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Light environment influences the flood tolerance in *Cordia americana* (L.) Gottschling & J.S.Mill.

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ABSTRACT

The subtropical riverine forests present a variation in soil water availability throughout the year, following precipitation seasonality. The objective of this work was to evaluate the responses of *Cordia americana* to different light intensities combined with soil flooding. Seedlings were acclimated to light treatments, with full sun and shade conditions. Sun and shade plants were subjected to soil flooding during periods of 10 (short) and 30 (longer) days. After 10 days, flooded plants had a higher root dry mass accumulation and soluble sugars content, regardless of the light condition. Shade plants presented higher shoot soluble sugars content in relation to the sun plants. After 30 days, a higher shoot soluble sugar content was observed in sun and shade flooded plants. In addition, a higher root soluble sugar content was also observed in sun plants under flood. Periods of short flooding, characterized in subtropical forests as from 5 to 15 days, favor the growth of shade plants and the roots sugar accumulation, fact that can explain the species distribution. However, long periods of flooding may be associated with light environment plasticity, suggesting that the sun plants present a higher flooding tolerance, directly associated with the ability to maintain the sugar content.

Key words: subtropical climate, soluble sugars, understory, water stress.

INTRODUCTION

Changes in the rainfall seasonality and fluctuations of the water column in riparian forests result in a specific forest structure - with plants tolerant to conditions which they are exposed - particularly associated with periods of drought or flood (Parolin et al. 2010). The flood frequency, among others traits of an ecosystem, influences the occurrence and distribution of plant species in riparian areas. Budke et al. (2010) points out that the flood frequency can be considered an extremely effective variable in predicting the differential occurrence of tree species.

The flood events occurring in riverine forests generate different impacts on arboreal populations

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distributed in these areas, including morphological, anatomical and physiological changes (Kozlowski 2002). In addition, Giehl and Jarenkow (2008) observed that in riparian forests from southern Brazil the tree species distribution is determined by the interaction between the light gradient and flood frequency. In fact, the soil moisture and light are crucial variables to the establishment and distribution of pioneer and secondary species in riverine forest communities (Maurenza et al. 2009, Gaburro et al. 2015) and the light conditions are considered as the limiting factor in growth of tree species (Valladares and Niinemets 2008). Thus, the composition of tree species in riparian forests may be associated with the light environment and flooding intensity (Poorter 2001, Arieira et al. 2016), and the satisfactory growth of some species in environments with low or high light associated to species plasticity depends on quick adjustment of their biomass allocation and physiological traits (Valladares and Niinemets 2008, Gaburro et al. 2015).

In riverine forests, the light may act as an environmental filter by selecting certain species and functional groups, setting a mosaic of occurrence of different tree species depending on the irradiance penetration more than on the frequency and flooding intensities (Valladares et al. 2008, Giehl and Jarenkow 2008). The species of study, *Cordia americana* (L.) Gottschling & J.S.Mill. is a tree of the family Boraginaceae, with occurrence restricted to areas rarely or not flood in subtropical riverine forests (Budke et al. 2010) and classified as early secondary and shade tolerant species (Villagra et al. 2013a). The aim of this study is to determine variables indicative of flooding and light plasticity in *C. americana* by evaluating the pattern of soluble sugars accumulation and morphophysiological traits in response to changes in light environment and soil flooding. The hypothesis tested in this study is based on the occurrence of *C. americana* in the understory in riparian forest fragments indicating that the plants acclimated to shade will show faster growth and higher soluble sugars accumulation in relation to sun plants in situations of flooding, and these differences are more pronounced after a long period of flooding.

MATERIALS AND METHODS

PLANT MATERIAL

For the study were used three months old *C. americana* plants acquired from Viveiro Florestal Biofértil. The seedlings were transferred to plastic tubes of circular cross section and volume of 100 cm^3 and acclimated in laboratory of Plant Systematic and Ecology of Universidade Regional Integrada do Alto Uruguai e das Missões (URI-Erechim) during 15 days, receiving irrigation every two days until the field water capacity. The average temperature during the initial growth period was 17.6 °C and the photosynthetic photon flux density (PPFD) was 100 μmol m^{-2} s^{-1}. After this period, the seedlings were then transferred to greenhouse conditions at a temperature and relative air humidity that accompanied the oscillations in the atmosphere, where they spent 10 min, three times a day for irrigation. These conditions were used for acclimation and initial growth. The average temperature during the experimental period was 18.9 °C and relative humidity of 71.9%.

FLOODING AND CONTRASTING LIGHT CONDITIONS

Seedlings were kept for 30 days in a greenhouse in contrasting light conditions: under sun and shade. Shading was obtained using a shade enclosure constructed with nylon mesh. Measurements were performed with a luximeter to determine the lighting conditions in the external environment to the greenhouse, in the internal environment of it, where the sun plants were placed and inside the shade enclosure. The sun seedlings were exposed in greenhouse to average of photosynthetic photon flux density (PPFD) of 633.2 μmol m^2 s^{-1}, which corresponds to 30% of external radiation interception, simulating understory light conditions, while plants under shading received an average of 9.1μmol m^{-2} s^{-1}, which corresponds a reduction of 99% of external radiation.

After 30 days of growth in sun and shade conditions (acclimation period) measurements were taken for morphological characterization at time zero of factorial experiment (light x flooding). The parameters evaluated were: stem length, stem diameter (using a digital paquimeter, measured five centimeters above the root-collar), and leaf number (by manual counting). For physiological characterization it was estimated the chlorophyll content using the ClorofiLOG CFL 1030 (Falker, Brazil).

Sun and shade plants were exposed to flooding treatments: 1) control (C), with plants placed in plastic tubes and irrigated every two days until the field water capacity; and 2) soil flooding (SF) in which the plants were placed in a vat where the flood level remained above the soil surface in the plant root collar. The treatments were performed during two time periods: 10 (short flooding) and 30 days (long flood). After these two experimental periods, morphological and physiological traits were analyzed, similarly to those analysis performed at time zero. Additionally to these assessments, the root, shoot and total dry mass (g) were assessed at 10 and 30 days after flooding treatments. For this, plants were removed from tubes, washed to remove the excess soil from roots and after it, the total root length and root-collar diameter were measured. Further, the plants were dried in an oven at 60 °C for 48 hours. After it, the shoots and roots were separated and weighed in an analytical scale. The pattern of biomass allocation was assessed by the root:shoot ratio (R:S ratio).

Each light treatment (sun and shade) consisted of 40 sample units (individual plants), totaling 80 plants. For the flooding treatments, they were used 10 replicates per treatment light (sun and shade) and flooding period (10 and 30 days).

TOTAL SOLUBLE SUGAR CONTENT

The extraction and quantification of soluble sugars was performed according to Dubois et al. (1956), with minor modifications. Samples with about 10 mg of dry weight, obtained after homogenization in liquid nitrogen and drying in an oven at 40 °C, were extracted with 1 mL of ethanol 80% (v/v) and incubated in a water bath at 75 °C for 15 min. The extracts were centrifuged at 12,000 rpm for 15 min and the supernatant was recovered. The sediment was re-extracted with 500 μL of ethanol 80% (v/v) and mixed with first extraction product. For quantification, 250 μL of samples were mixed with 250 μL of ethanol 80% (v/v), 2.5 mL concentrated sulfuric acid and 0.5 mL phenol 5% (v/v). After agitation, the solutions were kept for 20 min at room temperature. The absorbance at 490 nm was measured in a spectrophotometer. A standard curve was established with D-glucose.

STATISTICAL ANALYSIS

To detect the differences between growth parameters between light treatments (shade and sun), during acclimation period we run an analysis of variance (ANOVA one-way). Other analysis of variance (ANOVA two-way) were performed for each flooding periods (10 and 30 days). Treatments were: flooding with 2 levels, flooding and control and light with 2 levels, sun and shade. The response factors used were "x" (number of morphophysiological attributes). Differences were considered significant at $p \leq 0.05$. All analysis was performed using R software (R Core Team 2015).

RESULTS

Acclimation to light conditions - After 30 days of acclimation to the light conditions, the shade plants showed greater stem height, leaf number and chlorophyll content in relation to the sun plants (Table I). The stem diameter showed no difference between the two light treatments.

Interaction between flooding and light conditions - Plants under sun and shade exhibited differences in growth, biomass allocation and reserves when exposed to short (10 days) and long (30 days) flooding periods (Table II). Interactions among flooding and light condition were observed only for shoot soluble sugar content after 10 days of flooding and root soluble sugar content after 30 days of flooding (Table II).

After 10 days under soil flooding, sun and shade plants exhibited differences in stem diameter, leaf number, root length, root-collar diameter, chlorophyll content, shoot and root dry mass and R:S ratio but no difference was observed regarding flooded and control plants (Table II and Table III). Control plants under shade continued exhibiting higher chlorophyll content and leaf number over the control and flooded sun plants after 10 days, as was observed before starting the flooding treatments (time zero) ($p < 0.05$) (Tables I and III). After 10 days, flooded plants under sun and shade exhibited higher values of root sugar content over control plants ($p < 0.05$) (Table II, Figure 1a). Values of shoot soluble sugar content were highly variable among flooded and control plants under sun and shade after 10 days of flooding, but shaded flooded plants had higher shoot soluble sugars content than the other plants ($p < 0.002$) (Table II, Figure 1b).

Shaded plants continued exhibiting higher stem diameter, leaf number and chlorophyll content than sun plants after 30 days of flooding (Table II). The stem height, root length, root-collar diameter, shoot and root mass and R:S ratio did not differ between water and light treatments (Table III). Prolonged flooding had strong effect on root and shoot soluble sugars content. At this time, plants under shade showed decrease in the root soluble sugar content and not differed from the control plants under sun and shade whereas higher shoot sugar content was observed in flooding plants than in controls, independently of the light condition (Figure 1a, b).

TABLE I
Growth parameters in *Cordia americana* seedlings at time zero subjected to two light conditions (acclimation). Means followed by the standard deviation (n = 10).

Parameter	Sun	Shade	p
Stem length (cm)	3.85 ± 0.20	5.19 ± 0.13	<0.001*
Stem diameter (mm)	2.32 ± 0.08	2.32 ± 0.04	0.990
Leaf number	10.36 ± 0.59	13.98 ± 3.34	<0.001*
Chlorophyll content	10.87 ± 0.55	16.09 ± 0.72	<0.001*

* - indicate significant differences between sun and shade plants ($p < 0.05$).

DISCUSSION

This study simulated a two factors combination, water and light, which is known to affect the structure, composition and dynamic of plant communities of riverine forests (Giehl and Jarenkow 2008, Bender et al. 2017, Wittmann et al. 2017) and our results showed the high light plasticity of the studied species. Considering the distribution of *C. americana* in understory of subtropical riverine forests, the initial hypothesis of this study was that shade-acclimatized plants present greater flooding tolerance than plants growing under high irradiance, similar to what was observed for *Inga marginata* (Bender et al. 2017) that as well as *C. americana* is an early secondary species in ecological sucession (Villagra et al. 2013a). Despite the occurrence of *C. americana* in rarely flooding areas (Budke et al. 2010), the results of this study indicated that *C. americana* tolerates short (10 days) and long periods of flooding (30 days) and that tolerance was not directly associated with light environment, as observed by Bender et al. (2017) for *Inga marginata*, where the shade plants presented a temporal pattern of soluble sugars accumulation for the flooding tolerance. However,

TABLE II
Two-way ANOVA results in growth parameters for *Cordia americana* plants subjected to different light availability after 10 and 30 days of soil flooding.

		10 days		30 days	
	Factors	**F value**	**p value**	**F value**	**p value**
Stem lenght	Interaction	0.231	0.633	0.933	0.341
	Light	4.026	0.050	3.253	0.080
	Water	0.015	0.902	0.148	0.703
Stem diameter	Interaction	1.687	0.202	0.216	0.645
	Light	9.558	0.003*	4.802	0.035*
	Water	1.329	0.256	0.574	0.454
Leaf number	Interaction	0.178	0.675	1.079	0.305
	Light	9.512	0.003*	11.290	0.001*
	Water	1.949	0.171	0.239	0.628
Root length	Interaction	1.054	0.311	0.384	0.539
	Light	8.746	0.005*	2.685	0.110
	Water	1.233	0.274	0.051	0.823
Root-collar diameter	Interaction	0.001	0.974	0.006	0.941
	Light	5.075	0.030*	2.212	0.146
	Water	0.026	0.871	0.313	0.580
Chlorophyll content	Interaction	1.446	0.236	0.633	0.431
	Light	11.033	0.002*	9.264	0.004*
	Water	0.362	0.551	2.631	0.113
Shoot dry mass	Interaction	2.341	0.134	0.780	0.383
	Light	9.054	0.004*	2.528	0.121
	Water	0.973	0.330	1.157	0.289
Root dry mass	Interaction	0.007	0.931	0.144	0.707
	Light	8.136	0.007*	0.484	0.491
	Water	4.076	0.051	0.237	0.629
R:S ratio	Interaction	0.797	0.378	0.077	0.784
	Light	5.239	0.028*	1.463	0.234
	Water	1.851	0.182	0.683	0.414
Shoot soluble sugar content	Interaction	10.654	0.002*	3.783	0.057
	Light	14.201	<0.001*	3.849	0.060
	Water	0.004	0.947	28.724	<0.001*
Root soluble sugar content	Interaction	0.783	0.381	16.000	0.0003*
	Light	1.615	0.211	3.638	0.064
	Water	18.786	<0.001*	5.481	0.024*

* - indicate significant differences between flooding and light treatments ($p < 0.05$).

TABLE III

Growth parameters in *Cordia americana* plants subjected to different light availability after 10 and 30 days of soil flooding. Means followed by the standard deviation (n = 10).

Parameter	10 days				30 days			
	Sun		Shade		Sun		Shade	
	C	F	C	F	C	F	C	F
Stem lenght (cm)	7.03 ± 1.14Aa	6.70 ± 0.50 Aa	6.73 ± 0.68 Aa	6.47 ± 0.40 Aa	7.13 ± 0.96 Aa	6.78 ± 0.80 Aa	7.04 ± 0.71 Aa	6.04 ± 0.53 Aa
Stem diameter (mm)	2.05 ± 0.37Ba	2.61 ± 0.73Aa	2.61 ± 0.37Aa	2.57 ± 0.16Aa	2.59 ± 0.40Ba	2.65 ± 0.36Ba	2.64 ± 0.46Ba	2.73 ± 0.35Aa
Leaf number	12.71 ± 2.43Ba	9.25 ± 3.49Ba	14.30 ± 3.97Aa	11.50 ± 3.57Aa	12.14 ± 4.45Ba	11.75 ± 4.30Ba	15.70 ± 3.92Aa	13.20 ± 2.30Aa
Root length (cm)	10.61 ± 1.40Ba	12.50 ± 0.89Aa	12.18 ± 0.96Aa	12.28 ± 0.40Aa	14.23 ± 3.29 Aa	11.73 ± 1.20 Aa	11.41 ± 1.14 Aa	12.67 ± 1.60 Aa
Root-collar diameter (mm)	1.20 ± 0.22Aa	1.02 ± 0.22Ba	1.15 ± 0.32Aa	1.13 ± 0.27Aa	1.56 ± 0.63 Aa	1.21 ± 0.38 Aa	1.38 ± 0.39 Aa	1.27 ± 0.52 Aa
Chlorophyll content	16.39 ± 4.71Ba	17.44 ± 1.93Aa	21.58 ± 10.89Aa	18.08 ± 4.73Aa	18.39 ± 5.57Ba	14.44 ± 3.61Ba	20.32 ± 5.82Aa	15.92 ± 3.43Aa
Shoot dry mass (g)	0.21 ± 0.07Ba	0.27 ± 0.06Aa	0.28 ± 0.05Aa	0.26 ± 0.02Aa	0.26 ± 0.06 Aa	0.30 ± 0.03 Aa	0.26 ± 0.04 Aa	0.26 ± 0.06 Aa
Root dry mass (g)	0.16 ± 0.07Ba	0.22 ± 0.14Aa	0.21 ± 0.07Aa	0.28 ± 0.11Aa	0.24 ± 0.10 Aa	0.22 ± 0.01 Aa	0.18 ± 0.06 Aa	0.21 ± 0.03 Aa
R:S ratio	0.81 ± 0.48Aa	0.79 ± 0.41Ba	0.76 ± 0.23Aa	1.08 ± 0.41Aa	0.92 ± 0.19 Aa	0.73 ± 0.30 Aa	0.69 ± 0.17 Aa	0.81 ± 0.18 Aa

Uppercase letters (compare the parameters within each light treatment) and lowercase (compare the parameters within each flooding treatments) equal, do not differ in each evaluation time by test F ($p < 0.05$). C: control plants; F: Flooded plants.

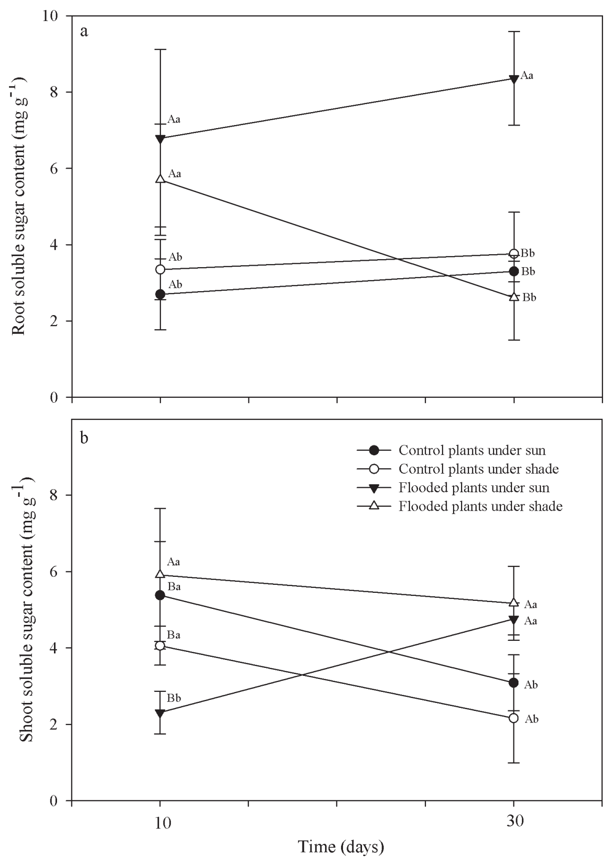

Figure 1 - Soluble sugar content in roots (**a**) and shoot (**b**) of *Cordia americana* plants subjected to different light availability after 10 and 30 days of soil flooding. Uppercase letters (compare the parameters within each light treatment) and lowercase (compare the parameters within each flooding treatments) equal, do not differ in each evaluation time by test F ($p < 0.05$).

when *C. americana* plants were exposed to a short flood, consistent with the frequency observed in subtropical riparian forests, both shade and sun plants under soil flooding showed higher growth and root accumulation of sugars, independent of the light treatment, rejecting the hypothesis of study. Additionally, shade plants showed higher stem growth compared to sun plants.

With the increase of the flooding period, it was expected that differences of shaded plants compared to sun plants would be more pronounced. However, light environment was not associated with a differential flooding response. After 30 days of flooding, sun and shade plants did not show differences in the majority of growth parameters analyzed. Shade plants continued to exhibit under 30 days of flooding a higher number of leaves and chlorophyll content, what allow increase in CO_2 uptake and may confer advantages to the survival of these plants in long-term flood.

After 10 days of flood, flooded plant of *C. americana* under sun and shade showed higher accumulation of soluble sugars in roots compared to control plants. However, after 30 days, it was observed that only sun flooded plants showed higher roots sugars accumulation when compared to control plants and flooded plants under shade. In general, stress events such as flooding and drought increase the concentrations of soluble sugar in plants (Chen et al. 2005, Rosa et al. 2009, Liu et al. 2014). Short flood periods, characterized in subtropical riparian forests such as 5 to 15 days (Budke et al. 2010), favor plants mainly in roots sugars accumulation allowing the maintenance of metabolic activity in roots (Chen et al. 2005), and thus, such ecophysiological response probably is associated with species distribution in the understory of riverine forests. When exposed to long flooding periods such response may be associated with light plasticity, suggesting that plants acclimated to sun shows greater flooding plasticity, especially in physiological characteristics, as observed by Gaburro et al. (2015). Thus, the greater plasticity of sun plants after a long period of flooding seems to be associated with the greater accumulation capacity of soluble sugars mainly in the roots. Flooding conditions limits the soil aeration as water occupies the previously gas-filled soil pores (Kozlowski 2002). Hence, the mobilization of reserves and soluble sugars in flooded plants are necessary to sustain the ATP generation, via respiration or fermentation (Bailey-Serres and Voeseneck 2008). In addition, flooded plants may present higher carbon consumption due to the morphoanatomic changes that they develop in response to flooding conditions, such as the formation of hypertrophic lenticels and adventitious roots (Kolb et al. 1998). Thus, flooded plants under shade conditions tends to consume more carbohydrate reserves than they produce since light is limited. It seems to be the case of *C. americana* plants that exhibited a reduction in soluble sugars under flooding and shade conditions. Therefore, the plasticity to the light environment seems to be determinant for flood tolerance when the plants were exposed to longer periods.

After a long-term flood under subtropical climate conditions, the sun plants presented similar growth to shade plants, suggesting that the growth recovery in sun plants may be directly associated with shoot sugar content and maintenance of metabolic activity (Panda et al. 2008, Mustroph and Albrecht 2003, Parent et al. 2008). The increase of root sugar content may be the main strategy to tolerate prolonged water saturation under high light conditions, associated with greater plasticity of physiological characteristics (Gaburro et al. 2015), which may involve functional traits such osmotic adjustment (Villagra et al. 2013a) and hydraulic efficiency (Cosme et al. 2017).

In subtropical riverine forests, the pattern of flood events is characterized as unpredictable and of low magnitude, differs from those observed in Cerrado and Amazonia riverine forests, where species are subjected to long periods of total submersion (Wittmann et al. 2017). Thus, the results of this work suggests that the ability of *C. americana* to tolerate successive periods of soil flooding due to the lack of precipitation seasonality is associated with the capacity to accumulate soluble sugars in roots and shoots.

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