model}
	6 days	16 or 14† days	21 days	35 days	Luvisol	Argisol	Spodosol						
Eh	− 186 ± 15.8 **a**	− 129.9 ± 20.3† **a**	NA	− 197.7 ± 7.8 **b**	− 178 ± 13.4 **b**	− 221 ± 7.4 **b**	− 114.6 ± 19.5 **a**	**	***	n.s	0.38	0.38	***
Ec	341.6 ± 27.6 **a**	205.8 ± 16.1 **b**	247.8 ± 22.6 **b**	224.3 ± 20.4 **b**	316.1 ± 26.9 **a**	256.4 ± 13.5 **a**	192.2 ± 13.9 **b**	***	***	n.s	0.30	0.36	***
pH	5.5 ± 0.06 **a**	5.3 ± 0.09 **b**	5.2 ± 0.06 **ab**	5.3 ± 0.09 **ab**	5.7 ± 0.03 **a**	5.4 ± 0.04 **a**	4.9 ± 0.05 **b**	***	***	n.s	0.69	0.71	***

Mean ± SE. Statistical significance among main effects and interactions was determined by a repeated measure two-way ANOVA

n.s.: $P > 0.05$; *: $P < 0.05$; **$P < 0.01$; ***$P < 0.001$; R^2_m: marginal coefficient of determination (the variance explained by fixed factors); R^2_c: conditional coefficient of determination (variance explained by both fixed and random factors); P_{model}: model probability. Means followed by different letters within rows (among time or soil types) indicate no significant difference according to a Tukey's HSD test ($P < 0.05$). Abbreviations: reduction–oxidation potential (E_h, mV) and electrical conductivity (E_c, µS cm^{-1})

for E_h, and no significant differences between 16, 21 and 35 DAF for E_c. The pH was fairly constant after treatments were initiated, with little change over time. Spodosol had the highest Eh and the lowest E_c and pH. However, Luvisol and Argisol had similar E_h, E_c, and pH. The non-significant interaction between T and S indicated that at each sampling date the same statistical differences in E_h, E_c, and pH was observed among soil types.

Cytharexyllum myrianthum seedlings subjected to flooding in Luvisol and Argisol had 100% survival after 35 days of flooding, whereas flooded seedlings in Spodosol had 10% mortality 14 days after flooding. From 2 to 11 days after flooding began, 70% of the plants in the Spodosol exhibited epinasty (abnormal downward leaf curvature, often associated with ethylene accumulation in flooded plants), a symptom not observed in plants in the Luvisol or Argisol. However, throughout the experiment, foliar abscission was observed in plants in all three soils, mainly during the first week after flooding. Nine days after flooding, hypertrophied stem lenticels and adventitious roots were observed in all flooded plants, except for the plants that did not survive in the Spodosol.

Overall, the non-flooded seedlings had higher A and g_s than the flooded seedlings (Table 3). Spodosol had the lowest A and g_s. However, Luvisol and Argisol had higher and similar A and g_s. There were significant statistical interactions between time, flooding treatment and soil types. After 7 days of flooding, for the non-flooded plants, there was no significant difference among soils for A (Fig. 2a), but a significant difference was observed among soils for g_s (Fig. 2b). At that time, the highest values of g_s were in the Luvisol, followed by Argisol and Spodosol. After 7 days of flooding, A (Fig. 2a) and g_s (Fig. 2b) were significantly higher in non-flooded than in flooded plants. After 14 days of flooding, no significant difference in A between flooded and non-flooded plants was observed in the Spodosol (Fig. 2a).

After 35 days of flooding, there was no effect of soil type on RGRd, NAR, or SMR (Table 4). The RGRm and RMR were significantly higher in the Luvisol and Argisol than in the Spodosol. On day 35, the LMR was significantly higher in the Spodosol than in the Luvisol or Argisol. The RGRm and NAR were significantly higher for plants in the non-flooded treatment than in the flooded treatment, whereas RGRd and SMR were significantly higher for plants in the flooded than in non-flooded treatment. No significant interactions between soil types and flooding treatment were observed for RGRd, RMR, SMR, or LMR.

The highest values of RGRm (Fig. 3a) and NAR (Fig. 3b) were observed in non-flooded plants in the Argisol, followed by the Spodosol and Luvisol. The mean RGRm of the non-flooded plants was significantly higher in the Argisol than in the Luvisol (Fig. 3a). However, the RGRm of the flooded plants was significantly higher in

Table 3 Effects of time (T, days after flooding), flooding treatment (F), soil type (S), and interactions between time, flooding treatment, and soil type on leaf-level photosynthetic characteristics of non-flooded (NF) and flooded (F) seedlings of *C. myrianthum*

Variable	Time (T, days after flooding)			Flooded (F)		Soil (S)			T	F	S	FxS	TxFxS	F_v	R^2	P_{model}
	7 days	14 days	28 days	Non-flooded	Flooded	Luvisol	Argisol	Spodosol								
A	8.81 ± 0.82 **b**	8.35 ± 0.57 **b**	12.09 ± 0.42 **a**	11.45 ± 0.31 **a**	8.05 ± 0.64 **b**	10.39 ± 0.6 **a**	10.08 ± 0.47 **a**	8.78 ± 0.9 **b**	***	***	**	n.s	***	19.5	0.82	***
g_s	0.44 ± 0.05 **a**	0.14 ± 0.02 **b**	0.22 ± 0.02 **b**	0.35 ± 0.04 **a**	0.18 ± 0.02 **b**	0.33 ± 0.04 **a**	0.27 ± 0.04 **ab**	0.2 ± 0.03 **b**	***	***	***	n.s	***	24.9	0.85	***

Mean ± SE. Statistical significance among main effects and interactions was determined by a three-way ANOVA

F_v Fisher value, R^2 coefficient of determination, P_{model} model probability

n.s.: $P > 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Means followed by different letters within rows (among time, flooded, or soil types) indicate no significant difference according to a Tukey's HSD test ($P < 0.05$). Abbreviations: net photosynthesis (A, μmol CO_2 m^{-2} s^{-1}) and stomatal conductance of water vapor (g_s, mol H_2O m^{-2} s^{-1})

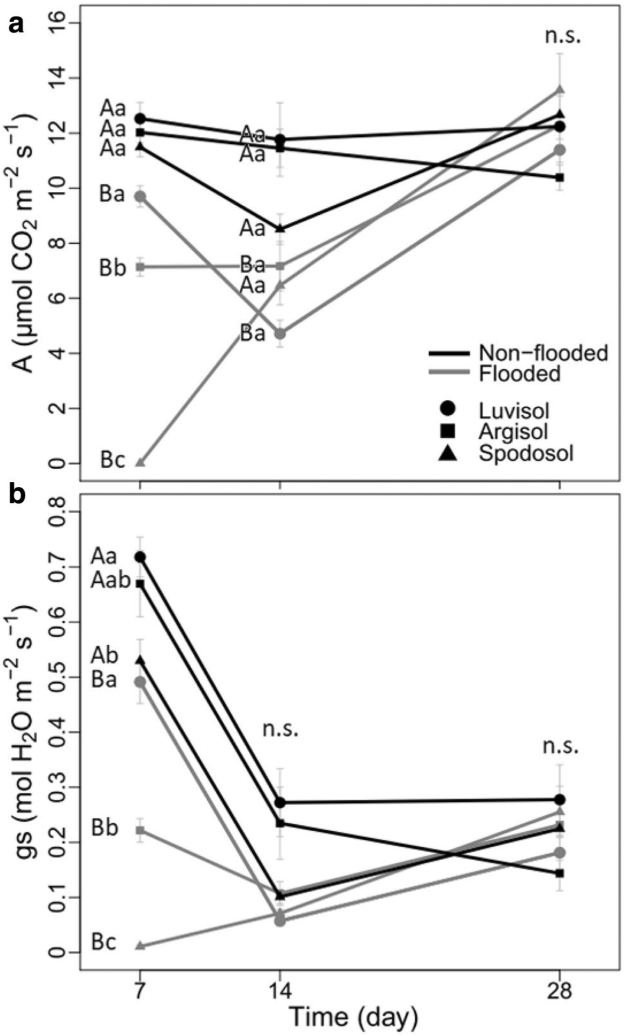

Fig. 2 Net photosynthesis (A, a) and stomatal conductance to water vapor (g_s, b) of non-flooded and flooded *C. myrianthum* seedlings in three different soils of the Almada River Watershed, southern Bahia, Brazil after 7, 14, and 28 days of flooding. $n = 5$. Means followed by different letters are significantly different according to a Tukey's HSD test ($P < 0.05$). Capital letters represent comparisons of flood effects within each soil and lower-case letters represent comparisons of soil effects within each flood treatment. Treatment means were compared separately on each date. n.s.: $P > 0.05$. Bars shows SE

the Luvisol and Argisol than in the Spodosol. The mean RGRm values in the Luvisol, Argisol, and Spodosol were 17%, 38%, and 75% higher in the non-flooded plants than in the flooded plants, respectively. No significant difference was observed among soil types for NAR in the non-flooded plants (Fig. 3b). In the flooded plants, the NAR was significantly higher in the Luvisol and Argisol than in the Spodosol. The NAR in the Luvisol, Argisol, and Spodosol was 27%, 51%, and 80%, respectively, and higher in the non-flooded plants than in the flooded plants.

Discussion

Spodosol had the highest E_h and the highest organic matter content of the three soils. This seems contradictory, because high organic matter content generally makes the soil more susceptible to changes in E_h under flooded conditions (Ponnamperuma 1984; Pezeshki and DeLaune 1998; Husson 2013; Tokarz and Urban 2015). However, the reduction capacity of different soils is also related to the availability of electrons accepted by the oxidants present in the soil, such as oxygen, nitrate, manganese, iron, and sulfate (Pezeshki and DeLaune 2012; Tokarz and Urban 2015). In the absence of oxygen, facultative and obligate anaerobic microorganisms use these other electron acceptors to maintain their respiration by decomposing organic matter (Pezeshki and DeLaune 2012). Therefore, these oxidant compounds are transformed into their reduced forms, contributing to a lower soil E_h (Pezeshki and DeLaune 2012). Thus, in the Spodosol, due to the low amount of electron acceptors such as manganese and iron, possibly microorganisms could not maintain sufficient respiration to decompose the organic matter and thereby reduce the Eh. In contrast, the more intense reduction in the Argisol may have been related to the greater amount of iron and sulfur available to be used as electron acceptors.

When flooded, most soils tend to reach pH neutrality, i.e., the pH of acidic soil increases, and the pH of alkaline soils decreases (Camargo et al. 1999). The increase in pH in acidic soils subjected to flooding can be attributed to reductions in Fe^{3+} and SO_4^{2-}, as well as the accumulation of ammonium and methane (Ponnamperuma 1972). Some chemical elements are more acidic when they are in the oxidized form than in the reduced form, such as Fe^{3+} which is more acidic than Fe^{2+} (Camargo et al. 1999). The low concentration of Fe in the Spodosol may have caused the higher pH stability in this soil, since Fe is the main factor in determining the pH change in acidic soils (Ponnamperuma 1984).

Flooding induced foliar abscission in *C. myrianthum* plants in all three soil types. This loss of leaves has been associated with the accumulation of ethylene in flooded plants (Voesenek et al. 2015). Ethylene is also involved in leaf epinasty and the formation of adventitious roots (Kozlowski 2002; Voesenek et al. 2015) and aerenchyma (Nuñez-Elisea et al. 2000; Voesenek et al. 2015). The formation of hypertrophied stem lenticels and adventitious roots provided the best acclimatization of the plants to flooding in all three soils. Flooded plants exhibited the same morphological adaptations in all soil types. The difference among soils was in the severity of the negative physiological responses to flooding prior to observing morphological changes in flooded plants, which were

Table 4 Effects of flooding treatment (F), soil type (S), and interactions between flooding treatment and soil type (FxS) on relative growth rate in diameter (RGRd) and mass (RGRm), net assimilation rate (NAR), root (RMR), stem (SMR) and leaf (LMR) dry mass ratios of non-flooded (NF) and flooded (F) seedlings of *C. myrianthum*

Variable	Flooded (F)		Soil (S)			F	S	FxS	F_v	R^2	P_{model}
	Non flooded	Flooded	Luvisol	Argisol	Spodosol						
RGRd	0.012 ± 0 **b**	0.015 ± 0.001 **a**	0.013 ± 0.001	0.015 ± 0.001	0.013 ± 0.001	**	n.s	n.s	5.7	0.35	***
RGRm	28.67 ± 1.32 **a**	16.33 ± 1.82 **b**	22.26 ± 1.8 **ab**	27.72 ± 2.03 **a**	17.58 ± 2.79 **b**	**	**	**	16.6	0.61	***
NAR	0.75 ± 0.05 **a**	0.36 ± 0.05 **b**	0.57 ± 0.07	0.67 ± 0.07	0.43 ± 0.07	**	n.s	*	13.2	0.56	***
RMR	0.39 ± 0.01	0.37 ± 0.01	0.43 ± 0.02 **a**	0.39 ± 0.02 **a**	0.34 ± 0.01 **b**	n.s	**	n.s	4.0	0.27	**
SMR	0.22 ± 0.01 **b**	0.25 ± 0.01 **a**	0.23 ± 0.01	0.24 ± 0.01	0.24 ± 0.01	**	n.s	n.s	2.5	0.19	**
LMR	0.38 ± 0.01	0.38 ± 0.01	0.35 ± 0.01 **b**	0.37 ± 0.01 **b**	0.42 ± 0.01 **a**	n.s	**	n.s	4.5	0.30	**

Mean ± SE

n.s.: $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

F_v Fisher value, R^2 coefficient of determination, P_{model} model probability

RGRd, mm mm^{-1} day^{-1} Relative growth rate in diameter, RGRm, mg g^{-1} day^{-1} relative growth rate in mass, NAR, mg cm^{-2} day^{-1} net assimilation rate, RMR root mass ratio, SMR stem mass ratio, RMR leaf mass ratio

Statistical significance among main effects and interactions was determined by a two-way ANOVA

Means followed by different letters within rows (among flooded or soil types) indicate no significant difference according to a Tukey's HSD test ($P < 0.05$)

greater in the Spodosol than in the other soils. Therefore, the positive effects of the morphological alterations were more notable in this soil. Flooded plants in the Spodosol appeared to be severely stressed after only a few days of flooding, but after morphological changes, only one individual did not recover. Hypertrophic stem lenticels and adventitious roots in flooded plants are morphological alterations that facilitate gas exchange between submerged roots and the atmosphere and are visual characteristics of flood-tolerant plants (Kozlowski 2002). Yamauchi et al. (2013) and Pires et al. (2018) reported that hypertrophied stem lenticels above the waterline are the main oxygen entry points in stems of flooded woody plants. In addition, these structures provide excretory sites for volatile phytotoxic compounds, such as acetaldehyde and ethanol (Kozlowski 1997; Larson et al. 1993) generated by anaerobic metabolism in roots under oxygen deficiency (Drew 1997). Adventitious roots also play a vital role in the oxidation of the rhizosphere, which contribute to the transformation of soil toxins into less harmful products (Nuñez-Elisea et al. 2000). The lack of significant differences in RMR between flooded and non-flooded plants in all three soils may be related to adventitious root formation in flooded plants, which compensates for part of the original root system destroyed during flooding. In addition, the formation of hypertrophic stem lenticels may have contributed to the maintenance of root metabolism (Kozlowski 1997).

The decrease in *A* observed in the flooded plants in the three soils may be explained by the decreases in g_s. Decreases in *A* and g_s after flooding are common even in species considered tolerant to soil flooding (Kozlowski 1997) and has been observed in many tropical tree species (Mielke et al. 2005; Bidala et al. 2018). On the other hand, the reopening of the stomata may be related to morphological adaptations to flooding. Adventitious root formation contributes to a greater efficiency in water absorption and may be positively correlated with reopening of stomata in flooded plants (Gomes and Kozlowski 1980), thus restoring carbon assimilation.

The higher RGRd of flooded plants compared to non-flooded plants can be explained by the swelling of the stem base. Andrade et al. (1999) also observed larger stem diameters in flooded than in non-flooded *C. myrianthum*. This enlargement of the stem base may have been caused by the formation of secondary aerenchyma. This type of aerenchyma is composed of white and spongy tissue (Yamauchi et al. 2013) of secondary origin, formed from the phellogen in flooded conditions, exhibiting morphology and anatomy different from the lysogenic or schizogenic (primary) cortical aerenchyma (Shimamura et al. 2014). Nuñez-Elisea et al. (2000) found that *Annona glabra* L., an extremely flood-tolerant woody tree, can tolerate prolonged flooding due to the development of increased stem aerenchyma compared to flood-sensitive *Annona* species which do not exhibit this increase in stem aerenchyma. The development of secondary aerenchyma can increase the formation of hypertrophic stem lenticels that leads to exposure of the aerenchyma to the atmosphere (Yamauchi et al. 2013), facilitating the entry of O_2 (Jackson and Armstrong 1999; Shimamura et al. 2014) into the plant. Hypertrophic lenticels also serve as excretory sites for potentially toxic metabolites, such as acetaldehyde,

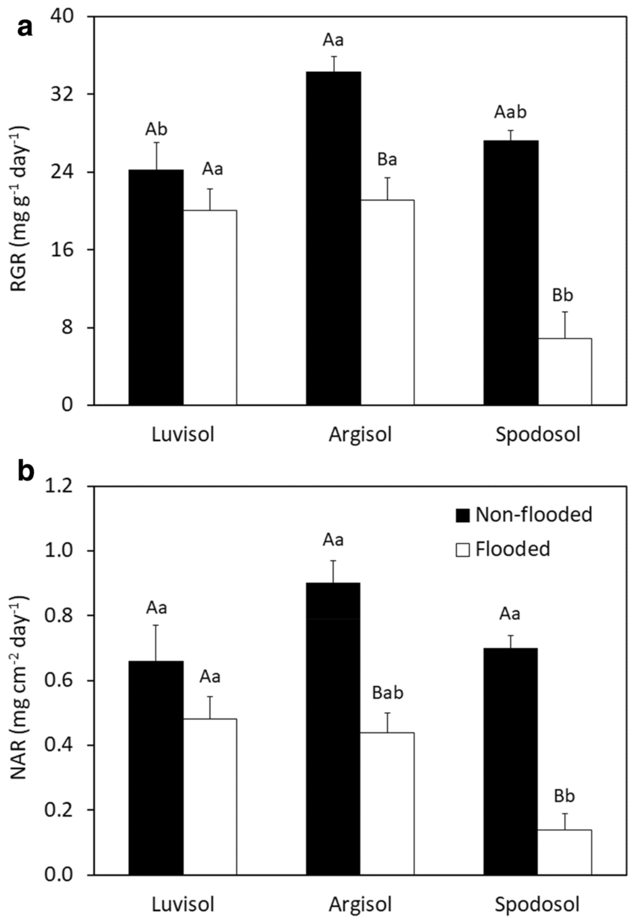

Fig. 3 Relative growth rate (RGR, **a**) and net assimilation rate (NAR, **b**) of non-flooded (NF) and flooded (F) seedlings of *C. myrianthum* in three different soils of the Almada River Watershed, southern Bahia, Brazil, after 35 days of flooding. $n = 10$. Means followed by different letters are significantly different according to by Tukey's HSD test ($P < 0.05$). Capital letters represent comparisons of flood effects within each soil type and lower-case letters represent comparisons of soil effects within each flood treatment

produced as in the roots as a result of anaerobic respiration under flooded soil conditions. This prevents these metabolites from being translocated to the leaves and damaging the plant canopy (Larson et. al. 1993).

The differences in the intrinsic characteristics of the different soils resulted in significant differences in E_h and pH under flooded conditions and these differences affected the physiology of young *C. myrianthum* plants. Pezeshki and DeLaune (2012) stated that E_h is the major factor in determining plant growth and survival under flooded conditions. In addition, low E_h induces a greater oxygen demand by plant roots and the microorganisms present in the soil, resulting in increased plant stress (Pezeshki 2001). Therefore, physiological responses of young *C. myrianthum* would be expected to correlate with changes in soil Eh. However, in the Spodosol, which had a higher E_h than the other soils after 35 days of flooding, flooding more negatively impacted the physiology and growth of young *C. myrianthum* plants compared to the other soils. This was evidenced by more leaf epinasty during the first week of flooding, greater plant mortality, and greater reductions in A, g_s and RGRm in the Spodosol than in the other soil types as a result of flooding. The greater plant stress observed in the Spodosol under flooded conditions may be associated with its low natural fertility and with the lower pH of this soil in relation to the other soil types tested. It is known that low pH values increase the solubility of some nutrients, which may be toxic to plants when in excess (Dubuis et al. 2013). The combined effect of low fertility, low pH and flooding on soil may have intensified the stress to which the plants were subjected. Although E_h is important, it alone does not explain the responses exhibited by young *C. myrianthum* plants when flooded in different soil types.

The use of native plant species in forest restoration projects facilitates the recovery of ecosystem processes, since those species are environmentally adapted and, together with their pollinators, seed dispersers and natural predators, help to restore ecological relationships. *C. myrianthum* is a pioneer tropical tree, with fast growth, producing a large number of fruit (Lorenzi 2002; Bueno and Leonhardt 2011; Amaral et al. 2013), with an extensive geographical distribution (Thode and França 2015). This species is considered tolerant to soil flooding and indicated for restoration of riparian forests (Andrade et al., 1999). Despite this, we found in this study that its ability to tolerate soil flooding depends on the type of soil. Plants grown in Spodosol had lower growth rates and less tolerance to flooding than plants grown in Luvisol or Argisol. In this case, the lowest physiological performance and the lowest growth rates can impact the competitiveness of seedlings planted in restoration areas, as well as their ability to respond to biotic stresses such as herbivory or pathogens. Ant predation, for example, is an important factor that can lead to seedlings mortality in forest succession (Silva et al. 2012) and forest restoration projects (Lima et al. 2016). Thus, even in a relatively small watershed, the selection of species for use in the restoration of riparian forests must consider the species' ability to tolerate soil flooding, as well as the type of soil prevalent in the place, where reforestation will be done.

In summary, the recovery of g_s and A as a function of morphological adjustments by young *C. myrianthum* plants allows this species to be classified as tolerant to up to 35 days of continuous flooding (root submergence). Considering that the ARW region has a humid tropical climate, with abundant but well-distributed rainfalls throughout the year (Gomes et al. 2013; Lopes et al. 2019), occasional floods do not last longer than 2–3 weeks. Thus, *C. myrianthum* can be indicated for the ecological restoration of riparian forests in the ARW. On the other hand, no significant differences were observed between non-flooded and flooded plants in the Luvisol for RGRm and NAR, but a strong decrease in the values of RGRm and NAR were observed for the flooded plants in the Spodosol. Throughout the flooding period, the Spodosol had higher E_h and lower pH and E_c than the other soils. In addition, the Spodosol had lower natural fertility than the Argisol or Luvisol. Thus, the physiological and growth responses of *C. myrianthum* seedlings to flooding was dependent on the characteristics of the soils. Our results demonstrated that the ability of seedlings of the same species to acclimate to flooded conditions may differ among soil types, and the characteristics of soils present in a watershed should be considered when selecting tree species for reforestation of riparian forests.

Author contribution statement LQA, MSM, ÂCD and RLG designed the experiment. LQA, ÂCD, KFP and AL performed the experiment. LQA and JPP-M performed statistical analysis. LQA, MSM, MSS, BS and JPP-M wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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