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# Photosynthetic efficiency of young *Rhizophora mangle* L. in a mangrove in southeastern Brazil

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## Abstract

The study proposes to evaluate the photosynthetic plasticity of *Rhizophora mangle* L. in four mangrove sites distributed along with the Great Vitória Estuarine System. The variation in organic matter content, which implies the higher essential nutrient availability, contributed to better energy flux performance related to electron transport. Furthermore, salinity damaged the reaction centers (RC), since the site with the highest salinity showed changes in the number and size of active photosynthetic RC and in the specific energy flows per active RC (absorption flux, trapped energy flux, and dissipated energy flux), but the plasticity of the species in response to salt stress was confirmed by the increase of performance index for energy conservation ($PI_{Total}$), net photosynthetic rate ($P_N$), and the water-use efficiency (WUE). Also, the results showed that the luminous intensity available compromises the functionality of PSII, in turn, it increases WUE. The results indicate the effect of the chlorophyll *a* content, which provides more substrate for light absorption, on the electron flow and $PI_{Total}$ is related to $P_N$ and WUE. The study indicates the ecological plasticity of *R. mangle* to the conditions of the evaluated area.

*Keywords*: gas exchange; JIP test; photosystems; tropical region.

## Introduction

Mangrove is a halophytic forest ecosystem growing in intertidal zones along tropical and subtropical coasts (Alongi 2009). Mangrove ecosystems are threatened all over the world by human pressures, leading to a demographic increase in the coastal zone, which, together with urbanization and industrialization, change the water

## Highlights

- Energy flux corresponds to electron transport associated with organic matter
- Adjustment of photosynthetic parameters occurs at high salinity
- Photochemical performance is related to net photosynthesis and conservative water use

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*Abbreviations*: ABS/RC – absorption flux per reaction center; Chl – chlorophyll; $C_i$ – intercellular $CO_2$ concentration; $DI_0$/RC – dissipated energy flux per RC; $E$ – transpiration rate; $ET_0$/RC – electron transport flux per RC; $F_0$ – initial fluorescence; $F_m$ – maximum fluorescence; $F_v/F_0$ – number and size of active photosynthetic RC; $g_s$ – stomatal conductance; GVES – Great Vitória Estuarine System; OM – organic matter; $PI_{abs}$ – performance index for energy conservation from exciton to the reduction of intersystem electron acceptors; $PI_{Total}$ – performance index for energy conservation from exciton to the reduction of PSI end acceptors; $P_N$ – net photosynthetic rate; $Q_{leaf}$ – luminous intensity incident on the leaf surface; $TR_0$/RC – trapped energy flux per RC; WUE – water-use efficiency; $\delta R_0$ – efficiency with which an electron from the intersystem reduces the final acceptor of PSI; $\varphi D_0$ – maximum efficiency of nonphotochemical de-excitation; $\varphi E_0$ – quantum yield for electron transport; $\varphi P_0$ – maximal quantum yield of PSII photochemistry; $\Psi_0$ – the probability of electron transport further than $Q_A^-$.

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regime and sediment/nutrient flow into the environment. Moreover, in some locations, these stressors may act synergistically with changes in the relative mean sea level, and, ultimately, climate change (Alongi 2015) may compromise ecosystem services. Understanding the *in situ* ecophysiology of mangrove plant species is important in determining how the ecosystem will behave in the face of environmental change and its long-term prospect of maintenance (Schaeffer-Novelli *et al*. 1990, Pascoalini *et al*. 2014), and contributing to coastal management.

Pioneering studies on the ecophysiology of mangroves focused on understanding plant behavior at different salinity levels (Ball *et al.* 1984, Ball 1986, 1988; Naidoo *et al*. 2002, Parida *et al*. 2004, Barr *et al*. 2009), because the salinity is considered the main abiotic factor determining the development of these forests (Parida and Jha 2010). Field and laboratory studies were carried out on various plant species, including *Avicennia marina* (Forssk.) Vierh., *Avicennia germinans* (L.) L., *Bruguiera gymnorrhiza* (L.) Lam., *Kandelia candel* (L.) Druce, *Laguncularia racemosa* (L.) C. F. Gaertn., *Rhizophora mangle* L., and *Rhizophora mucronata* Lam. (Ball *et al.* 1984, Sobrado 1999, 2000; Naidoo *et al*. 2002, Krauss *et al*. 2006, Barr *et al*. 2009, Ru *et al*. 2009, Hoppe-Speer *et al*. 2011, Bompy *et al*. 2014). The relationship with salt differentiates mangrove species into salt-secretor, salt-accumulator, and salt-excluder (Parida and Jha 2010). However, more recent approaches have assessed species tolerance as a function of daily salinity variation (Bompy *et al.* 2014), contributing to an understanding of these species' ecological niches.

In addition to the influence of salinity on plant development, several studies address other variables that can influence biomass acquisition. Nonetheless, in general, these studies conducted in the laboratory or the field address extremes such as hypersaline and/or nutrient deficient mangrove areas (Lovelock *et al*. 2006a,b; Martin *et al*. 2010). Therefore, studies approaching the *in situ* behavior of species subjected to a variety of environmental conditions independently of stress occurrence are necessary.

*R. mangle*, a mangrove tree widely distributed on the American Atlantic coast, is among the species that have been the subject of ecophysiological studies. In general, *R. mangle* colonizes the low and middle intertidal zone, with a high frequency of flooding, and muddy substrates subjected to low salinity (Alongi 2009, Barr *et al*. 2009, Bompy *et al*. 2014, Lima *et al*. 2018, Lopes *et al*. 2019). *R. mangle* is considered a salt-excluder species, preventing a considerable amount of sodium and chlorine from being absorbed (Parida and Jha 2010). This is a strategy of less salt-tolerant plants. Moreover, the species exhibits the least conservative water- and nutrient-use efficiency compared to other neotropical mangroves (McKee 1995, Parida and Jha 2010, Soares *et al*. 2015, Tognella *et al*. 2016).

Chlorophyll (Chl) *a* fluorescence is a technique used to evaluate the plant photochemical performance providing us with information about the structure and functioning of PSII, the reaction center (RC), and the electron transport between PSII and PSI. By inducing fluorescence in dark-adapted leaves, Strasser *et al.* (2000) derived several equations for the photochemical apparatus that are translated through the JIP test. Although the technique has been applied to several studies related to water and salt stress, its use in mangal areas is still restricted, but it can provide relevant information on the ecophysiological dynamics of mangrove species under field conditions (Naidoo *et al.* 2002, Gonzalez-Mendoza *et al*. 2007, Falqueto *et al.* 2008, 2012; Pascoalini 2014, Lopes *et al*. 2019, Tognella *et al*. 2022). Furthermore, gas-exchange measurements of mangroves have been widespread and very useful because they provide information on photosynthesis and water-use efficiency quickly and reliably in field conditions (Medina 1999, Soares *et al*. 2015, Larcher *et al*. 2016). Assessing the photochemical process through Chl *a* fluorescence measurements and photosynthesis through gas exchange allow the understanding of sink effects on photosynthesis, from leaf light capture to release of chemical energy. Falqueto *et al.* (2008, 2012) and Pascoalini (2014) conducted studies in the mangrove swamp of the Great Vitória Estuarine System (GVES) and found increased photochemical efficiency with salinity, however lower carbon assimilation for *R. mangle* (Pascoalini 2014).

Mangrove photosynthesis is mainly controlled by salinity. But, the availability of nutrients and light, substrate oxygenation, and sediment contamination also affect the photosynthetic process to a greater or a lesser extent, depending on the limitation imposed. This paper proposes to identify and better understand the photosynthetic plasticity of *R. mangle* in field conditions and some of the factors controlling it, including salinity, organic matter – which indicates nutrient availability, luminosity – related to canopy variation, chlorophyll content, and photochemical performance. The study is guided by the hypothesis that biotic and abiotic factors act directly or indirectly on parameters of the photosynthetic process, reflecting on the photosynthetic efficiency of *R. mangle* growing in the GVES.

## Materials and methods

**Study area**: The study was conducted in the Great Vitória Estuarine System (Fig. 1), on the central Brazilian east coast (20°10'44.0"S and 20°16'31.1"S–40°15'11.0"W and 40°20'44.0"W). The region's climate is Am (Köppen's climate classification), *i.e.*, tropical with seasonal precipitation, the annual mean rainfall is approximately 1,350 mm (Alvares *et al*. 2013). The wettest and driest months extend from October to April, and from May to September, respectively (Alvares *et al.* 2013, INCAPER 2018). Rebello *et al.* (2011) indicate that the area experiences water scarcity almost every month of the year and a water surplus above 100 mm in November and December. The estuary presents dynamics dominated by the tides, mainly by the ebb tide, and they are classified as microtides with semidiurnal frequency, which is less than 2 m in amplitude (Rigo and Chacaltana 2006, Neves *et al.* 2012). The Santa Maria da Vitória River is the main freshwater source of the estuary (Teubner Júnior *et al.* 2018).

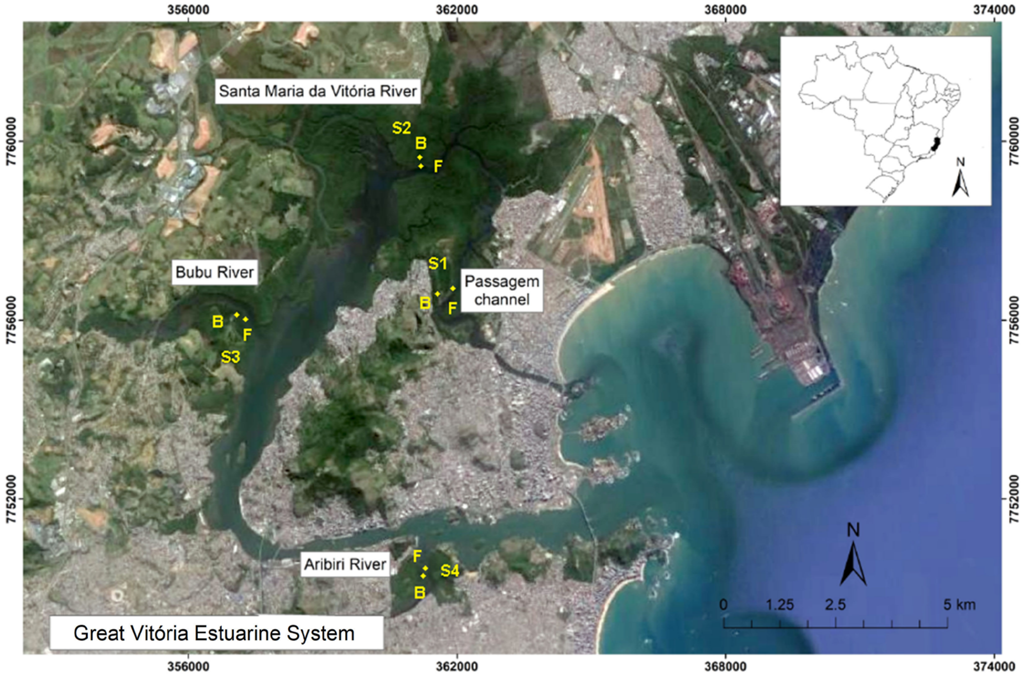

Fig. 1. Study sites in the Great Vitória Estuarine System (GVES), Espírito Santo, Brazil, which are located in the anticlockwise direction from the north entrance (S1) to the south entrance (S4). F – fringe; B – basin.

The GVES mangrove has an extension of 24.8 km$^2$ (Teubner Júnior *et al*. 2018) and is inserted in a wide protection area together with its buffer areas that make up the Vitória Bay Mangrove Protected Areas Mosaic established by state Decree no. 2625-R of 23 November 2010 (Espírito Santo 2010). The mangrove structural diversity is associated with the frequency of flooding, salinity, sediment characteristics, and anthropogenic pressures (Lima 2011, Zamprogno *et al.* 2016, Pascoalini *et al*. 2019).

**Study sites and plant material**: All parameters were measured at four sampling sites (S1, S2, S3, and S4) in the GVES, according to their location in the bay, *i.e.*, in the anticlockwise direction from the north entrance to the south entrance. Each site was divided by physiographic type as fringe (F) and basin (B) (Schaeffer-Novelli *et al.* 2000), totaling eight sampling points (S1F, S1B, S2F, S2B, S3F, S3B, S4F, and S4B). At each site, five completely expanded leaves (the second pair from the apex) were sampled from twelve individuals. Sample collections were carried out at low tide in spring between July and October 2016 and March and June 2017, starting at 08:00 h. The samples characterize the dry period, as the region went through a period of precipitation below expectations for two years (INCAPER 2018).

**Abiotic variables**: Organic matter (OM) analysis and the interstitial water salinity measurements were performed concurrently with the measurements of photosynthetic parameters and pigment indices. The salinity of interstitial water was determined using a 5-cm diameter and 0.5 m in length PVC tube inserted at least –0.3-m sediment depth according to the method of Zamprogno *et al.* (2016) using a *Hach Multiparameter Meter* (*model HQ40d*) previously calibrated with a standard solution.

For OM analysis, samples of surface sediment (first 2 cm) were collected after the removal of the deposited macroscope material (standing crop). The samples were kept at –20°C until the lyophilization procedure. The content of lyophilized organic matter was determined using dry mass after samples were ignited and ashed in a muffle furnace for 4 h at 550°C (Mook and Hoskin 1982). The samples were treated individually, consisting of three samples per site and year.

**Chl index** was measured using a portable Chl meter *ClorofiLOG* (*Falker*, *model CFL 1030*); this equipment provides reliable and dimensionless information and its results are strongly related to those obtained by the classical method (Barbieri Júnior *et al.* 2012). The parameters obtained through the *ClorofiLOG* are Chl index *a* ($Chl_a$), *b* ($Chl_b$), and total ($Chl_{total}$). These variables were collected only in 2016.

**Chl *a* fluorescence** was measured using a *Plant Efficiency Analyzer* (*Handy-PEA*, *Hansatech*, King's Lynn, Norfolk, UK) with a high-resolution time (10 µs). Leaves were dark-adapted for 30 min using leaf clips (Falqueto *et al.* 2008, 2012) for oxidation of all reaction centers (RC) (Strasser *et al.* 2000). Light intensity reaching the leaf was 3,000 µmol(photon) m$^{-2}$ s$^{-1}$ (650 nm) which was sufficient to generate maximal fluorescence for all the samples. The fast fluorescence kinetics ($F_0$ to $F_m$) was recorded from 10 µs to 1 s. The initial fluorescence intensity at 50 µs ($F_0$), 100 µs, 300 µs, 2 ms ($F_J$), 30 ms ($F_I$), and maximum fluorescence ($F_m$) were recorded and used to obtain the parameters of JIP test (Strasser *et al.* 2000, Yusuf *et al.* 2010). The selected parameters were: Area, $F_0$, $F_m$, $F_v/F_0$ (number and size of active photosynthetic RC), specific energy flows per active RC, *i.e.*, ABS/RC (absorption flux), $TR_0/RC$ (trapped energy flux), $ET_0/RC$ (electron transport flux), and $DI_0/RC$ (dissipated energy flux); $\varphi P_0$ (maximal quantum yield of PSII photochemistry), $\Psi_0$ (probability of electron transport further than quinone A – $Q_A^-$), $\varphi E_0$ (quantum yield for electron transport), $\delta R_0$ (efficiency with which an electron from the intersystem reduces the final acceptor of PSI), $\varphi D_0$ (maximum efficiency of nonphotochemical de-excitation), $PI_{abs}$ (performance index for energy conservation from exciton to the reduction of intersystem electron acceptors), $PI_{Total}$ (performance index for energy conservation from exciton to the reduction of PSI end acceptors).

**Gas exchange**: Net photosynthetic rate ($P_N$ [µmol m$^{-2}$ s$^{-1}$]), stomatal conductance ($g_s$ [mol($H_2O$) m$^{-2}$ s$^{-1}$]), intercellular $CO_2$ concentration ($C_i$ [µmol($CO_2$) mol$^{-1}$]), transpiration rate ($E$ [mmol($H_2O$) m$^{-2}$ s$^{-1}$]), and luminous intensity incident on the leaf surface ($Q_{leaf}$ [µmol(photon) m$^{-2}$ s$^{-1}$]) were measured using infrared gas analyzer *LCi* (*ADC, BioScientific Ltd*., Hoddesdon, UK). The gas chamber was maintained in ambient conditions, the average photon flux density in the chamber was 257 µmol m$^{-2}$ s$^{-1}$, with an average $CO_2$ concentration of 372 µmol($CO_2$) mol$^{-1}$, and leaf temperature reaching 32°C on average. $P_N$ and $g_s$ were used to calculate and determine water-use efficiency (WUE = $P_N/g_s$ [µmol($CO_2$) mol($H_2O$)$^{-1}$]) (Sobrado 2005).

**Data analysis**: Because the abiotic and physiological data were not normally distributed, the nonparametric *Kruskal–Wallis* test was used for comparisons between study sites and followed by multiple posterior comparisons. The *Mann–Whitney*'s test was used in the comparison between the physiographic types (fringe and basin) (Zar 1996). The relationship between the variables was assessed by the correlation analysis, for this, the mean of the variables in each site was obtained, followed by a normality test (*Shapiro–Wilk*), taking into account this assumption, a *Pearson*'s correlation analysis was conducted. The $PI_{Total}$ variable did not meet normality, being normalized through the natural logarithm and, consequently, its pair in the correlation was also transformed. Correlations were calculated between the abiotic variables ($Q_{leaf}$, interstitial water salinity, OM) and biotic variables, and also between biotic variables. The data were presented as the mean ± standard error (SE). The significance level was $p<0.05$.

## Results

**Abiotic variables**: The salinity was higher in the fringe forest in S4 (Table 1). The highest content of organic matter in the sediment occurred in S2 (basin forest). Statistically, differences in salinity occurred between the sites (Table 1), confirming the highest mean observed for S4, which is located near the south entrance of the system. OM percentage varied among the sites, with the lowest values observed in S1 (north entrance). No statistical difference was obtained when the physiographic types (fringe and basin) were compared (Table 1).

Table 1. Mean (± standard error) of sediment variables including the parameters interstitial salinity and organic matter referring to sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p<0.05$).

| Sites | Interstitial salinity | Organic matter [%] |
|---|---|---|
| S1F | 27.85 ± 0.94$^B$ | 13.14 ± 0.99$^B$ |
| S1B | 32.28 ± 0.84$^B$ | 11.90 ± 2.06$^B$ |
| S2F | 32.00 ± 0.99$^B$ | 34.02 ± 0.86$^A$ |
| S2B | 27.92 ± 1.59$^B$ | 49.55 ± 0.82$^A$ |
| S3F | 32.42 ± 1.32$^B$ | 32.57 ± 0.67$^A$ |
| S3B | 30.93 ± 0.60$^B$ | 31.58 ± 1.97$^A$ |
| S4F | 37.88 ± 0.22$^A$ | 34.29 ± 1.06$^A$ |
| S4B | 35.38 ± 1.40$^A$ | 34.91 ± 2.42$^A$ |

**Chl index**: The $Chl_a$ and $Chl_b$ index differed between the sites (Fig. 2*A,B*). The $Chl_a$ index was the highest in S4 and the $Chl_b$ index was in S1 and S2. No statistical difference was recorded for the $Chl_{total}$ index between the sites. Plants of the basin forest had higher values of $Chl_a$ and $Chl_{total}$ (Fig. 2*C*).

**Chl *a* fluorescence – JIP test**: The results of the JIP test are shown in Fig. 3. The area above the curve decreased in S1, S3, and S4 (Fig. 3*A*). Sites S1, S3, and S4 exhibited the highest $F_0$ values. The $F_m$ and $F_v/F_0$ were highest at S1. For the physiographic types, the highest $F_0$ value was recorded in the fringe forest and $F_v/F_0$ was the highest in the basin forest (Fig. 3*B,D*). The values of the specific energy fluxes expressed per RC, ABS/RC, $TR_0/RC$, $ET_0/RC$, and $DI_0/RC$ were the highest in S3 and S4 (Fig. 4). S1 also had a higher mean for $TR_0/RC$, along with S3 and S4 (Fig. 4*B*). The highest values of ABS/RC, $TR_0/RC$, and $DI_0/RC$ were recorded for fringe forests compared to basin forests (Fig. 4).

The maximum quantum yield of PSII photochemistry ($\varphi P_0$) was the highest in S1 and S2 and higher $\Psi_0$ and $\varphi E_0$ values were obtained in S2, S3, and S4 (Fig. 5*A–C*). The efficiency with which an electron from the intersystem reduces the final acceptor of PSI ($\delta R_0$) was the greatest in both S2 and S4 followed by S3 (Fig. 5*D*). The maximum efficiency of nonphotochemical de-excitation ($\varphi D_0$) values was the highest in S3 and S4 and the lowest in S1 (Fig. 5*E*). The highest $PI_{abs}$ and $PI_{Total}$ values occurred in S2 and S4 (Fig. 5*F,G*). The comparison between the basin and fringe

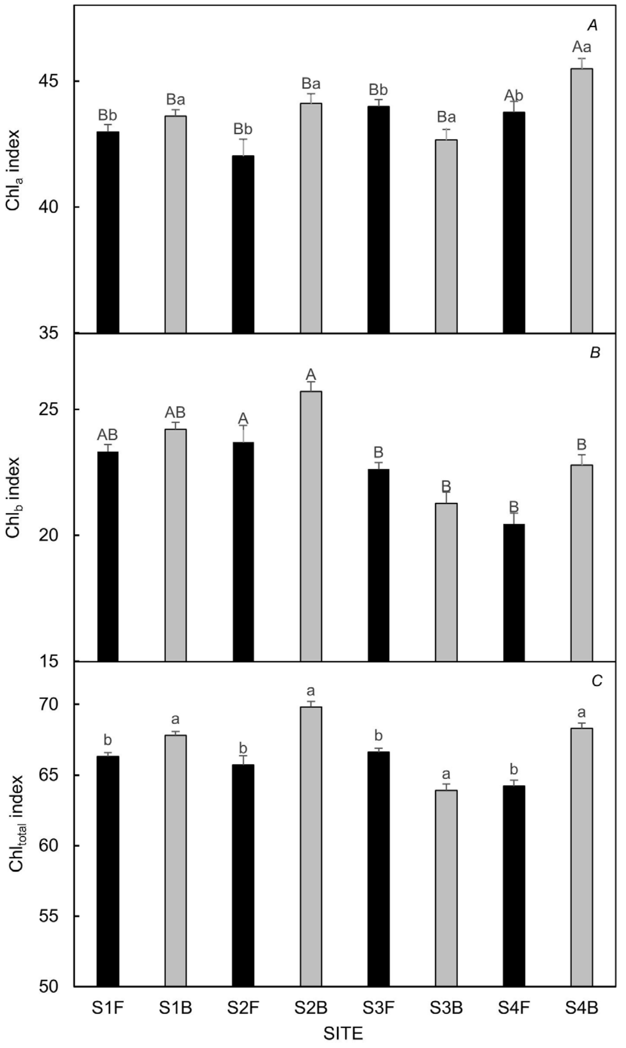

Fig. 2. Mean (± standard error) of chlorophyll (Chl) index collected in the sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. (*A*) Chl$_a$ index, (*B*) Chl$_b$ index, (*C*) Chl$_{total}$ index. *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p<0.05$).

forests indicates that the plants of the basin forest had higher values of $\varphi P_0$, $\Psi_0$, $\varphi E_0$, $PI_{abs}$, and $PI_{Total}$. In contrast, the fringe forest showed a higher value of $\varphi D_0$ (Fig. 5).

**Gas exchange**: The net photosynthetic rate ($P_N$) was significantly the highest in S2 and S4, followed by S3, with the basin forest exhibiting a greater value than that of the fringe (Fig. 6*A*). The highest values of $C_i$ were reported in S1 and it was statistically similar to those values obtained in S2 and S3 (Fig. 6*B*). The highest $g_s$ was recorded in S2. No statistical difference was recorded for *E*. Concerning the water economy, the WUE was statistically similar among S2, S3, and S4 (Fig. 6*E*). Statistical analysis for $Q_{leaf}$ is displayed in Fig. 1S (*supplement*). Difference between sites was recorded, with S1 having the lowest value.

**Linear correlation analysis**: Table 2 shows a significant linear correlation between abiotic (interstitial salinity, OM, and $Q_{leaf}$) and biotic variables, and also between biotic variables. The correlation established between OM and Chl$_a$ and the parameters related to the electron flow stands out; $Q_{leaf}$ is intrinsically correlated with several steps in the photosynthetic process. $PI_{Total}$ seems to act on $P_N$ and, consequently, on WUE.

## Discussion

Understanding the ecophysiology of plant species is important in the context of climate change as the rise in temperature and relative mean sea level will induce expansion/shrinkage of biomes and ecosystems (Wong *et al.* 2014). In addition, they can also lead to loss of habitat quality through the introduction/extinction of populations and communities. The species distribution responses in mangrove systems are closely related to environmental variables, such as flood frequency, salinity, and nutrient distribution (Cunha *et al.* 2006, Krauss *et al.* 2006, Lovelock *et al.* 2006b, Medina *et al.* 2010, Tognella *et al.* 2016). Yet, very few studies have examined the interactions between biochemical processes at energy flux level, photochemical efficiency, carbon, and nutrient assimilation that influence the incorporation of biomass by the individual.

Chl *a* fluorescence assessment determines the light-use efficiency in plants under ambient light conditions. The variable Area is proportional to the size of the electron acceptor pool on the reducing side of the PSII. If the electron transfer from the reaction center to the plastoquinone pool is blocked, the Area will be drastically reduced (Mehta *et al.* 2010). In this study, we found the lowest values for the Area of S3, which was followed by S1 and S4. Reductions in Area have already been reported in plants growing under high irradiance and salinity (Gonçalves and Santos Júnior 2005, 2007; Mehta *et al.* 2010). In this study, note that S4 had the highest salinity level, S1 had the lowest OM content, and, consequently, lower nutrient availability (Bai *et al.* 2005, Khadka 2016), and S3 had the highest mean of $Q_{leaf}$, indicating that the parameters interfere with light-use efficiency. Furthermore, S1 and S3, followed by S4, showed the highest $F_0$ values. Increased $F_0$ values may result from the impaired energy transfer between the light-harvesting complex and the reaction center, induced by low energy connectivity and damage to PSII reaction centers (Yamane *et al.* 1997, Tóth *et al.* 2007). Thus, increased $F_0$ may indicate some environmental stress. Falqueto *et al.* (2008, 2012) observed that salinity-tolerant species, *e.g.*, *R. mangle*, may show decreased $F_0$ values with an increase in salinity, but this pattern was not observed here. Reduction in maximal fluorescence in S2, S3, and S4 may indicate inhibition of PSII donor side electron transport resulting in $P_{680}$* accumulation and/or decreased $Q_A$ pool (Mehta *et al.* 2010).

The ABS/RC parameter is calculated as the total number of photons absorbed by chlorophyll molecules from all RCs divided by the total number of active RCs. Thus, ABS/RC values are affected by the ratio of active to

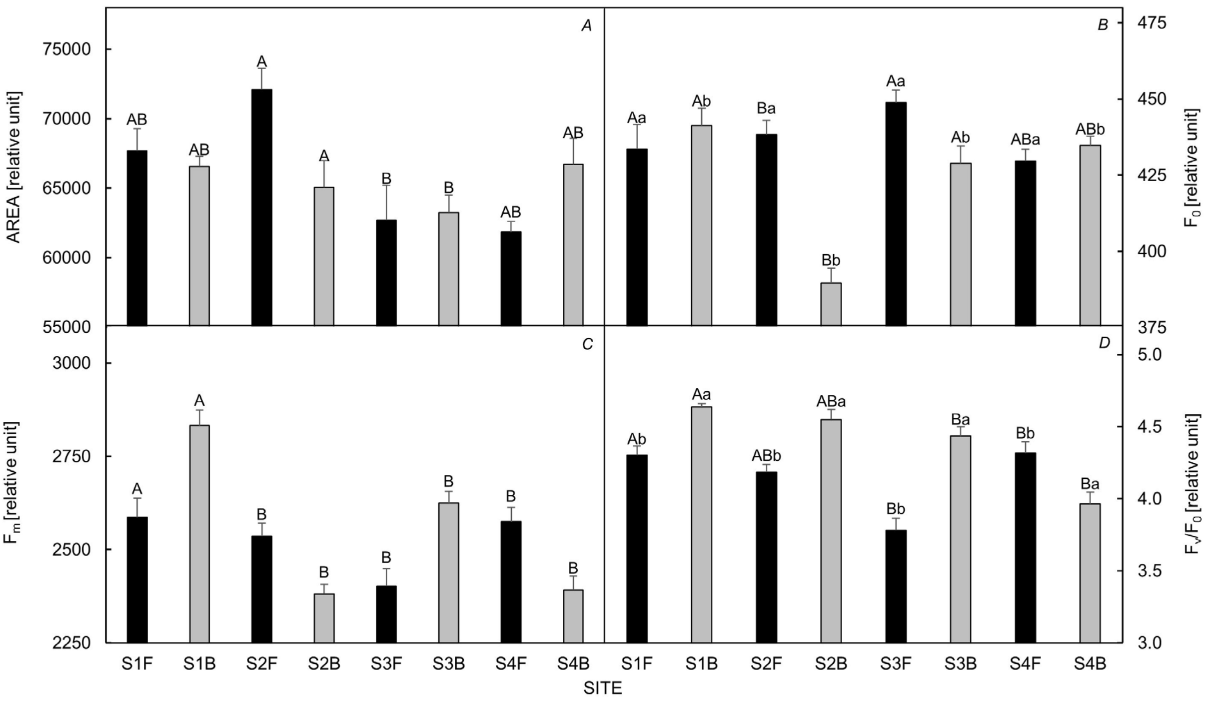

Fig. 3. Mean (± standard error) of Area, initial fluorescence ($F_0$), maximum fluorescence ($F_m$), number and size of active photosynthetic reaction centers ($F_v/F_0$) collected in the sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p<0.05$).

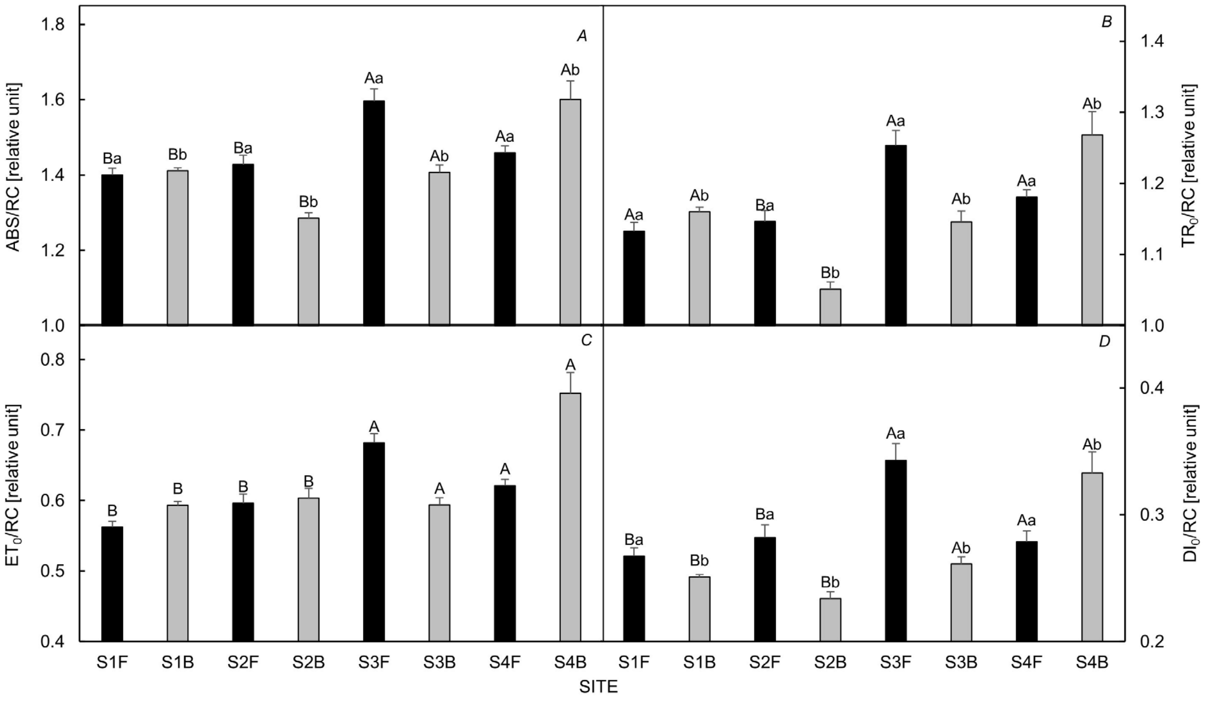

Fig. 4. Mean (± standard error) of specific fluxes (ABS/RC – absorption; $TR_0/RC$ – trapping, $ET_0/RC$ – transport; and $DI_0/RC$ – dissipation) per reaction center (RC) collected in the sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p<0.05$).

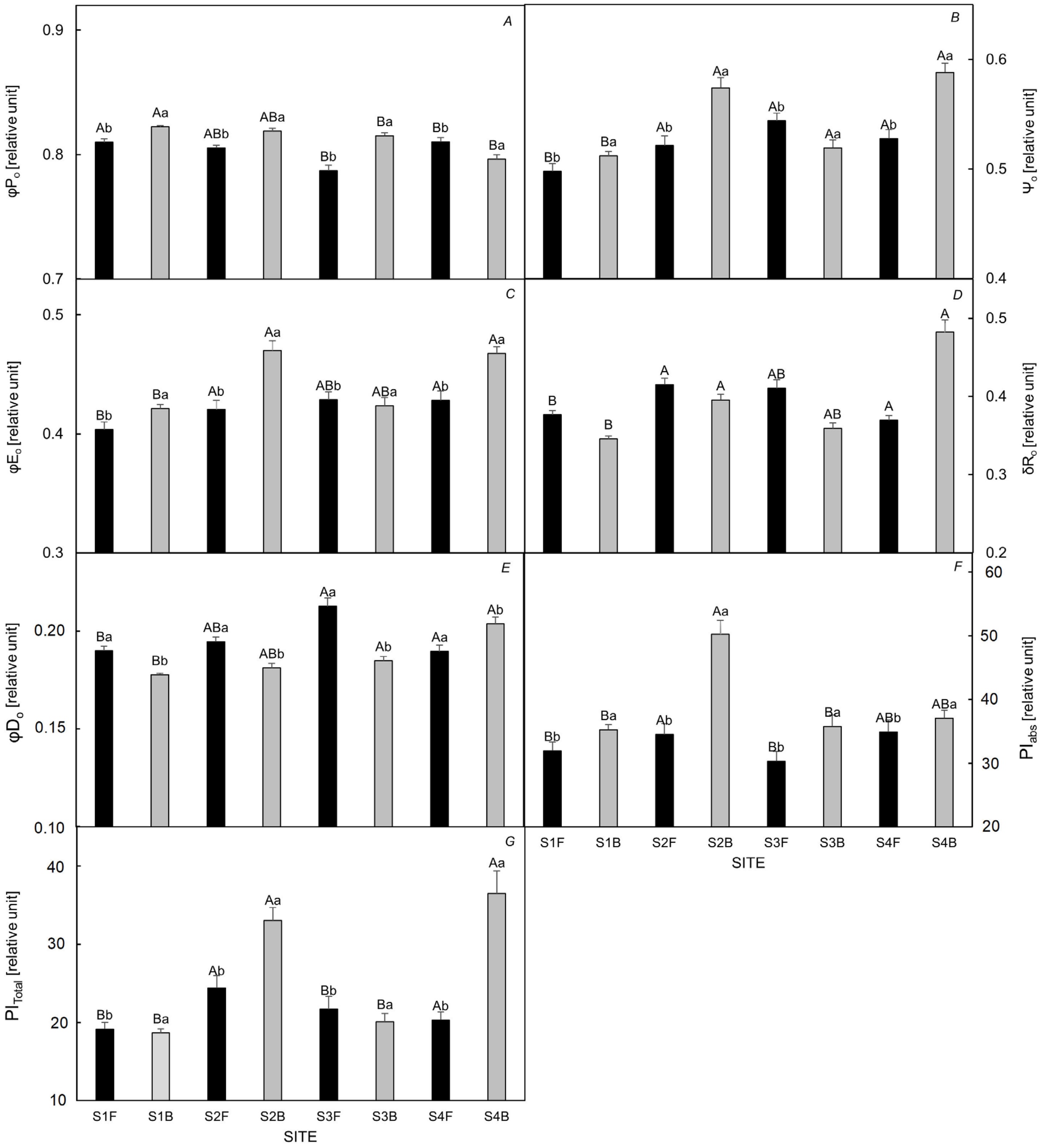

Fig. 5. Mean (± standard error) of JIP test parameters collected in the sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. (*A*) Maximum quantum yield of PSII photochemistry ($\varphi P_0$), (*B*) probability of electron transport further than quinone A – $Q_A^-$ ($\Psi_0$), (*C*) quantum yield for electron transport ($\varphi E_0$), (*D*) efficiency with which an electron from the intersystem reduces the final acceptor of PSI ($\delta R_0$), (*E*) maximum efficiency of nonphotochemical de-excitation ($\varphi D_0$), (*F*) performance index for energy conservation from exciton to the reduction of intersystem electron acceptors ($PI_{abs}$), (*G*) performance index for energy conservation from exciton to the reduction of PSI end acceptors ($PI_{Total}$). *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p$<0.05).

inactive RCs (Mehta *et al*. 2010). High values of ABS/RC are interpreted in two ways: (*1*) increase in antenna size, which is responsible for photon absorption and transfer of the excitation energy to the reaction center; (*2*) reduction in stress-active reaction centers (Strasser and Stirbet 1998, Yusuf *et al*. 2010). In the present study, increases in ABS/RC values observed in S3 and S4 indicate a reduction in active reaction centers, considering the highest $DI_0/RC$ values and the lowest $F_v/F_0$ values recorded in both sites. $DI_0/RC$ indicates energy loss as heat or fluorescence or

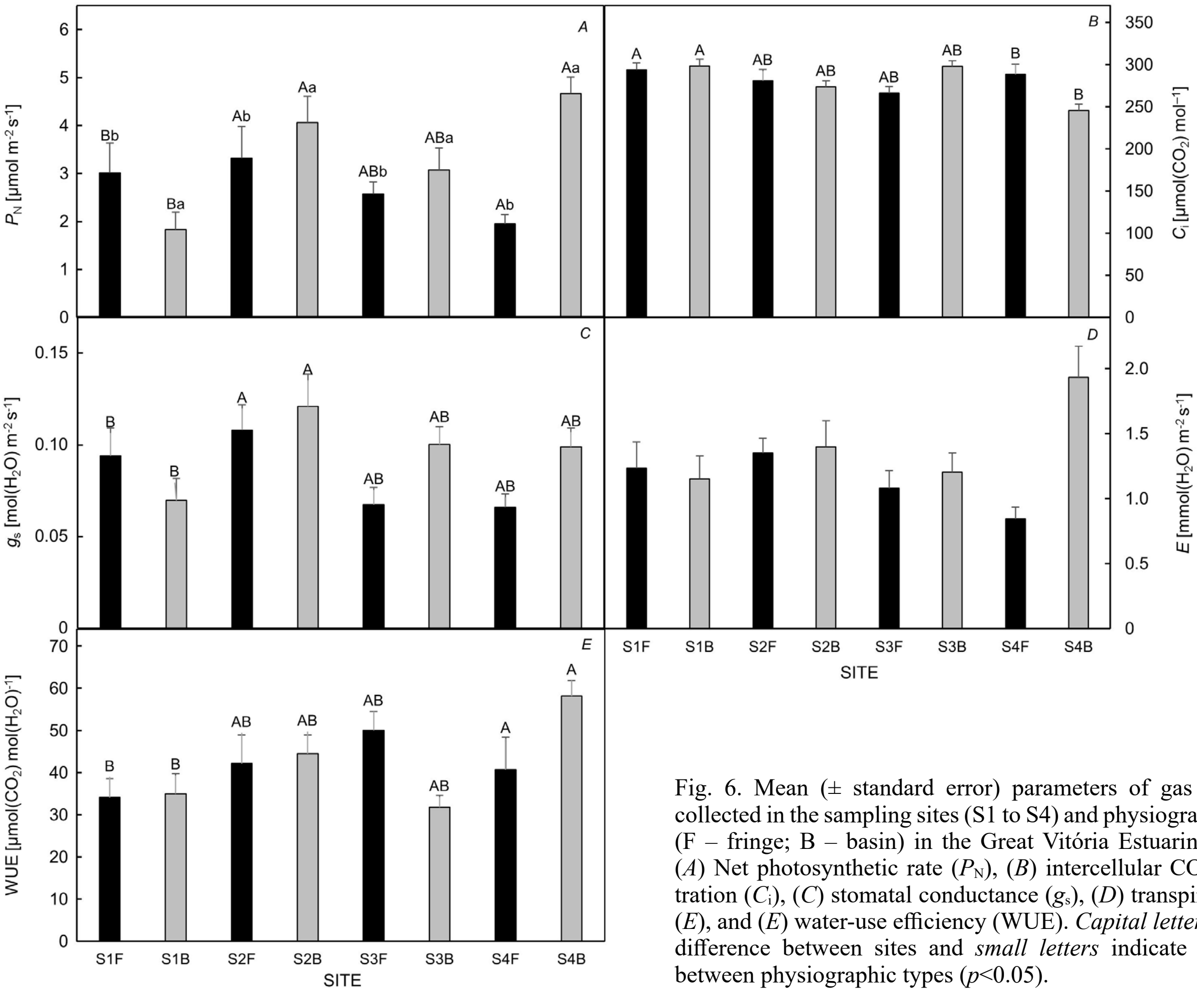

Fig. 6. Mean (± standard error) parameters of gas exchange collected in the sampling sites (S1 to S4) and physiographic types (F – fringe; B – basin) in the Great Vitória Estuarine System. (*A*) Net photosynthetic rate ($P_N$), (*B*) intercellular CO$_2$ concentration ($C_i$), (*C*) stomatal conductance ($g_s$), (*D*) transpiration rate (*E*), and (*E*) water-use efficiency (WUE). *Capital letters* indicate difference between sites and *small letters* indicate difference between physiographic types ($p$<0.05).

energy transfer to other systems such as nitrate reduction or generation of reactive oxygen species (Strasser *et al.* 2000). In contrast, reduction in $F_v/F_0$ expresses the inactivation of RC. So, these three parameters ($DI_0$/RC, $F_v/F_0$, and ABS/RC) may indicate susceptibility to high irradiance in S3 and S4. Similar results have also been associated with water stress, as recorded by Mehta *et al.* (2010) and Falqueto *et al.* (2017). However, we observed an apparent recovery of the energy flux due to the increases in energy flux corresponding to electron transport ($ET_0$/RC, $\Psi_0$, and $\varphi E_0$).

The maximal quantum yield of PSII ($\varphi P_0 = F_v/F_m$) is used to evaluate plant stress. In this study, $\varphi P_0$ was the highest at S1. Moreover, S1 exhibited the lowest $\Psi_0$, indicating less efficient production of reducing power (NADPH), as well as reduction of the oxidized plastoquinone pool, and inhibition of reoxidation of the $Q_A$ ($\varphi E_0$). The lowest $ET_0$/RC, $\Psi_0$, $\varphi E_0$, and $\delta R_0$ values obtained in S1 suggest damage to energy flux corresponding to electrons transport (Gonçalves and Santos Júnior 2005). These parameters can be considered indicators of the nutritional status of plants (Swoczyna *et al.* 2019, Meng *et al.* 2021), since the reduction of nutrients directly influences the photosynthetic apparatus, mainly through the biosynthesis and functioning of the main photosynthetic components, with a direct effect on the synthesis of proteins involved in photosynthetic reactions and synthesis of chlorophyll (Kalaji *et al.* 2014). The performance indices ($PI_{abs}$ and $PI_{Total}$) have been used to identify strategies for energy use in plants (Gonçalves *et al.* 2010). $PI_{abs}$ evaluates the variables $\varphi P_0$ and ABS/RC, as well as $\Psi_0 = ET_0/TR_0$ (Mehta *et al.* 2010, Yusuf *et al.* 2010). $PI_{Total}$ also considers the reduction of PSI acceptors by incorporating the $\delta R_0$ parameter (Yusuf *et al.* 2010). Thus, analysis of $\varphi P_0$ alone can disguise the actual condition of the plant. For example, the highest $\varphi P_0$ values were found in S1, but this site had the lowest $PI_{abs}$ and $PI_{Total}$ values indicating that electron flow after $Q_A^-$ and from the intersystem for PSI final acceptor reduction is not in good condition, which was evidenced by the analysis of $\Psi_0$ and $\delta R_0$.

Plants subjected to water and salt stresses lead to a reduction in $\Psi_0$, $\varphi E_0$, $PI_{abs}$, and $PI_{Total}$ and an increase in ABS/RC and $DI_0$/RC (Mehta *et al.* 2010, Redillas *et al.* 2011, Silvestre *et al.* 2014, Falqueto *et al.* 2017), as well as high irradiance stress. In the present study, we found that the site with the highest salinity level (*i.e.*, S4) exhibited the highest specific energy fluxes per reaction center (ABS/RC, $TR_0$/RC, $ET_0$/RC, and $DI_0$/RC). But also,

Table 2. Linear correlation between abiotic and biotic variables and between biotic variables collected in the mangrove forest of the Great Vitória Estuarine System. ABS/RC – absorption flux per reaction center; $C_i$ – intercellular $CO_2$ concentration; $DI_0$/RC – dissipated energy flux per RC; $ET_0$/RC – electron transport flux per RC; $F_m$ – maximum fluorescence; $F_v/F_0$ – number and size of active photosynthetic RC; $P_N$ – net photosynthetic rate; $PI_{Total}$ – performance index for energy conservation from exciton to the reduction of PSI end acceptors; $Q_{leaf}$ – luminous intensity incident on the leaf surface; WUE – water-use efficiency; $\delta R_0$ – efficiency with which an electron from the intersystem reduces the final acceptor of PSI; $\varphi D_0$ – maximum efficiency of nonphotochemical de-excitation; $\varphi E_0$ – quantum yield for electron transport; $\varphi P_0$ – maximal quantum yield of PSII photochemistry; $\Psi_0$ – probability of electron transport further than $Q_A^-$.

| Variables | | *r* | *p* |
|---|---|---|---|
| Organic matter | $F_m$ | –0.76 | 0.0274 |
| | $\Psi_0$ | 0.73 | 0.0393 |
| | $\varphi E_0$ | 0.74 | 0.0354 |
| $Q_{leaf}$ | $F_v/F_0$ | –0.86 | 0.0054 |
| | $\varphi P_0$ | –0.86 | 0.0056 |
| | $\varphi D_0$ | 0.86 | 0.0056 |
| | ABS/RC | 0.76 | 0.0267 |
| | $ET_0$/RC | 0.85 | 0.0075 |
| | $DI_0$/RC | 0.85 | 0.0062 |
| | $\delta R_0$ | 0.93 | 0.0007 |
| | $C_i$ | –0.91 | 0.0015 |
| | WUE | 0.89 | 0.0028 |
| $Chl_a$ index | $\Psi_0$ | 0.79 | 0.0188 |
| | $\varphi E_0$ | 0.74 | 0.0339 |
| | $ET_0$/RC | 0.80 | 0.0166 |
| | $C_i$ | –0.73 | 0.0394 |
| | WUE | 0.75 | 0.0320 |
| $PI_{Total}$ | $P_N$ | 0.82 | 0.0126 |
| | WUE | 0.78 | 0.0222 |

the highest energy flux corresponds to electron transport ($ET_0$/RC, $\Psi_0$, and $\varphi E_0$). This finding shows the sensitivity of the species to salinity, at least concerning the reduction in the active reaction centers (ABS/RC and $F_v/F_0$) and greater entrapment in energy flux ($TR_0$/RC) (Strasser *et al.* 2004), since S4 exhibited the highest $PI_{Total}$ value.

*In situ* studies are difficult to identify a single cause of stress observed, although there is an indication of irradiance stress at S3, this evaluation can be done taking into account the parameters ABS/RC, $DI_0$/RC, $F_v/F_0$, $\varphi P_0$, $PI_{abs}$, and $PI_{Total}$, as well as the negative linear correlation between $Q_{leaf}$ and $F_v/F_0$. None of the evaluated sites presented high $Q_{leaf}$ values. In any case, S1 and S3 are assumed to have some energy sink. S1 is more closely linked to the energy flux corresponding to electron transport beyond $Q_A^-$ and, and S3 to PSII and PSI, in addition to the lowest $Chl_a$ and $Chl_b$ content. Reduction in photosynthetic pigments may represent a protective strategy in which photon trapping is reduced (Christian 2005). The forest at S3 showed the highest $Q_{leaf}$, which compromises photosynthetic efficiency. In addition, Teubner Júnior *et al.* (2018) point out that the Bubu River, the location of S3, has one of the lowest nutrient inputs (nitrogen and phosphorus) to the GVES. Farnworth and Ellison (1996) considered *R. mangle* as a sun-and-shade flexible species, with ontogenetic variations.

High sand content and lower MO content in sediment were observed by Zamprogno *et al.* (2016) in the mangrove area around S1. In general, sites with coarser sediment favor *L. racemosa* because the species can more efficiently use nutrients, which are scarcer in sandy areas (Cintrón and Schaeffer-Novelli 1983).

The Chl index is largely used in agronomy because it provides a reliable relationship between chlorophyll content and leaf nitrogen concentration (Pariz *et al.* 2011, Haim *et al.* 2012, Conforto *et al.* 2014, Schlichting *et al.* 2015). Nitrogen is considered one of the most important nutrients for plants and around the world, there are mangrove areas with limited growth/structure due to this nutrient deficiency (Lovelock *et al.* 2006a,b; Alongi 2011). In the present study, a relationship was established between the $Chl_a$ and the electron flux variables ($\Psi_0$, $\varphi E_0$, $ET_0$/RC) and WUE by linear correlation, showing the highest values for the variables in S4 compared with the other sites evaluated. Thus, we can consider that a greater nutrient contribution to a given region may favor energy flux and water-use efficiency. In contrast, for S1, which is considered a nutrient-poor region within the study due to its sediment characteristics, this would explain the reductions in $Chl_a$ and $Chl_b$, electron transport chain energy fluxes, and performance indices ($PI_{abs}$ and $PI_{Total}$). In addition, the linear correlation also confirmed the relationship between OM content and variables related to the energy flux in the electron transport chain.

Mangrove species are recognized for their conservative behavior in water use, *i.e.*, an increase in salinity is usually accompanied by a reduction in water loss, reflecting greater efficiency in water use. The intensity of this relationship depends on the species (Sobrado 2000, Soares *et al.* 2015) and the level of salinity and its variation (Ball 1988, Bompy *et al.* 2014). *R. mangle* is described in the literature as the most sensitive species to salinity among neotropical species. In general, it shows less assimilation and low water-use efficiency under high salinity conditions compared to other species (Ball 1988, Sobrado 2000). However, new studies have shown that in some sites, it is the dominant species in high-salinity conditions (Estrada *et al.* 2013, Bompy *et al.* 2014). Therefore, regarding *R. mangle*, more research on photosynthetic behavior in field conditions is needed, as well as contemplating a greater population diversity.

Pascoalini (2014) evaluated net photosynthesis by *R. mangle* in the Vitória Bay and found a reduction in carbon assimilation with increasing salinity (average salinity of 21 and 28). The present study found no similar pattern, but found responses to new stressors in the system, for example, the lesser $P_N$ at the site with the lowest organic matter content (S1). $P_N$ was statistically similar at both sites S2 and S4, followed by S3. However, two locations stand out: S2 and S4. S4 is the site with the highest salinity level. It has a mixed forest including *A. schaueriana*, *L. racemosa*, and *R. mangle* and is subject to anthropic interference (Pascoalini *et al.* 2019). This mangrove area is adjacent to a port complex and, consequently, it is near the dredging along the estuary's central channel, as well as all contamination from the port activities. It also receives urban and industrial effluents from a metropolitan municipality (Vila Velha) *via* the Aribiri River and through direct sewage disposal in the mangrove. The literature highlights the presence of heavy metals above the expected for the region in both the mangrove and estuary sediment samples, with the presence of organic contaminants in the mangrove's sediment (Jesus *et al.* 2004, Zamprogno 2015). Nonetheless, individuals at S4 were photosynthetically efficient for both chlorophyll fluorescence parameters and gas exchange, a reflection of the species' photosynthetic plasticity. One of the characteristics of *R. mangle* is the possibility of excluding salts and contaminants at the root level (Souza *et al.* 2014), preserving the photosynthetic apparatus of energy sinks.

S2 also stands out. It is located in a region of the estuary in which the organic matter content reaches 50%, although being statistically similar to S3 and S4. In addition, the site has been undergoing estuarine salinization from climate variability. In the years 2015, 2016, and 2017, the municipality of Vitória had rainfall below 1,000 mm per year, with 2016 being the most critical (INCAPER 2018). $PI_{abs}$, $PI_{Total}$, $P_N$, and WUE were similar to site S4 and the vegetation would be expected to respond to increased salinity, since the low rainfall affected the salinity of the estuary, as pointed out by Leite (2018) and Teubner Júnior (2016). According to the literature, in the years 2000/2001, the salinity of the estuarine region near S2 was lower than 10 (Jesus *et al.* 2004) and in 2015 reached about 30 (Leite 2018). Zamprogno *et al.* (2016) measured the salinity of the interstitial water in the mangrove sediment and recorded values ranging from 11 to 21 for the years 2012 and 2013.

Among the variables analyzed, photosynthetic efficiency seems to be controlled by $Q_{leaf}$, since there is a relationship between it and the variables of chlorophyll *a* fluorescence and WUE, which was confirmed by linear correlation. The Chl concentration, observed in this study through the index $Chl_a$, controls the performance of plants at the level of energy flux in the electron transport chain and WUE. Variables related to the energy flux in the electron transport chain are also controlled by OM. Furthermore, $PI_{Total}$ controls net photosynthesis and WUE. The results indicate that salinity has less control over photosynthetic efficiency and is visible only in variables related to reaction centers, showing negative interaction. On the other hand, the site (S4), with the highest salinity level, has the highest photosynthetic performance, same as S2, reaffirming the role of mangrove plants' efficiency in water economy, under conditions of significant nutrient input.

The input of nitrogen (5.6 t $km^{-2}$ $year^{-1}$) and phosphorus (2.8 t $km^{-2}$ $year^{-1}$) to GVES is high when compared to other intermediate-size watersheds in Brazil. The contribution of nutrients from the Santa Maria River to Vitória Bay is more significant when compared to the other basins that contribute to the system. Cattle livestock is the largest source of nutrients for GVES and then is followed by domestic effluents (Teubner Júnior *et al.* 2018). However, considering the areas of the basins evaluated, Teubner Júnior *et al.* (2018) pointed out that domestic effluents account for the highest pressure in the system. The authors recognize the Aribiri River (S4) among other urban basins of the site as the region with the highest population density and highest nutrient yield, especially nitrogen.

Nitrogen-enriched sediments favor the increase of electron transport efficiency in *A. germinans* and *R. mangle*, as well as accumulation of the element in senescent leaves (Feller *et al.* 2003). S4 had the highest $Chl_a$ values and carbon assimilation, and the literature points to the eutrophication of the estuary. Still, if there is a relationship between chlorophyll index and leaf nitrogen concentration in mangrove plants, one can assume that vegetation is responding to nutritional enrichment.

At first, the mangrove is favored by the nutritional enrichment as already reported in the literature (Lovelock *et al.* 2006a). However, Lovelock *et al.* (2009) found an increase in mortality with long-term nutritional enrichment, and this increment of mortality was observed in the Aribiri River mangrove, through the density of dead individuals in S4 (Zamprogno *et al.* 2016, Pascoalini *et al.* 2019). As previously mentioned, this mangrove area has high levels of organic and metal contaminants and the short-term response of vegetation, especially in the young compartment, may be indifferent to these high concentrations. This unresponsive behavior is related to the fact that *R. mangle* has morphophysiological mechanisms such as precipitated iron plates in the roots. These occur since plants exposed to anoxic sediments, such as mangrove plants, release oxygen from the roots to tolerate flooding, which causes precipitation of metals in the sediment and on the root surface. This iron-rich root precipitate forms a physical barrier to heavy metal absorption (Souza *et al.* 2014).

In the present work, light saturation was not achieved, but, possibly, individuals can increase their assimilation under more favorable conditions. The low assimilation recorded in this work might be related to light attenuation by the vegetation occurring in the study sites, in addition to the other environmental factors mentioned. Attenuation of visible light confers protection to $Chl_a$ from photooxidation, a strategy the species uses to remain long periods under the canopy until gaps are formed increasing intraspecific competition and reducing growth in low light conditions (Lima *et al.* 2018). The species will remain in the system as a source of contribution to processes of regeneration/replacement of individuals. The leaf area index of mangroves is one of the lowest among tropical forests and their leaves are mostly clustered in the upper part of the crown, with a phyllotactic pattern that minimizes leaf overlapping (Tomlinson 1986). Moreover, the ecosystem lacks the understory characteristic of humid tropical forests (Cintrón and Schaeffer-Novelli 1983). Despite these singularities, some forests are more closed than others, resulting in light control for young individuals. Therefore, this forest compartment may exhibit less photosynthesis when compared with the canopy (Alongi 2009).

In the comparison of the physiographic types, the plants in the basin showed higher values for $Chl_a$ and $Chl_{total}$, $F_v/F_0$, $\varphi P_0$, $\Psi_0$, $\varphi E_0$, $PI_{abs}$, and $PI_{Total.}$ The plants of the basin had higher photochemical performance than those in the fringe. This behavior is reflected in the $P_N$, with the basin plants recording the highest value. In contrast, the parameters with higher values recorded in the fringe are related to stress in plants and include $F_0$, $\varphi D_0$, ABS/RC, $TR_0$/RC, and $DI_0$/RC. The mangrove area around GVES has the basin forests more structurally developed and the fringe areas are more vulnerable, having characteristics of forest-changing variations in flood patterns, erosive and depositional processes, and irregular freshwater flow (Zamprogno 2015, Zamprogno *et al*. 2016, Teubner Júnior *et al*. 2018).

The combination of gas exchange, chlorophyll *a* fluorescence, and chlorophyll index measurements in association with abiotic data that control mangrove growth and species competition reinforce the results obtained among the different sites and comparatively analyzed to assess the species plasticity to occupy different habitats in the mangrove. These findings corroborate the importance of the management of these species in metropolitan regions, contributing to the maintenance of ecosystem services and, consequently, biological, habitat, and genetic diversity (Millennium Ecosystem Assessment 2005).

**Conclusion**: The study indicates the photosynthetic plasticity of *R. mangle* in a complex mangrove area. The photosynthetic efficiency of the species is controlled by the available incident radiation and organic matter content. Salinity acts by reducing or inactivating the reaction centers. On the other hand, concerning gas exchange, salinity acts on water loss, which leads to reduced stomatal conductance and, thus, increased water-use efficiency in high salinity conditions. The higher availability of OM seems to be directly related to nutrients and, consequently, to a greater energy flux to the electron transport chain in the photochemical phase of photosynthesis. $Q_{leaf}$ is an important factor controlling photosynthetic efficiency by mainly acting on chlorophyll fluorescence variables and water-use efficiency. The biotic variables identified as controlling the photosynthetic efficiency are $Chl_a$ concentration (observed here through the Chl index) and $PI_{Total}$. The former for contributing to the performance of plants at energy flux level to the electron transport chain and conservative use of water and the latter for acting on $P_N$ and also conservative use of water. The results obtained show that the fluorescence of Chl *a*, gas exchange, and Chl index, together with sediment analysis, are suitable parameters to evaluate *R. mangle* photosynthetic plasticity in metropolitan mangroves.

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