



Seasonal changes in leaf chlorophyll *a* content and morphology in a sub-tropical mangrove forest of the Mexican Pacific

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ABSTRACT: Changes in chlorophyll *a* (chl *a*), leaf area, and leaf length need to be considered when developing ecological assessments of mangrove forests where distinct seasons occur. The purpose of this study was to assess such changes between the dry and rainy seasons in a variety of mangrove classes. Six different classes were examined, consisting of 3 species (white mangrove *Laguncularia racemosa*, red mangrove *Rhizophora mangle*, and black mangrove *Avicennia germinans*) that were either healthy or in poor condition. In total, 360 leaf samples were taken from the upper and lower canopy for chl *a* content. Additionally, leaf area index (LAI) was recorded at the same locations. For all the poor-condition classes, we observed an increase in the chl *a* content during the rainy season in both the upper and lower canopies. Moreover, dwarf black mangrove was the only poor-condition class which did not show an increase in leaf length during the rainy season. The healthy white mangrove showed no seasonal difference in chl *a* in the upper canopy, but the lower canopy did have higher chl *a* content during the dry season as well as a lower LAI. The healthy red mangrove also did not show any seasonal difference in chl *a* content, but the upper canopy had a higher chl *a* content. For the healthy black mangrove, no seasonal differences were found in chl *a* content, LAI, or leaf morphology in both upper and lower canopies. Consequently, for future endeavors we recommend that seasonal changes in the upper canopy be considered, especially when examining stands in poor condition.

KEY WORDS: Mangrove · Seasonal changes · Chlorophyll *a* · Leaf area index · LAI

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INTRODUCTION

Leaf chemical properties are the principal determinants of plant physiology and of highly active biochemical processes such as photosynthesis (Evain et al. 2004). Among the most common variations that interact with plant photosynthesis are diurnal changes of incident irradiance, ambient temperature, and humidity (Schulze & Caldwell 1994). Additionally, seasonal changes in the availability of water and nutrients (Gilman et al. 2008) affect the effectiveness of pigments in light capture and utilization (Evain et

al. 2004). Amongst the various leaf pigments, chlorophyll *a* (chl *a*) is a key compound responsible for photosynthesis, physiology, and other biological functions in plants. Consequently, changes in chl *a* can indicate plant growth (Raven et al. 1992) or disturbances from stressors (Blackburn 2007).

The aforementioned disturbances are commonplace in high, locally stressed canopies such as mangrove forests. These forested wetlands are predominantly intertidal and occur worldwide in the sub-tropics and tropics (Nagelkerken et al. 2008) along sheltered and shallow water coastlines (Ho-

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garth 1999) where high irradiation is the norm (Evain et al. 2004) and natural and anthropogenic disturbances are common. The importance of ecological field surveys of these systems may have implications in developing fast and accurate assessments regarding the state of these highly productive forested habitats for future conservation measures. Mangroves are an essential resource for a variety of local activities (Walters et al. 2008), provide for a variety of macrofaunal interactions (Cannicci et al. 2008), are highly productive (Komiyama et al. 2008), and provide habitat for a variety of terrestrial and marine fauna (Nagelkerken et al. 2008).

For mangroves, the concentrations of leaf pigments can be associated with environmental factors such as ambient temperature/sunlight (Saenger 2002), water availability (Lacerda 2002), and salinity (Steinke et al. 1993). Thus, in a sub-tropical mangrove forest where fresh water availability is seasonal, precipitation patterns could affect the physiological development of the mangrove trees, resulting in an increase or decrease of ground salinity (Field 1995). As a consequence, in sub-tropical regions there could be a seasonal decrease in net primary productivity (Saenger 2002) and growth (Raven et al. 1992). As well, a seasonal increase in the availability of sulfate in water may occur, which could increase anaerobic decomposition (Saintilan & Wilton 2001, Rogers et al. 2005) and thus potentially alter the competition between mangrove species (Lacerda 2002) resulting in decreasing diversity within mangrove areas (Duke et al. 1998). In anthropogenically stressed mangroves, these conditions (e.g. hypersalinity) may be exasperated, resulting in large-scale mangrove loss or degradation as shown in a mangrove forest just south of our study area (Kovacs et al. 2005).

Each species of mangrove has a particular range of tolerance to environmental factors such as water salinity. For example, some species are relatively intolerant to hypersaline conditions (e.g. *Rhizophora mangle*), whereas others are quite capable of tolerating very high salinities of over 60 (e.g. *Avicennia germinans*; Moroyoqui-Rojo & Flores-Verdugo 2005). These differences among the species could be assessed using leaf biophysical variables such as leaf area index (LAI), leaf area, leaf length, and chl *a* concentration. Specifically, seasonal differences in LAI and chl *a* concentration could be related to organic carbon dynamics such as litterfall decomposition rates (Flores-Verdugo et al. 1987, Kristensen et al. 2008), nutrient cycling characteristics (Feller et al. 1999), and mangrove paleoecological reconstructions (Ellison 2008). The variability of inter-species leaf

morphology (e.g. leaf area, leaf length) could be associated with faunal retention rates (Cannicci et al. 2008), mangrove ecosystem seasonal dynamics (Berger et al. 2008), and differences in canopy ecological habitat for faunal species (Nagelkerken et al. 2008). Moreover, all of these data could be valuable in describing and predicting seasonal patterns of forest productivity (Raven et al. 1992).

Yet another potentially important characteristic to consider is seasonal change in the vertical distribution of pigments within the mangrove canopy. Such potential variability could depend on many factors, including acclimation to light penetration (Saenger 2002), characteristics of each species (Raven et al. 1992), and the environment itself (Ciganda et al. 2009). Moreover, it could provide key information regarding our understanding of the role that mangrove species play in response to a variety of factors, including climate change. The main objective of this investigation was to compare the leaf biophysical parameters (chl *a* content, leaf area, and leaf length) between the rainy and dry seasons in a degraded mangrove forest of the Mexican Pacific. This would also include assessing whether any seasonal differences can occur in the upper and lower canopies. These data can be of utmost importance when trying to establish effective monitoring programs of mangrove forest productivity. In particular, these data can be used to determine the optimal times to map estimated mangrove biomass from remotely sensed data. This is extremely important given that the spectral vegetation indices used in such operations are directly dependent on the leaf canopy structure and leaf chl *a* concentration.

MATERIALS AND METHODS

Study area

Data were collected along the south end of the Urias mangrove system (Fig. 1) during 2 seasons, the dry season of May 2010 (mean precipitation of 0.1 mm) and at the end of the rainy season in October 2010 (mean precipitation of 190 mm; INEGI 2010). According to the federal government (INEGI 2010), the historical metrological data (1986 to 2010) indicates that the 2010 dry and rainy seasons were normal in regards to precipitation and ambient temperature. The driest and rainiest years were 1994 and 2000, respectively.

The Urias system is a shallow, saline, vertically mixed body of water of approximately 18 km²

which is located in the coastal plain of the south-eastern Gulf of California (23° 10' N, 106° 20' W). Previous authors have indicated that during the dry season, this estuary becomes fully inversed (Alvarez 1977, Agraz-Hernández 1999, Moroyoqui-Rojo & Flores-Verdugo 2005). In other words, the salinity increases monotonically from the mouth to the head. It has also been suggested that the removal of water by the mangrove trees (Hogarth 1999) and the high estuarine evaporation rates (Ridd & Stieglitz 2002) may combine to raise the soil salinity during the dry season, resulting in areas characterized by a hypersaline state which are common in this system. The fringe mangroves, which consist of healthy trees, receive ample water from the adjacent river at high tide during the rainy season. The basin mangrove communities, consisting primarily of dwarf trees and/or trees in poor condition, receive runoff water from the mainland, decreasing soil salinity during this season. Healthy mangrove trees located along the

fringe are exposed to frequent full strength tidal influence (up to 1.5 m; Hogarth 1999), while the poor/dwarf mangrove trees are located more inland exposed to infrequent tidal inundation (Saenger 2002).

The surface of the substrate in the mangrove is generally smooth with a few small channels and depressions, with a relatively gentle overall slope extending towards the open water of the main tidal channel (Moroyoqui-Rojo & Flores-Verdugo 2005). The lagoon is partly bordered by a mangrove forest ecosystem, which is best developed along the edge and supports 3 dominant species: red mangrove *Rhizophora mangle*, black mangrove *Avicennia germinans*, and white mangrove *Laguncularia racemosa*. Based on height and distance to water, the mangroves in this arid sub-tropical region differ considerably from their wet tropical counterparts in 2 major ways. Firstly, river discharge into the wetlands is highly seasonal, with very large flows in the wet season followed by several months of negligible discharge. Secondly, large areas of mangrove and saltpan often infringe on this coastal type lagoon. As a result, many of these arid coastal lagoons become hypersaline for much of the year.

Similar to the mangrove system just south of this region, anthropogenic changes, particularly related to hydrological modifications (e.g. roads, aquaculture diversion) have resulted in a degraded system with prominent areas now consisting of dwarf and poor-condition stands of each species (Kovacs et al. 2008, 2009). Consequently, 6 classes of mangrove have been identified for this system: dwarf and poor-condition red, black, and white mangrove and healthy red, black, and white mangrove. Although the descriptions of these classes are qualitative, their classification has been done quantitatively utilizing standard image-processing methods based on their unique spectral properties as identified from remotely sensed digital data (Kovacs et al. 2008, Zhang et al. in press). Moreover, a similar remotely sensed mangrove classification scheme based on identical spectral data was recently justified using statistical methods based on *in situ* biophysical parameter data for a forest just south of this region (Kovacs et al. 2011).

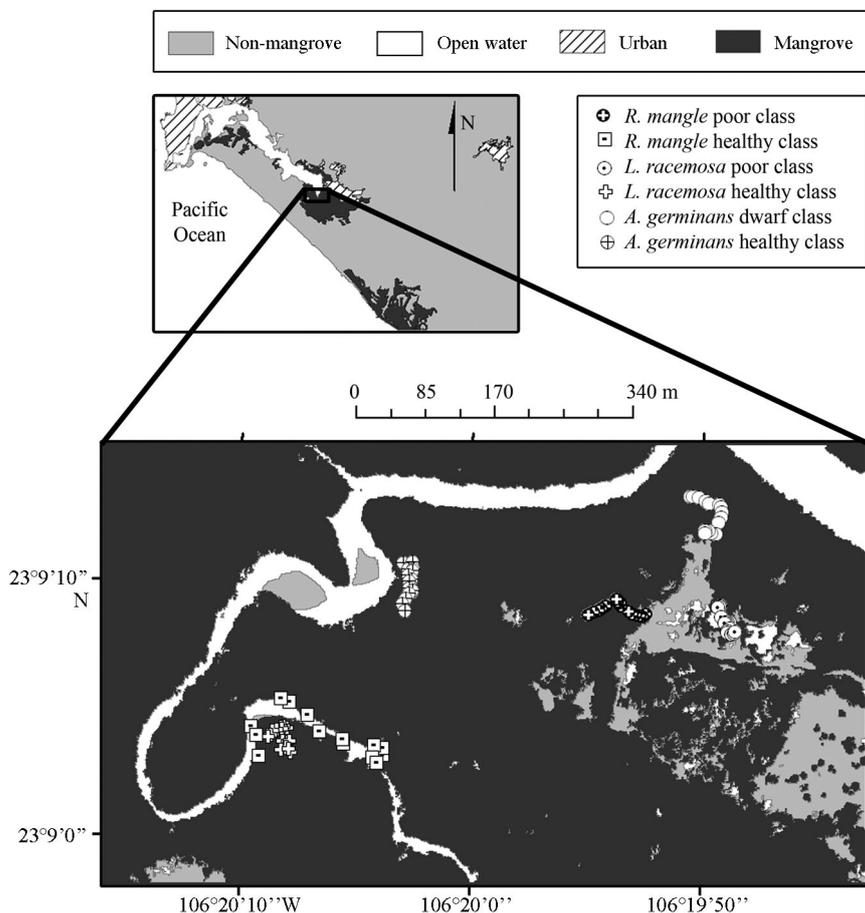


Fig. 1. Data collection sites at the south end of the Urias mangrove system

LAI collection

LAI is defined as the 1-sided leaf area per ground surface area (Wilhelm et al. 2000) found in the near-infrared spectrum of the canopy reflectance properties. With regards to the LAI measurements, an AccuPAR LP-80 (Decagon Devices) ceptometer was used to quantify *in situ* LAI for every species of mangrove in this system. The device measures the incoming photosynthetically active radiation (PAR) through 80 sensors incorporated along the linear probe. We quantified LAI based on 1 above- and >1 below-canopy reading using the following equation:

$$\text{LAI} = \frac{\left[\left(1 - \frac{1}{2K} \right) fb - 1 \right] \ln \tau}{A(1 - 0.47fb)} \quad (1)$$

where *fb* is beam fraction. (*A*) is determined by the instrument based upon the leaf distribution and the canopy leaf absorption qualities. For this sampling routine it was assumed to be 0.9. Tau (τ) is the ratio of PAR measured below the canopy to PAR above the canopy, and the extinction coefficient (*K*) is determined automatically by the LP-80 using the latitude, longitude, and the minutes of the day to calculate the zenith angle (θ):

$$K = \frac{1}{2\text{Cos}\theta} \quad (2)$$

The beam fraction (*fb*) depends on the high and low limits of the potential PAR and the zenith angle with the following set of equations:

$$r = \frac{\text{PAR}}{2550(\text{Cos}\theta)} \quad (3)$$

$$fb1 = 48.57 + r[-59.024 + r(24.835)] \quad (4)$$

$$fb = 1.395 + r[-14.47 + r(fb1)] \quad (5)$$

A stratified random sampling method was employed to make sure each mangrove class within the system was analyzed. For each class, we sampled 15 sites in a longitudinal pattern taking approximately 8 LAI readings per site. A post-processing GPS was used to ensure that seasonal readings could be collected for each site.

Leaf chl *a* concentration and leaf morphology

As with the LAI sites, we selected 3 mangrove trees from each class for the pigment analysis. For each tree, 10 leaves were taken from the top of the canopy (i.e. upper canopy) and 10 leaves from the lower canopy using an extendable pole with a cutter. In order to select just the mature leaves, each of the

samples was chosen between the third and fifth leaves from the tip. A sub-meter GPS location was recorded so that the same leaf collection site could be used for both seasons.

Once cut, each leaf was stored in a plastic bag within a small cooler at 4°C for transportation to the laboratory. The leaf area and length were analyzed using an LI-3000C Portable Area Meter device.

Due to the difference in leaf morphology between the mangrove species, we followed the method of F. Flores-de-Santiago et al. (unpubl.), in which we normalized chl *a* per unit area (mg m⁻²) using the dimensions of the diameter of a copper cylinder. Specifically, 1 leaf circle (1.25 cm in diameter) from each leaf of each sample was cut out with the cylinder. Care was taken to avoid the circles that included main leaf veins. Plant material for each sample was then dissolved with 100 ml of 80% acetone. A spectrophotometric assay was then conducted to extract information of peak absorption at 646 and 663 nm.

Statistical analysis

Normality test

We used a Q-Q plot to test the normality of error of estimates for all data (i.e. LAI, chl *a*, leaf area, leaf length). This test is based on an ordered plot of residual errors of an equation against normal quantiles $q_{(j)}$. In this test, if the data lie in proximity to a straight line, then we cannot reject the null hypothesis of normality. To measure the straightness of the Q-Q plot, we used the correlation coefficient of the Q-Q plot, which is defined as follows:

$$r_Q = \frac{\sum_{j=1}^n (x_j - \bar{x})(q_j - \bar{q})}{\sqrt{\sum_{j=1}^n (x_j - \bar{x})^2} \sqrt{\sum_{j=1}^n (q_j - \bar{q})^2}} \quad (6)$$

where (*x*) is the theoretical quantile, (*q*) is the sample quantile, (*j*) are the points of paired quantiles, and (*n*) is the total observation number. Consequently, at the 5% significance level ($\alpha = 0.05$) and *n* = 60, we used the critical value of 0.98 (Johnson & Wichern 1992).

Seasonal changes and LAI statistical testing

Differences in chl *a* concentrations, leaf area, leaf length, and LAI were tested using Minitab® and Origin® software. When the data were not normally distributed, each of the 3 parameters was tested using non-parametrical statistics (Mann-Whitney *U*-test).

However, averages and standard deviations are provided though not analyzed for comparison between the mangrove classes. The tests were used to examine for differences between the upper and lower canopies for both seasons.

RESULTS

Seasonal assessment and LAI

Of all comparisons for normality, most r_Q values were below the critical value; therefore, we used non-parametric tests. Significant differences in chl *a* concentration ($p < 0.05$, $n = 30$) were found between seasons for the upper and lower canopies of the white poor, red poor, and black dwarf classes (Table 1). Among these differences, it is clear that all 3 species experienced an increase in leaf chl *a* concentration during the rainy season (Fig. 2). By contrast, for healthy mangroves of all 3 species, no significant differences in chl *a* concentration were observed between seasons ($p < 0.05$, $n = 30$) in the upper leaves (Table 1). With the exception of the ‘white healthy’ class, which had higher chl *a* concentration during the dry season (Fig. 2), a lack of seasonal differences was also observed for the lower canopy leaves of the healthy mangroves.

With regards to the leaf area and leaf length, no data were recorded for the white poor upper leaves during October due to data loss (corrupt file). Most of the classes showed no significant seasonal differences ($p < 0.05$, $n = 30$) in leaf area. In the case of

Table 2. *Laguncularia racemosa*, *Rhizophora mangle*, and *Avicennia germinans*. Mann-Whitney *U*-test for the leaf area index (LAI) between seasons ($n = 15$). *Significant *U* value at $p \leq 0.05$ (2-tailed)

Class	— Median LAI —		<i>U</i>
	May	October	
<i>L. racemosa</i>			
Poor	1.4	1.2	106
Healthy	2.5	3.6	28*
<i>R. mangle</i>			
Poor	2.1	2.4	68
Healthy	5.7	5.1	151
<i>A. germinans</i>			
Dwarf	1.5	1.5	95
Healthy	3.6	2.9	137

white and black healthy upper leaves (Table 1), a significant increase in leaf area was recorded during the rainy season (Fig. 3). Moreover, the length of the leaves in the upper canopy increased significantly ($p < 0.05$, $n = 30$) for white healthy, red poor, and red healthy mangroves during the rainy season (Table 1, Fig. 4). No significant differences ($p < 0.05$, $n = 30$) were found in the lower canopies of black healthy, black dwarf, and red healthy (Table 1).

With regards to LAI, no significant difference ($p < 0.05$, $n = 15$) was observed between the seasons for the white poor, red poor, red healthy, black dwarf, and black healthy mangrove classes (Table 2). However, a significant difference ($p < 0.05$, $n = 15$) was found in the white healthy mangrove with an increase in LAI occurring during the rainy season (Fig. 5).

Table 1. *Laguncularia racemosa*, *Rhizophora mangle*, and *Avicennia germinans*. Mann-Whitney *U*-test median values for chlorophyll *a* (chl *a*), leaf area, and leaf length between seasons ($n = 30$). LR: *L. racemosa*; RM: *R. mangle*; AG: *A. germinans*. *Significant *U* values at $p \leq 0.05$ (2-tailed)

Species and class	Chl <i>a</i> (mg m ⁻²)			Leaf area (cm ²)			Leaf length (cm)		
	May	Oct	<i>U</i>	May	Oct	<i>U</i>	May	Oct	<i>U</i>
Upper									
LR poor	20.9	26.6	15*	No data			No data		
LR healthy	31.6	30.9	536	14.7	18.2	301*	6	10	48*
RM poor	24.9	33.3	117*	34.7	29.0	541	9.6	12.3	94
RM healthy	43.2	42.6	418	48.1	50.6	420	11.3	14.6	90*
AG dwarf	24.7	36.2	15*	10.9	10.4	503	99.5	9.7	430
AG healthy	32.0	36.7	341	20.2	24.0	306*	13.0	13	479
Lower									
LR poor	23.5	26.5	160*	19.1	19.2	424	6.7	9.2	65*
LR healthy	33.4	27.0	809*	14.3	15.5	371	6.2	9.6	41*
RM poor	31.3	39.9	194*	27.9	25.8	406	8.4	12.5	42*
RM healthy	36.7	37.8	376	49.1	46.9	529	15.5	15.4	500
AG dwarf	32.1	36.7	225*	13.1	10.2	583*	8.8	9.1	454
AG healthy	32.2	33.2	354	29.6	29.0	514	13.5	12.3	543

Upper versus lower canopy

Dry season

During the dry season, chl *a* concentration shows no significant difference ($p < 0.05$, $n = 30$) between upper and lower canopy leaves for the white healthy and the black healthy mangroves (Table 3). The white poor, red poor, and black dwarf classes showed a higher chl *a* concentration within the lower leaves when compared to the red healthy, which presented higher chl *a* content in the upper leaves (Table 3). With regards to leaf area, the white healthy, red healthy, and black dwarf mangroves did not show any significant differences ($p < 0.05$,

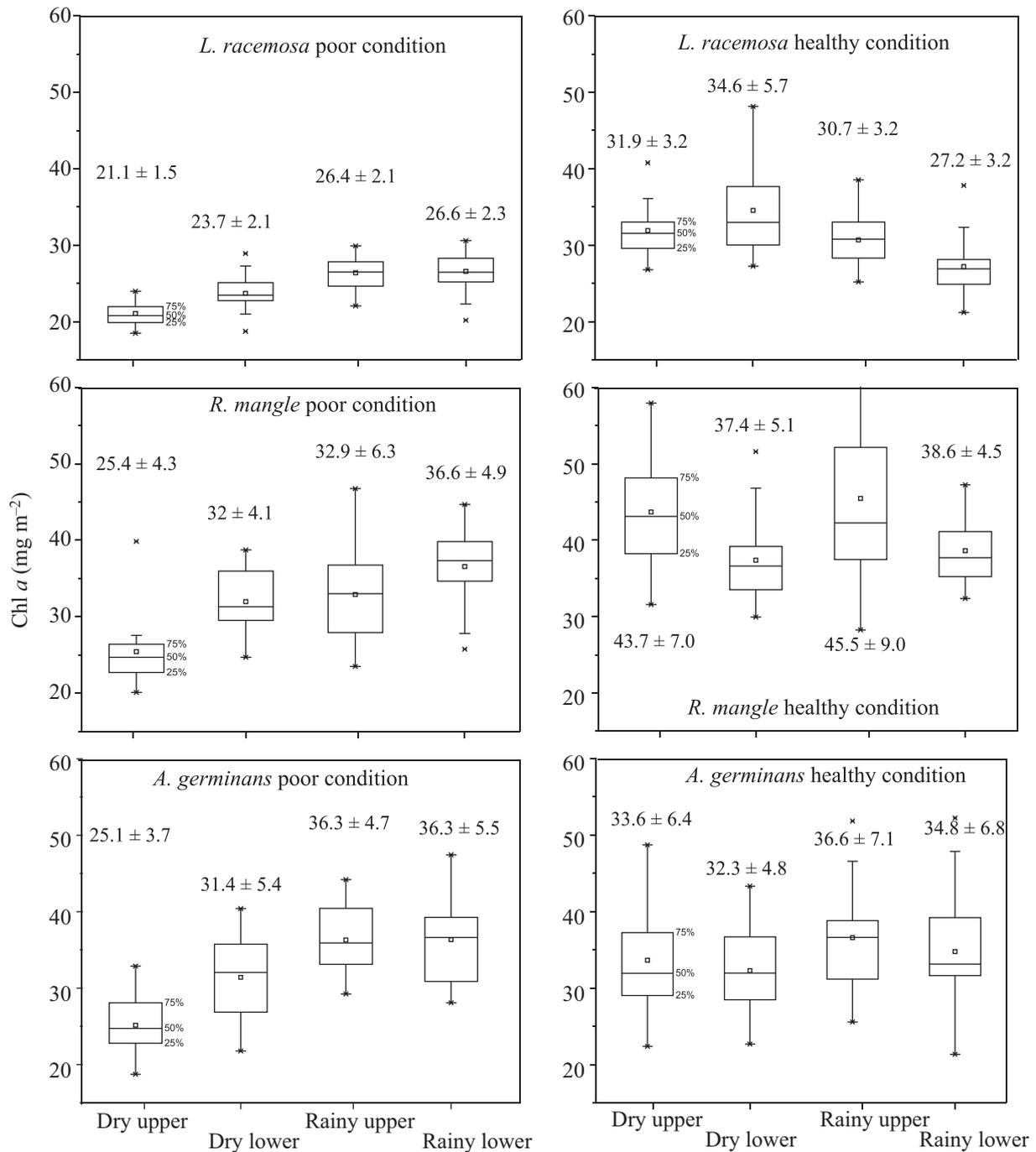


Fig. 2. *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans*. Upper and lower canopy leaf chlorophyll a (chl a) concentration by season. Dry and rainy seasons are represented by the months of May and October, respectively. Each box plot depicts the mean (small square), the minimum sample, the lower quartile (25%), the median (50%), the upper quartile (75%), the maximum sample, and the lowest and highest sample within the 1.5 interquartile ranges of the lower and upper quartile (x). Also, mean ± SD is shown at the top of each box plot

n = 30). The red poor mangroves did have significantly higher leaf area in the upper leaves. In contrast, the white poor and black healthy showed an increase in leaf area in the lower leaves. The length of leaves showed no significant difference ($p < 0.05$, n = 30) in

the white healthy, black dwarf, and black healthy classes. The white poor and the red healthy did have significantly higher leaf lengths in the lower leaves, whereas the red poor had significantly higher leaf lengths in the upper canopy.

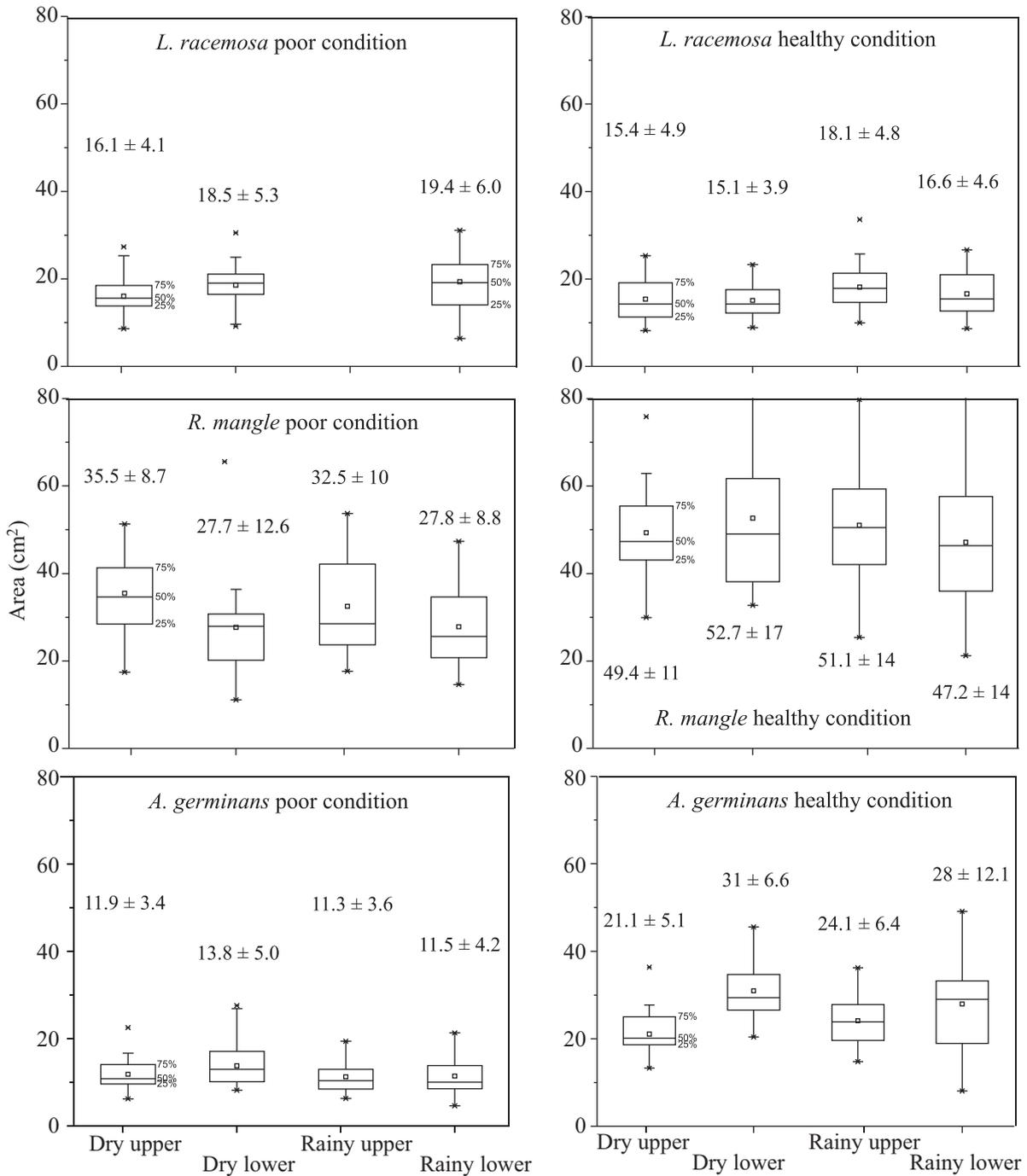


Fig. 3. *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans*. Upper and lower canopy leaf chlorophyll a (chl a) concentration by season. Dry and rainy seasons are represented by the months of May and October, respectively. Each box plot depicts the mean (small square), the minimum sample, the lower quartile (25%), the median (50%), the upper quartile (75%), the maximum sample, and the lowest and highest sample within the 1.5 interquartile ranges of the lower and upper quartile (x). Also, mean ± SD is shown at the top of each box plot

Rainy season

With regards to the rainy season (Table 3), the chl a concentration showed no significant difference ($p < 0.05$, $n = 30$) between the lower and

upper leaves in the white poor, black dwarf, and black healthy mangroves. The white healthy and the red healthy classes presented higher chl a concentration in the upper leaves, and the red poor showed higher content in the lower leaves.

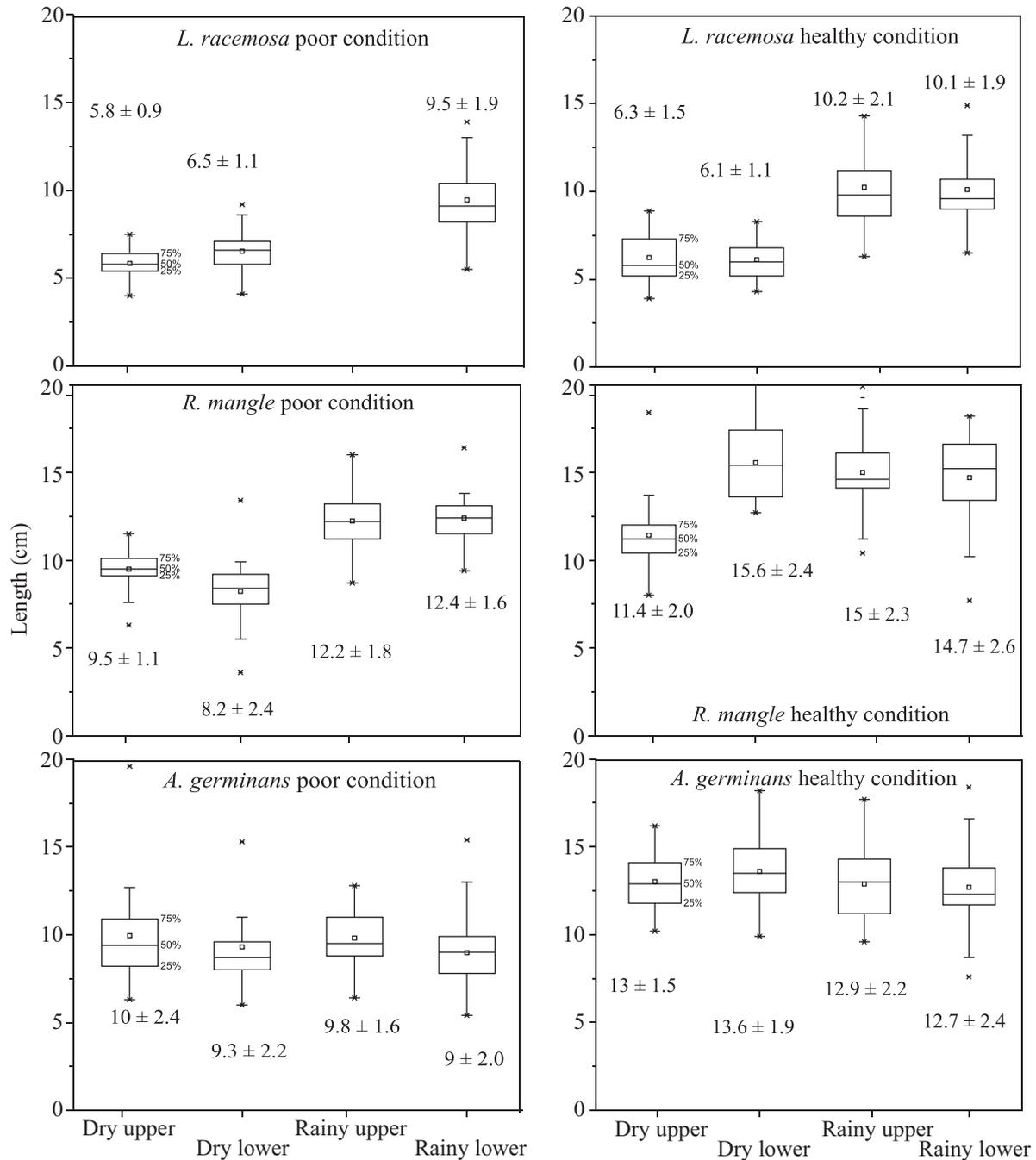


Fig. 4. *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans*. Upper and lower canopy leaf chlorophyll a (chl a) concentration by season. Dry and rainy seasons are represented by the months of May and October, respectively. Each box plot depicts the mean (small square), the minimum sample, the lower quartile (25%), the median (50%), the upper quartile (75%), the maximum sample, and the lowest and highest sample within the 1.5 interquartile ranges of the lower and upper quartile (x). Also, mean ± SD is shown at the top of each box plot

No significant differences in leaf area were found among all 6 classes. Regarding leaf length, no significant differences were found with the exception of the black dwarf, which had significantly larger leaves in the upper canopy during this season.

DISCUSSION AND CONCLUSIONS

Mangrove community

Where seasonal gradients are involved, the pattern of chl a concentration and leaf morphology can be

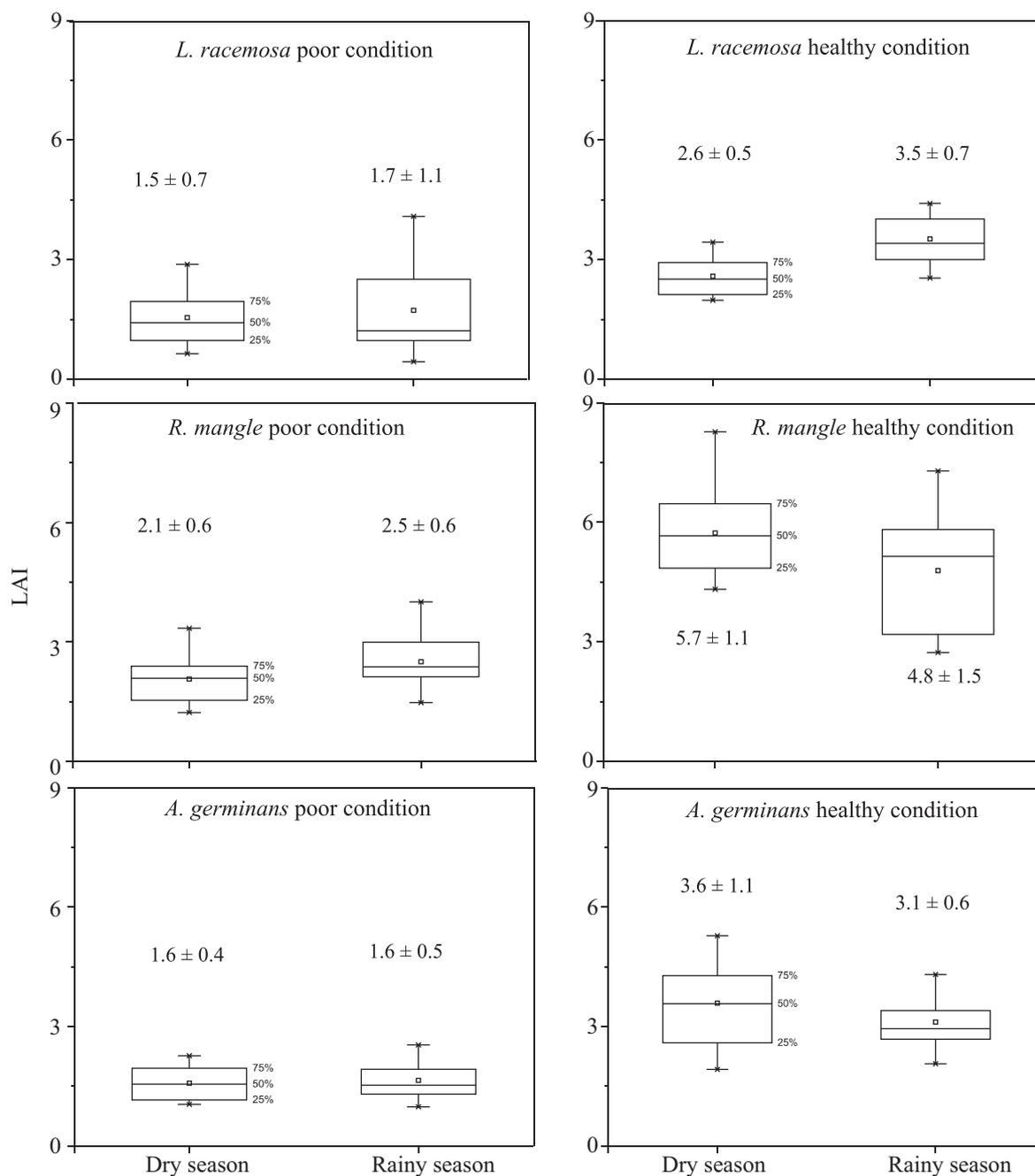


Fig. 5. *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans*. Upper and lower canopy leaf chlorophyll a (chl a) concentration by season. Dry and rainy seasons are represented by the months of May and October, respectively. Each box plot depicts the mean (small square), the minimum sample, the lower quartile (25%), the median (50%), the upper quartile (75%), the maximum sample, and the lowest and highest sample within the 1.5 interquartile ranges of the lower and upper quartile (x). Also, mean ± SD is shown at the top of each box plot

used to express the ecological changes of species as key indicators of the physiological stage, productivity, and stress of a mangrove forest. In this investigation, we determined that variability in chl a can occur amongst various mangrove classes found within a degraded forest of the sub-tropics. Specifically, in this study area, the chl a concen-

tration of all 3 mangrove species in poor condition showed seasonal dependence, unlike those that were healthy. As previously described by Kovacs et al. (2011), the fringe mangrove of this region of Mexico is typically healthy, whereas basin mangrove is more often found in a poor/dwarf condition.

The leaf morphology patterns observed in this study agree with Tomlinson (1986), in that we found bigger leaves in the healthy classes, in particular red and black mangrove, while black dwarf and white poor showed the lowest leaf area and length (Figs. 3 & 4). This is suggestive of a direct relationship between the leaf morphology and the physical state of the trees.

White mangrove

It has been noted that different light and shade requirements in adults of *Laguncularia racemosa* are indicative of a shade-intolerant response (Smith 1992, McKee 1995), suggesting a pattern in which leaves from the lower canopy and under thicker cover receive less light during the rainy season. As seen with the increase in LAI during the rainy season in healthy stands, this could decrease chl *a* concentration in the lower leaves and therefore result in more stress because of the low irradiances as depicted in Fig. 2. By contrast, the apparent lack of change in the chl *a* concentration in healthy leaves from the upper canopy suggests that the aforementioned shade-intolerant pattern from the lower canopy is present in this type of healthy forest. However, the higher leaf area and leaf length during the rainy season may indicate that at the top of the canopy, the chl *a* concentration has no apparent dependence on the morphology of the leaves.

Table 3. *Laguncularia racemosa*, *Rhizophora mangle*, and *Avicennia germinans*. Mann-Whitney *U*-test median values for chlorophyll *a* (chl *a*), leaf area, and leaf length between the upper and lower canopy in both seasons (*n* = 30), viz. rainy (October) and dry (May). LR: *L. racemosa*, RM: *R. mangle*, AG: *A. germinans*. *Significant *U* values at *p* ≤ 0.05 (2-tailed)

Species and class	Chl <i>a</i> (mg m ⁻²)			Leaf area (cm ²)			Leaf length (cm)		
	Upper	Lower	<i>U</i>	Upper	Lower	<i>U</i>	Upper	Lower	<i>U</i>
May									
LR poor	20.9	23.5	142*	15.6	19.1	291*	5.9	6.7	269*
LR healthy	31.6	33.4	338	14.7	14.3	449	6	6.2	463
RM poor	24.9	31.3	110*	34.7	27.9	658*	9.6	8.4	661*
RM healthy	43.2	36.7	697*	48.1	49.1	425	11.3	15.5	68*
AG dwarf	24.7	32.1	154*	10.9	13.1	357	9.5	8.8	551
AG healthy	32.0	32.2	485	20.2	29.6	91*	13.0	13.5	368
October									
LR poor	26.6	26.5	419	No data			No data		
LR healthy	30.9	27.0	723*	18.2	15.5	536	10	9.6	482
RM poor	33.3	37.5	266*	29.0	25.8	581	12.3	12.5	440
RM healthy	52.2	41.6	676*	50.6	46.9	523	14.6	15.4	451
AG dwarf	36.2	36.7	453	10.4	10.2	454	9.7	9.1	594*
AG healthy	36.7	33.2	518	24.0	29.0	346	13	12.3	455

Regarding the white mangrove in poor condition, the shade-intolerant pattern (Smith 1992, McKee 1995) was not observed, as there was no change in LAI. Moreover, the higher chl *a* concentration and leaf length during the rainy season indicate that this poor-condition forest is distinctly seasonal in its development. Tomlinson (1986) indicated that for this species, branching occurs during the rainy season, with an extended period of inactivity during the dry season, suggesting that at high irradiances and lack of fresh water, the vegetative survival and competitiveness of *Laguncularia racemosa* could depend on an efficient display of foliage and the ability to respond to environmental changes and stress.

Red mangrove

Regarding the poor condition, the increases in chl *a* concentration and leaf length during the rainy season in both upper and lower canopies suggest that this type of forest greatly depends on fresh water availability and shade as previously reported by Farnsworth & Ellison (1996). In contrast, the lack of seasonal change within the healthy forest in LAI and leaf morphology suggests a moderate sun-shade flexibility. Ellison & Farnsworth (1993) reported that *Rhizophora mangle* is capable of adapting to different light levels, including gaps within the canopy. It was noted in the field that the majority of healthy *R. mangle* were found in a continuous stand along the main channel where no other species of mangrove could constrain the availability of light. The lack of observed seasonal change in LAI, chl *a*, and leaf area in this study would suggest an adaptation of fringe *R. mangle* to constant tidal flushing.

In this study, a high chl *a* concentration was found in the upper leaves of healthy red mangrove during the rainy season. Lugo et al. (1975) indicated that the non-shaded leaves (i.e. upper canopy) of this species may show a net photosynthetic rate twice as high as that of the shaded leaves (lower canopy). Regardless of canopy composition, it has been reported that *Rhizophora mangle* trees can assume a shade-tolerant (Farnsworth & Ellison 1996) and shade-intolerant (Snedaker 1995) pattern. In this study, the red mangrove in poor condition could

be indicative of a shade-tolerant pattern, with higher concentrations of chl *a* in the lower canopy. By contrast, the healthy red mangrove in this study would indicate a more shade-intolerant trend, with higher chl *a* concentration in the upper canopy where the availability of light is higher as compared to the shaded leaves in the lower canopy.

Black mangrove

The patterns of the black dwarf mangrove suggest a distinctive seasonal pattern similar to the red mangrove in poor condition, with the only difference being no significant seasonal change in LAI. The low chl *a* concentration during the dry season could be the result of increasing soil temperature and decreasing humidity (Sherman et al. 2000), as these trees are typically close or adjacent to drier uplands (i.e. salt-pan). Ball & Critchley (1982) reported that shaded leaves of *Avicennia germinans* can have a higher chl *a* content during the dry season, suggesting a more intolerant pattern to light availability (Feller et al. 2007), and thus revealing a high vulnerability to photoinhibition (Cheeseman 1994).

Within healthy black mangrove forest, Gratani (1997) suggested that the major adaptation of leaves in a lower canopy with low irradiance is the development of thinner leaves. In our study, we did not measure leaf thickness. However, the apparent lack of change in leaf morphology may suggest that healthy *Avicennia germinans* is well adapted to shaded conditions as mentioned by Attiwill & Clough (1980). In the present study, the lack of change in LAI and chl *a* for the shaded leaves may suggest that this forest does not present significant seasonal changes.

Monitoring the seasonal development of mangrove species and conditions along a mixed environment is important for future research, particularly when dealing with studies that examine remotely sensed data, carbon allocation, or biomass. The observed differences between seasons for some of the species and conditions examined would indicate a clear pattern that this study site is dependent primarily on fresh water availability. Given the large geographic extent and inaccessibility of this type of sub-tropical canopy, remote-sensing image acquisitions are commonly used to monitor and map mangroves. In particular, for degraded systems, remotely sensed imagery is often used to monitor parameters directly related to the LAI and/or chlorophyll content. For example, many estimates of biomass or LAI from remote sensing platforms are dependent on standard vegetation

indices (e.g. the normalized difference vegetation index) which are calculated from spectral reflectance directly related to the canopy thickness and leaf chl *a* content (Jensen 2005).

Consequently, knowing the seasonal changes in these parameters would allow remote sensing specialists to identify the optimal time to acquire imagery for accurate biomass or LAI mapping and monitoring. Moreover, collecting these data on an annual basis could be beneficial for monitoring potential impacts on these particular ecosystems resulting from abnormal years of precipitation and/or temperature.

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