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# Variations in photo-physiological responses of shaded and non-shaded mangrove, *Rhizophora mucronata* tree parts from Mauritius Island, western Indian Ocean

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**Abstract.** *Kaullysing D, Jogee SY, Mundil SP, Soondur M, Gopeechund A, Ricot M, Jeetun S, Chinta T, Chockalingum J, Mungur D, Kowal B, Kristnama L, Gunness V, Balgobin A, Fakun ZR, Munbodhe V, Nohur MB, Ramdhun D, Ramsurrun LK, Rase S, Seetohul TK, Mattan-Moorgawa S, Ramah S, Bhagooli R. 2023. Variations in photo-physiological responses of shaded and non-shaded mangrove,* Rhizophora mucronata *tree parts from Mauritius Island, western Indian Ocean. Indo Pac J Ocean Life 7: 71-78.* This study assessed and compared the photo-physiological responses of the tree parts of juvenile and adult mangrove, *Rhizophora mucronata*, under shaded and non-shaded conditions in the northern coast of Mauritius Island. Chlorophyll *a* fluorescence of mature (dark) leaves, young and mature propagules, lichen, buds, and sepal of adult *R. mucronata* trees, and of mature and young (pale) leaves of juveniles under natural shaded and non-shaded conditions was measured using a field-portable Diving Pulse-Amplitude-Modulated (D-PAM) fluorometer. Commonly used chlorophyll fluorescence parameters such as $F_v/F_m$, $rETR_{max}$, $NPQ_{max}$ were calculated. The tree parts of adult and juvenile *R. mucronata* showed considerable variations in their photosynthetic responses. $F_v/F_m$ of adult tree leaves was 30% higher in shaded condition as compared to non-shaded condition. The combined effect of mangrove tree parts and conditions (shaded; non-shaded) resulted in significant differences in mean values of $F_v/F_m$ (three-way ANOVA, $p<0.001$). Leaves of adult trees had 52% higher $rETR_{max}$ in shaded condition. While a significant difference ($p<0.001$) was noted in the mean $rETR_{max}$ values of various tree parts, the shaded and non-shaded conditions did not have any significant effect on $rETR_{max}$ ($p>0.05$). Non-shaded parts of *R. mucronata*, including the leaves, exhibited higher $NPQ_{max}$ values as compared to shaded conditions. Mean $NPQ_{max}$ varied significantly among mangrove parts ($p<0.001$), between tree stage ($p<0.001$) and between conditions ($p<0.05$). These findings revealed differences in the photosynthetic activities of various mangrove parts of juvenile and adult trees under shaded and non-shaded conditions, a first attempt for the tropical island of Mauritius.

**Keywords:** Chlorophyll *a*, mangrove, Mauritius, photo-physiology, shaded and non-shaded conditions

## INTRODUCTION

Mangroves are unique and complex vascular plants inhabiting tropical and sub-tropical coasts (Cheeseman et al. 1997; Polidoro et al. 2010). An estimated 14.79 million hectares of mangrove forests are present in 113 countries around the world (FAO and UNEP 2020). Mangrove plants of the world consist of approximately 70 species of trees and shrubs (Spalding and Leal 2021). In Mauritius, only two species of mangroves occur, namely, *Bruguiera gymnorrhiza* and *Rhizophora mucronata* (Appadoo 2003). However, only species belonging to the genera *Avicennia*, *Lumnitzera*, *Bruguiera*, *Ceriops*, *Kandelia*, *Rhizophora* and *Sonneratia*, and the species *Nypa fruticans* and *Laguncularia racemosa* are considered as "true mangroves" and are the main components of mangrove forests worldwide (Tomlinson 2016 cited in Quadros and Zimmer 2017). This implies that they are woody plants, facultative or obligate halophytes inhabiting the intertidal region and are not found in terrestrial communities (Komiyama et al. 2008; Quadros and Zimmer 2017). Mangrove trees are usually associated with other organisms such as lichens, microbes, other plants, and animals (Kathiresan and Bingham 2001), and mangrove forests are composed of both autochthonous (local) and allochthonous (external) organic carbon, as evidenced by the analysis of sediment cores (Suello et al. 2022).

Tang et al. (2018) used Geographic Information System (GIS)-based geospatial analysis and high-performance parallel computing and estimated the total area, biomass (including above- and below-ground), and associated carbon stock of global mangroves as 130,420 km$^2$, 1.908

Pg, and 0.725 Pg C, respectively, for the year 2000. The averaged above-ground biomass density of global mangroves was estimated as 146.3 Mg $ha^{-1}$ for the same year (Tang et al. 2018). From 1990 to 2020, mangrove area has decreased by 1.04 million hectares (FAO and UNEP 2020), contributing significantly to loss of carbon stocks (Monga et al. 2022) and associated ecosystem services (Goldberg et al. 2020). It is estimated that mangrove deforestation results in emissions of 0.02-0.12 Pg C per year, which is as much as around 10% of emissions from deforestation globally, despite accounting for merely 0.7% of tropical forest area (Donato et al. 2011). This highlights the importance of protecting mangrove forests from destructive anthropogenic activities, as well as natural causes of degradation.

Mangroves are physiologically interesting as prospective models for stress tolerance (Cheeseman et al. 1997) as they have adapted to live in extreme conditions such as high temperature, anaerobic soil, tidal influx, and high salinity (Kathiresan and Bingham 2001). A convenient way of measuring stress in mangroves is by estimating their photosynthetic activities through the measurement of the chlorophyll *a* fluorescence. Mangroves perform C3 photosynthesis and the photosynthetic activity of mangroves differs from one species to another (Basak et al. 1996) depending on several external environmental factors such as salinity level, ambient temperature, and ambient light levels (Cheeseman et al. 1991; Cheeseman 1994). Photosynthetic pigments such as chlorophylls are also found in the propagules (Duke and Watkinson 2002), stems and branches (Saveyn et al. 2010; Schmitz et al. 2012) of mangroves. Therefore, different parts of mangrove trees are capable of performing photosynthesis which is a key process for their survival and sustainability of the ecosystem as a whole. Globally, numerous studies have investigated photo-physiological responses of mangrove leaves (Rovai et al. 2013; Naidoo et al. 2014), while fewer studies investigated that of the stem (Schmitz et al. 2012). The photosynthetic activity of other parts such as the pegs, flowers and epiphytic lichens are yet to be thoroughly understood. It is noteworthy that plant parts in other marine seaplants have been studied. For instance, the photosynthetic performance was found to be variable among the leaf, transition part between leaf and stem (transit), the stem of the seagrass *Thalassodendron ciliatum*, and between the frond and the stolon of the macroalga *Caulerpa cupressoides* (Bhagooli et al. 2021a).

Mangrove afforestation programmes in Mauritius have enabled the declining area to increase from 45 ha in the year 1980 to 145 ha in 2013 (Bosire et al. 2016). However, such programmes are carried out without an assessment of the photo-physiological responses of mangroves to the local conditions and climate. Furthermore, though there are several scientific studies related to mangrove areas around Mauritius (Sadally et al. 2016; Armance et al. 2019; Soondur et al. 2020, 2021), no information is available about the differential photo-physiological responses in the different parts of adult and juvenile mangrove. Thus, with the intention of contributing to providing new and additional information on tropical mangroves of Mauritius, this study assessed and compared the photo-physiological responses of the photosynthetic tree parts of juvenile and adult *R. mucronata*, the dominant species of mangroves in the tropical island of Mauritius, under shaded and non-shaded conditions.

## MATERIALS AND METHODS

### Study site

The study was conducted in a mangrove patch at Poudre d'Or situated in the north-east coast of Mauritius Island (Figures 1A,B) in September 2020. Juvenile and adult trees of *R. mucronata* extended along the intertidal zone within the barachois and seedlings were mostly found under the canopy of the adult trees. Saplings and some more developed seedlings were found along the supratidal zone (Figure 1C). For the purpose of this study, mangrove trees taller than 3 m were considered as adults (Clarisse et al. 2016), while juvenile trees were defined as those individuals with a height greater than 0.3 m but smaller than 3 m (Osland et al. 2020). Adult and juvenile trees/parts in the non-shaded condition were those that were exposed continuously to sunlight over maximum duration of the day. Shaded juvenile trees were sheltered from direct sunlight under the adult trees over maximum duration of the day, while shaded adult trees were constantly protected from direct sunlight among other taller adult trees.

### Measurement of photosynthetic activity

Measurement of photosystem II fluorescence represents the best approach to estimating the photosynthetic activity of mangroves. The use of Pulse Amplitude Modulated (PAM) fluorometry (Genty et al. 1990; Bhagooli et al. 2021b) as a non-invasive method is well suited for studying the photo-physiology of photosynthetic organisms, including mangroves (Falqueto et al. 2008). During the present study, chlorophyll *a* fluorescence was measured using a field-portable Diving-PAM fluorometer (Heinz Walz GmbH, Effeltrich, Germany). Following dark adaptation of 30 minutes, measurements were taken between 1130 to 1430 hrs on three random samples/individuals (triplicate) of mature (dark) leaves, young and mature propagules, lichen, buds, and sepal of adult *R. mucronata* trees, and of mature and young (pale) leaves of juveniles under natural shaded and non-shaded conditions in the mangrove stand at the study site. The commonly used fluorescence parameters $F_v/F_m$ (maximum photochemical efficiency of photosystem II), $rETR_{max}$ (maximum relative electron transport rate), $NPQ_{max}$ (maximum non-photochemical quenching), as well as $\alpha$ (initial slope of the Rapid Light Curve before the onset of saturation), $\beta$ (slope of the RLC after saturation) and $I_k$ (minimum saturating irradiance) were calculated from the fluorescence parameters measured (Bhagooli et al. 2021b). $rETR_{max}$, $NPQ_{max}$, $\alpha$ and $\beta$ values were obtained after fitting curves to the RLCs through Sigmaplot (Version 12.0).

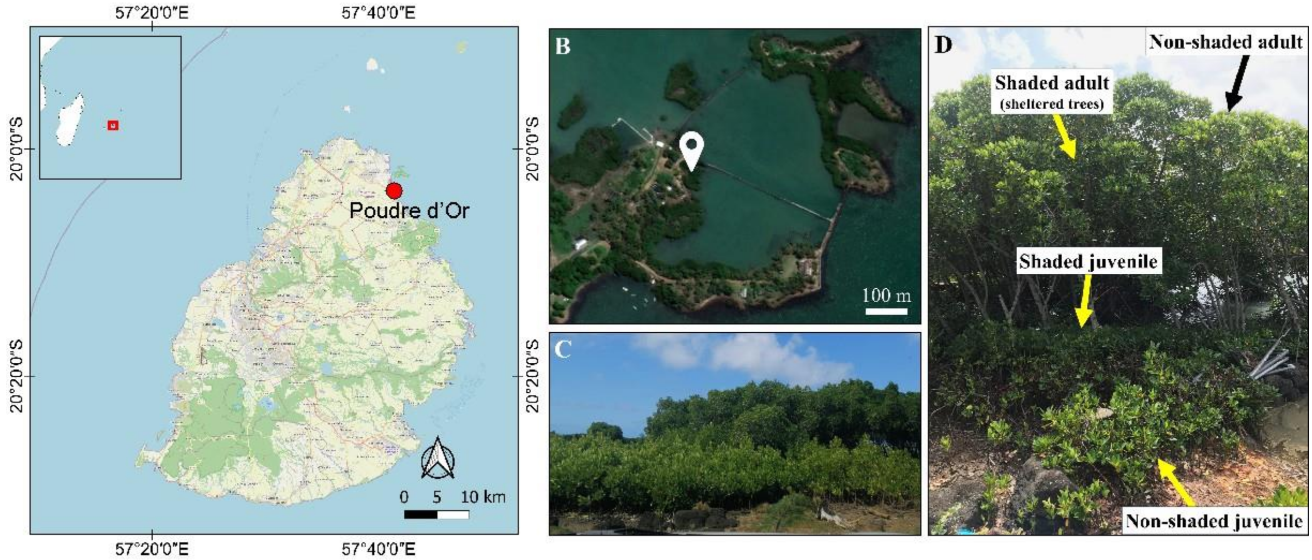


**Figure 1.** A. Map of Mauritius showing the study site located in the north-east of Mauritius, B. Satellite image of Poudre d'Or barachois with mangrove patch indicated by a white pin (Source: Google Earth Pro 2022), C. The study site with a mangrove patch composed of adult (background) and juvenile (foreground) trees, D. Adult mangrove trees and juveniles in shaded and non-shaded conditions

**Measurement of physico-chemical parameters**

To quantify the characteristics of the shaded and non-shaded conditions, air temperature and light intensity levels were recorded in situ using data loggers (HOBO, Pendant) which were affixed with cable ties on shaded and non-shaded adult and juvenile trees. Seawater salinity was also measured using a salinity logger. Measurements were taken at an interval of 15 minutes over the study period.

**Statistical analyses**

The normality of the data was determined by the Shapiro-Wilk test. Non-normal data were arcsine (sqrt) transformed to meet the assumptions of normality. A three-way Analysis of Variance (ANOVA) was used to determine differences in mean $F_v/F_m$, $rETR_{max}$, $NPQ_{max}$, α, β and $I_k$ values of different parts of adult and juvenile mangroves, including in the epiphytic lichens under shaded and non-shaded conditions, followed by LSD post hoc test. All statistical analyses were conducted using SPSS statistical software (PASW Statistics 18.0.0).

## RESULTS AND DISCUSSION

**Temperature and light intensity variations**

In Mauritius, the annual mean temperature in summer is 24.7°C (Bhagooli and Kaullysing 2019). During the study period, air temperature and light intensity varied between 23.29-24.06°C (Figure 2A) and 3444.5-11022.3 Lux (Figure 2B), respectively where the shaded adult mangrove trees were located. At the non-shaded or exposed zone of adult mangrove trees, air temperature and light level ranged between 27.08-31.88°C (Figure 2A) and 33066.9-121245.2 Lux (Figure 2B), respectively. At the shaded juvenile mangrove patch located under the adult mangrove canopy, air temperature and light intensity varied between 23.97-24.64°C (Figure 2C) and 4822.3-18600.1 Lux (Figure 2D), respectively. In contrast, non-shaded juvenile trees experience an air temperature and light intensity between 28.45-34.80°C (Figure 2C) and 46844.8-286579.7 Lux (Figure 2D), respectively. Non-shaded adult *R. mucronata* trees received light intensity almost 11-fold higher than shaded ones, while non-shaded juvenile trees received light intensity more than 15-fold higher than shaded ones. Seawater salinity varied between 34.5-35.5 PSU during the study period.

**Photo-physiology of *Rhizophora mucronata***

The tree parts of adult and juvenile *R. mucronata* showed considerable variations in their photosynthetic responses. The leaves of adult trees had the highest $F_v/F_m$ followed by the young propagules, both under shaded and non-shaded conditions (Figure 3A). A significant difference was noted in $F_v/F_m$ values under shaded and non-shaded conditions (three-way ANOVA, $p<0.05$). $F_v/F_m$ of adult leaves, juvenile leaves (young and mature), and propagules (young and mature) were higher under shaded condition. $F_v/F_m$ of adult tree leaves was 30% higher in shaded condition as compared to non-shaded condition. In contrast, the lichen associated with the bark of the mangrove trees showed higher $F_v/F_m$ in non-shaded condition. Buds and sepal of adult trees, measured only under non-shaded condition, also exhibited comparable $F_v/F_m$ to the other tree parts under the same condition. The combined effect of mangrove tree parts and condition (shaded; non-shaded) resulted in significant differences in mean values of $F_v/F_m$ ($p<0.001$; Table 1). $rETR_{max}$ was higher in young leaves of juvenile *R. mucronata* in shaded condition, while the mature leaves had higher maximum relative electron transport rate in non-shaded condition. Leaves of adult trees had 52% higher $rETR_{max}$ in shaded condition. Young and mature propagules and lichen on the bark had lower $rETR_{max}$ in shaded condition (Figure 3B). While a significant difference ($p<0.001$) was noted in the mean $rETR_{max}$ values of various tree parts, the shaded and non-shaded conditions did not have any significant effect on $rETR_{max}$ ($p>0.05$; Table 1). Overall, mean $NPQ_{max}$ varied significantly among mangrove parts ($p<0.001$), between tree stage ($p<0.001$) and between conditions ($p<0.05$). In general, non-shaded parts of *R. mucronata* exhibited higher $NPQ_{max}$ values as compared to shaded conditions (Figure 3C). No significant differences in mean α and ß values were noted among the mangrove parts, however, there were significant differences in α between juvenile and adult *R. mucronata* ($p<0.05$; Figure 3D). No significant differences were noted in ß under any treatment ($p<0.05$; Figure 3E). $I_k$ values were lower for leaves of juvenile *R. mucronata* and higher for leaves of adult trees in shaded condition (Figure 3F) with significant differences between mangrove parts and tree stages ($p<0.05$).

## Discussion

Being one of the most productive ecosystems on the planet, mangrove forests sequester a significant amount of carbon dioxide, thus, representing a globally important carbon sink (Sanderman et al. 2018). A thorough understanding of mangrove physiological conditions, community structure, and ecosystem processes is crucial to efficiently channel efforts toward the conservation of this highly threatened ecosystem, especially in data-deficient regions such as the western Indian Ocean, including the tropical island of Mauritius which relies heavily on its surrounding natural coastal and marine ecosystems for the protection of its coastal zones. This study revealed the photosynthetic activity of various mangrove parts of juvenile and adult trees under shaded and non-shaded conditions.

**Table 1.** Three-way ANOVA for effects of different mangrove parts, tree stage (juvenile and adult) and condition (shaded and non-shaded) on the photo-physiological parameters ($F_v/F_m$, $rETR_{max}$, $NPQ_{max}$, α, ß and $I_k$). * - p<0.05, ** - p<0.01, *** - p<0.001

| Dependent variable | Source of variation | *df* | *MS* | *F* | *p value* | |
|---|---|---|---|---|---|---|
| $F_v/F_m$ | Mangrove part | 5 | 0.132 | 21.549 | 0.000 | *** |
| | Tree stage | 1 | 0.001 | 0.132 | 0.719 | NS |
| | Condition | 1 | 0.134 | 21.929 | 0.000 | *** |
| | Mangrove part * Tree stage | 1 | 0.001 | 0.082 | 0.777 | NS |
| | Mangrove part * Condition | 3 | 0.062 | 10.169 | 0.000 | *** |
| | Tree stage * Condition | 1 | 5.140E-7 | 0.000 | 0.993 | NS |
| | Mangrove part * Tree stage * Condition | 1 | 0.006 | 1.056 | 0.313 | NS |
| $rETR_{max}$ | Mangrove part | 5 | 0.084 | 10.065 | 0.000 | *** |
| | Tree stage | 1 | 0.012 | 1.385 | 0.250 | NS |
| | Condition | 1 | 0.001 | 0.154 | 0.698 | NS |
| | Mangrove part * Tree stage | 1 | 0.057 | 6.830 | 0.014 | * |
| | Mangrove part * Condition | 3 | 0.024 | 3.623 | 0.026 | * |
| | Tree stage * Condition | 1 | 0.030 | 5.232 | 0.030 | * |
| | Mangrove part * Tree stage * Condition | 1 | 0.028 | 3.349 | 0.078 | NS |
| $NPQ_{max}$ | Mangrove part | 5 | 0.066 | 37.187 | 0.000 | *** |
| | Tree stage | 1 | 0.006 | 3.467 | 0.000 | *** |
| | Condition | 1 | 0.024 | 13.553 | 0.001 | ** |
| | Mangrove part * Tree stage | 1 | 1.913E-6 | 0.001 | 0.974 | NS |
| | Mangrove part * Condition | 3 | 0.013 | 7.491 | 0.001 | ** |
| | Tree stage * Condition | 1 | 0.000 | 0.147 | 0.704 | NS |
| | Mangrove part * Tree stage * Condition | 1 | 0.007 | 3.796 | 0.062 | NS |
| α | Mangrove part | 5 | 0.004 | 1.676 | 0.174 | NS |
| | Tree stage | 1 | 0.012 | 4.755 | 0.038 | * |
| | Condition | 1 | 0.005 | 2.204 | 0.149 | NS |
| | Mangrove part * Tree stage | 1 | 0.026 | 10.388 | 0.003 | ** |
| | Mangrove part * Condition | 3 | 0.004 | 1.796 | 0.172 | NS |
| | Tree stage * Condition | 1 | 0.001 | 0.463 | 0.502 | NS |
| | Mangrove part * Tree stage * Condition | 1 | 0.003 | 1.174 | 0.288 | NS |
| ß | Mangrove part | 5 | 0.016 | 1.305 | 0.291 | NS |
| | Tree stage | 1 | 0.011 | 0.914 | 0.347 | NS |
| | Condition | 1 | 0.012 | 0.993 | 0.328 | NS |
| | Mangrove part * Tree stage | 1 | 0.028 | 2.248 | 0.145 | NS |
| | Mangrove part * Condition | 3 | 0.034 | 2.790 | 0.060 | NS |
| | Tree stage * Condition | 1 | 0.017 | 1.364 | 0.253 | NS |
| | Mangrove part * Tree stage * Condition | 1 | 0.001 | 0.097 | 0.758 | NS |
| $I_k$ | Mangrove part | 5 | 0.033 | 3.503 | 0.014 | * |
| | Tree stage | 1 | 0.057 | 6.088 | 0.020 | * |
| | Condition | 1 | 0.024 | 2.589 | 0.119 | NS |
| | Mangrove part * Tree stage | 1 | 0.061 | 6.536 | 0.017 | * |
| | Mangrove part * Condition | 3 | 0.106 | 11.336 | 0.000 | *** |
| | Tree stage * Condition | 1 | 0.261 | 27.895 | 0.000 | *** |
| | Mangrove part * Tree stage * Condition | 1 | 0.006 | 0.653 | 0.426 | NS |

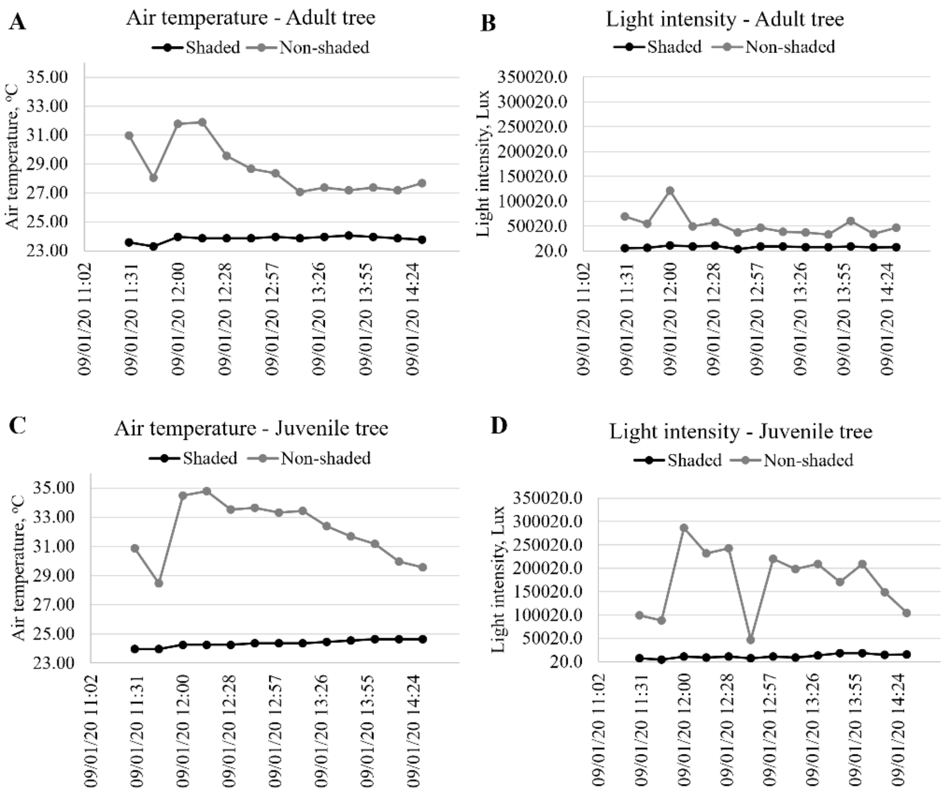


**Figure 2.** Variations in air temperature and light intensity for adult (A, B) and juvenile (C, D) *R. mucronata* at shaded and non-shaded zones within the studied mangrove patch

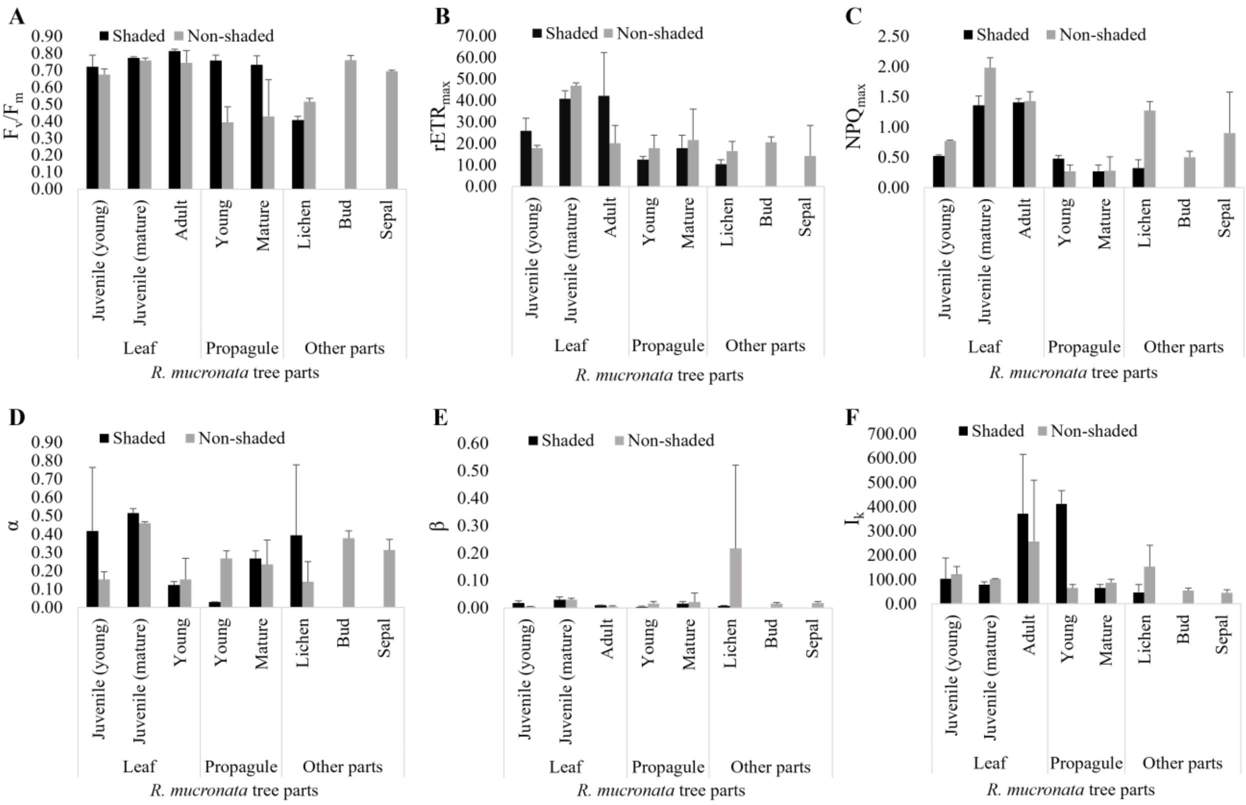


**Figure 3.** A. $F_v/F_m$, B. $rETR_{max}$, C. $NPQ_{max}$, D. α, E. β and F. $I_k$ of the different parts of juvenile and adult *R. mucronata* trees under shaded and non-shaded conditions. Bars represent mean ± standard deviation

Mangroves are physiologically interesting plants thriving in a harsh environment where conditions are expected to reduce their photosynthetic capacity through photoinhibition. In the natural habitat, mangroves receive high luminosity which is much more than the saturation point of photosynthesis, indicating that mangrove leaves often receive a large amount of excess light energy and may be prone to photo-inhibition (Cheeseman et al. 1994; Kitao et al. 2003; Attiwill and Clough 2018). Mangrove photosynthesis can reach light saturation under the incident photosynthetic photon flux density of 40% sunlight (800-1000 µmol photon.$m^{-2}$.$s^{-1}$) or lower in harsh tropical intertidal environmental conditions (Andrews et al. 1984; Carter et al. 1990; Cheeseman 1994).

Despite the extreme conditions, most species of mangroves have adapted their leaves and maintain this main active photosynthetic organ under optimum conditions to reduce photoinhibition and to sustain productivity. The shaded condition of the mangroves at Poudre d'Or led to the availability of 11- to 15-fold lower light intensity for the photosynthesizing mangrove parts, going as low as 3444.5 Lux (64 µmol photon.$m^{-2}$.$s^{-1}$). The mangrove parts exposed to higher intensities of light had lower photosynthetic activities as compared to the shaded parts, as evidenced by higher values of $F_v/F_m$ under non-shaded conditions. Low light conditions may not necessarily imply reduced photosynthetic activities.

Additionally, the photosynthetic apparatus of mangroves are also adapted to recover rapidly from high light levels such that $F_v/F_m$ reaches 0.8 shortly after sunset without occurrence of chronic photoinhibition and quantum efficiencies of PSII were high up to 500 µmol quanta.$m^{-2}$.$s^{-1}$, indicative of well-protected PSII activity, as demonstrated by Cheeseman (1994). In contrast to the findings of this study, Björkman et al. (1988) reported a large decrease in $F_v/F_m$ when leaves of a number of mangroves were directly illuminated in the field, while Cheeseman et al. (1991) reported no evidence of photoinhibition in exposed leaves of *Bruguiera parviflora* under natural illumination. This aspect of the metabolism of mangroves might be crucial for photosynthesis.

Leaves of *R. mucronata* when exposed to high illumination (non-shaded condition) at Poudre d'Or exhibited higher $NPQ_{max}$, indicating the dissipation of excess radiation through non-damaging heat emissions (Bhagooli et al. 2021b). NPQ is an important photo-protective mechanism of plants in response to the high light irradiance damage, which quenches excess energy absorbed as Photosynthetically Active Radiation (PAR) and converts and dissipates it as heat to avoid the harmful effects of excessive photon absorption (Murchie and Niyogi 2011; Esteban et al. 2013). Similar observations have been made for *Abies alba* (Pinaceae, Coniferales) by Dörken and Lepetit (2018) whereby sun leaves had higher NPQ as compared to shade leaves.

While eco-physiological responses of mangroves to excess luminosity vary between different species and may considerably affect the survival rate and spatial distribution of the mangroves, the difference in their photosynthetic capacity is closely related to salinity also (Naidoo and Von Willert 1995; Naidoo et al. 2001; Panda et al. 2006; Dittmann et al. 2022; Wang et al. 2022). A decrease may be noted in stomatal conductance when mangrove ecosystems are exposed to high illumination and high salinity conditions, resulting in reduced $CO_2$ fixation to generate excess energy. Chen et al. (2022) demonstrated that *Kandelia obovata* and *Rhizophora stylosa* when treated with 30 ppt salinity exhibited lower photosynthetic rate but higher NPQ and heat quenching values, followed by increases in the excess energy and photoprotective effects. In the present study, salinity did not vary considerably. The results of this study suggest remarkable difference between the photosynthetic activities of various mangrove parts of juvenile and adult trees under shaded and non-shaded conditions at a tropical site like Mauritius. However, it is important to also consider the effect of salinity and other parameters on the photosynthesis of mangroves. Therefore, further studies are warranted to assess the diurnal variations in fluorescence parameters under the effect of varying salinities with different tidal levels under field conditions.

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