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Does the Extent of Photosynthetic surface and Potential Gross Primary Productivity (GPP) of Mangrove Ecosystems Depend on Climate? : A Case Study from Sri Lanka

K. A. R. S. Perera[1], M. D. Amarasinghe[2]

[1] Department of Botany, The Open University of Sri Lanka, Nawala, Nugegoda, Sri Lanka
[2] Department of Plant and Molecular Biology, University of Kelaniya, Sri Lanka

*Corresponding Author: email: kaper@ou.ac.lk, Tele: +94112881269

Abstract – *Mangrove forests characterized as an important agent of carbon sequestration due to its rapid rate of primary production and slow rates of sediment organic carbon decomposition. Mangrove productivity has shown a wide variation among sites due to variations in many factors, including climate. Comparison of the Leaf area index (LAI) and Gross Primary Productivity (GPP) of mangrove ecosystems located in different climatic zones in Sri Lanka and its relationship with rainfall and the vegetation structure are the main objectives of the study. Absorption of photosynthetically active radiation (PAR) is governed by the extent of photosynthetic surface which is estimated with LAI of vegetation canopies and then calculated the GPP of respective area. Intensity of PAR above (I_0) and below (I) the canopy of the study areas was recorded using LI-191SA line Quantum sensor. Mangrove vegetation structure was characterized with species richness, plant density, basal area and stand height of study areas were quantify with standard methods The GPP was performed in seven mangrove ecosystems representing wet, intermediate and dry climatic zones in Sri Lanka. Highest average values of LAI and GPP were recorded from the mangroves in the wet and the intermediate zone. and the lowest average values for LAI and GPP were recorded for the dry zone mangroves. Statistically significant positive linear relationship with high coefficient of determination (r^2>0.7) were revealed to occur between GPP values of wet and dry periods of mangroves and GPP with vegetation structural complexity. The average LAI of mangrove ecosystems in Sri Lanka was 5.66, with a GPP of 24.74 Mg ha^{-1} y^{-1}. A positive correlation was revealed between estimated average annual gross primary productivity (GPP) values and annual rain fall of the areas. Results revealed that LAI and GPP of mangroves are potentially driven by annual rainfall pattern among other factors, by climate.*

***Keywords**: Mangroves, Leaf area index (LAI), Gross Primary Productivity (GPP), Climate*

1 INTRODUCTION

Gross primary productivity (GPP) is the rate at which an ecosystem's producers capture from a given amount of chemical energy during a given length of time. Net production is the balance between gross photosynthesis and leaf dark respiration and represents the amount of carbon available for growth and tissue maintenance. High primary productivity of mangroves facilitates the high carbon sequestration function of mangrove ecosystems (Perera et al., 2012). Mangrove forests have been recognized as an important agent of carbon sequestration with reported half of the biomass content organic carbon (Lovelock et al., 2015). The rapid rate of primary production and slow rates of sediment carbon decomposition bring about the preservation of huge amounts of organic carbon in mangrove forests (Alongi,2014). GPP represents the rate at which an ecosystem's producers capture from a given amount of chemical energy during a given length of time.

Photosynthetically active radiation (PAR) absorbed by the plant canopies/ leaves gives a reliable measure of its gross primary production. The light response curves of mangroves are similar to other plants, with a steep linear increase up to 300 -400 μ mol photons m^{-2} s^{-1} after which saturation is reached (Alongi 2009) Extent of photosynthetic surface (leaf area) solar zenith angle, which is a function of time, day length and latitude also plays a part in determining the total quantum of PAR absorbed by plant leaves (Okimoto et al., 2007; Jayakody et al., 2008). Measurement of PAR absorption by the mangrove canopy is used to estimate the LAI and then it can be converted to gross primary productivity in mangrove forests. Amount of light absorbed by the mangrove canopy is related to the total canopy chlorophyll concentration and was then multiplied by a rate of carbon fixation per unit of chlorophyll to give an estimate of GPP. The method described by Bunt et al. (1979) has been used widely in recent years to estimate GPP of mangroves (Jayakody et al., 2008; Kathiresan and Khan, 2010). However recent work suggests that potential GPP calculated using this method (Bunt et al., 1979), significantly underestimates the photosynthetic capacity of mangroves. English et al., (1997) proposed theoretically, that measuring photosynthetic capacity of mangroves is a more robust method in estimating canopy LAI (with the ratio of PAR below and above the canopy), that can be used to estimate GPP.

Although a low extent of mangroves in Sri Lanka, supports 23 true mangrove plants species (Amarasinghe and Perera, 2017) and present study was conducted with the objective of estimating the GPP of Sri Lankan mangrove ecosystems by capturing of solar energy through photosynthesis. Although number of services and traditional uses of Sri Lankan mangroves were reported, quantifiable measures of primary productivity of mangroves are inadequate. Present study focused on estimates the gross primary productivity of Sri Lankan mangroves and its dependency on main climatic factor i.e., rainfall which vary in coastal zone in Sri Lanka. Findings of the study may be helpful to making of decisions in maintain mangrove areas for carbon sequestration process in order to mitigation the effects of climatic changes.

2. MATERIALS AND METHOD

2.1 Study area

Intensive data collection was carried out in two mangrove areas, Kadolkele and

Wedikanda located in Negombo estuary on west coast of Sri Lanka. Other than that total of six (6) study areas i.e, Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar and Batticaloa lagoons, were selected around the Sri Lanka to represent all the climatic zones found along the coastal line of the country (Fig.1). Data was collected form 2014 – 2016 period. Study locations and their basic climatic characteristics are presented in Table 1.

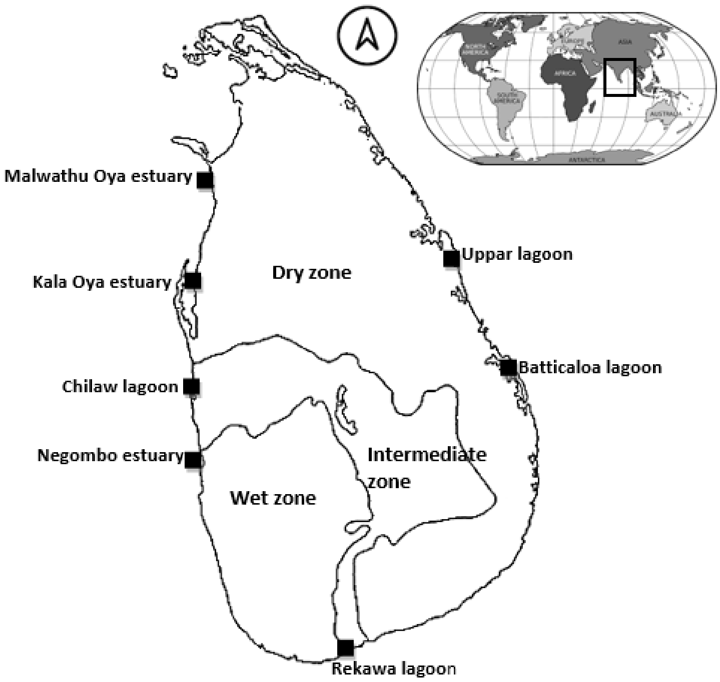


Fig 1. Study areas located along the coastal line of the Sri Lanka.

2.2 Sampling strategy

In order to gather data on photosynthetically active radiation (PAR) and mangrove vegetation structure, 10 m wide belt transects were laid perpendicular to the shoreline across the environmental gradient in randomly selected locations in each of study area. Each belt transects then divided in to 10m x 10m (100m^2) sampling plots. Total of hundred and thirty-seven (137) sampling plots, including forty (40) permanent sampling plots at Negombo estuary and ninety-seven (97) sampling plots at other six study areas, Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar and Batticaloa lagoons. were used to collect the data.

2.3 Mangrove vegetation structure

Standard methods were adopted to quantify the vegetation structure of the mangrove ecosystem, as described by Kathiresan and Khan, (2010). Data on mangrove structural properties including species richness, tree diameter at breast height (dbh) and tree height of the stands were gathered from each sampling plot. Complexity index (CI), indicates the diversity and abundance of flora within the forest community and it is calculated using data on the number of species, stand density, basal area and height (Kathiresan and Khan, 2010; Perera and Amarasinghe, 2016; Umayangani, Perera, 2017). For the present study, CI was calculated as, Number of species x stand density x stand basal area x stand height x 10^{-5}.

Study area	Climatic zone	Location	Annual rainfall (mm) *	Relative humidity (%)	Annual temperature (^0C)
Negombo estuary	Wet zone	$7^0$11′50.48" N; 79^0 50′47.50" E	2161	87-93	25.6 – 28.5
Chilaw lagoon	Intermediate zone	$7^0$30′46.40" N; 79^0 49′11.70" E	1507	86-93	25.2 – 29.3
Rekawa lagoon		$6^0$02′ 51.70" N; 80^0 50′ 57.92" E	1082	86-90	25.6- 29.0

Table 1: Study locations and their climatic characteristics

Kala Oya estuary	Dry zone	$8^0$17′ 11.31" N; 79^0 50′ 45.65" E	1200	83-95	25.6 - 29.8
Malwathu Oya estuary		$8^0$49' 02.64" N; 79^0 55' 09.24" E	923	83-88	26.2 - 29.8
Uppar lagoon		8^0 05′ 13.25″ N; 81^0 26′15.92 E	1786	76-88	25.8 - 30.5
Batticaloa lagoon		7^0 44′ 50.70" N; $81^0$41′17.67" E	1810	76.88	25.8 - 30.5

*Source - Bastiaanssen and Chandrapala (2003)

2.4 Leaf area index (LAI)

Leaf area index (LAI), the total area of (one side) leaf surface per unit ground-surface area, has been used to calculate the potential GPP of mangrove ecosystems. Measurement of photosynthetically active radiation (PAR) absorption by the canopy used to estimate the leaf area index. The method described by Jayakody et al., (2008); Kathiresan and Khan (2010) has been used to calculate the leaf area index.

$$I = I_0 \, e^{-k \, LAI \, I}$$

$$LAI^I = \frac{\log e \, (I/I_0)}{-k}$$

$$LAI = LAI^I \times \text{Cos} \, (\theta \times 3.141593/180)$$

I = photon flux density beneath the canopy; Io = photon flux density incident on the top of the canopy or fully exposed position outside the canopy; LAI^I = Leaf area index correction; LAI = Leaf area index; θ = zenith angle of sun; k = canopy light extinction coefficient.

Light intensity of above canopy or in open space of the study area (I_0) and under canopy (I) was recorded between 10.00 and 14.00 hr. using LI-191SA line Quantum sensor. Approximately 50 readings of I were taken from each study plot (100 m^2). Values of zenith angle (angle of the sun from the vertical) at the time that measurements of I were made, obtained from the Metrological Dept. of Sri Lanka and website www.solardat.uoregon.edu.

Photosynthetically active radiation (PAR) absorption data of study sites of Negombo estuary, were collected during a two-year period, once in three months, which encompassed the two monsoon periods and inter monsoon periods, i.e., total study period covered four monsoon periods. The PAR data of other mangrove areas, Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar lagoon and Batticaloa lagoon were once in dry period only, during same year.

2.5 Gross primary productivity (GPP)

Gross primary productivity (net rates of maximum light saturated leaf photosynthesis) of mangrove ecosystems in Negombo estuary was estimated by using the LAI. The potential gross primary productivity of the canopy per unit area was calculated with the following formula (Bunt et al., 1979; Clough and Dalhaus., 1997; Kathiresan and Khan, 2010).

$$GPP = A \times d \times LAI$$

Where d is the day length in hours, LAI is the leaf area index and A is the average rate of photosynthesis per unit area (g C m^{-2} hr^{-1}) for all leaves in the canopy. This value A varied with climatic conditions. While it is desirable to measure the actual rate of photosynthesis at each site and according to the explanation by English et al., (1997), approximate rate of 0.216 g C m^{-2} hr^{-1}can be used for dry period, and 0.648 g C m^{-2} hr^{-1} for wet/raining conditions. Accordingly, potential GPP of estuarine mangroves at Negombo was calculated during wet and dry periods separately by using the data of two consecutive years. Ratio of GPP of wet period to dry period was also calculated.

2.6 Rainfall data

Considering the local daily rainfall data, (obtained from nearest station of the Meteorological Department of Sri Lanka), number of rainy and dry months was separated. Actual dry and wet/raining months were enumerated with the criteria used by the Department of Meteorological, Sri Lanka i.e., daily rainfall recorded to be less than 1 mm in 15 consecutive days of a month is considered a dry month and daily rainfall recorded to be more than 3 mm in 15 consecutive days of a month is considered as wet month. The mean annual GPP was then calculated for each mangrove area at Chilaw, Rekawa, Kala Oya, Malwathu Oya, Uppar, Batticaloa lagoons and estuaries.

2.7 Data analysis

Statistical analyses were carried out by using of SPSS Ver. 20 (SPSS, 2012). Initially, all the data was tested using Shapiro-Wilk normality test and results indicated that there was no violation of normality ($p \leq 0.05$). Mean and standard errors were calculated and presented along with number of samples used for the purpose.

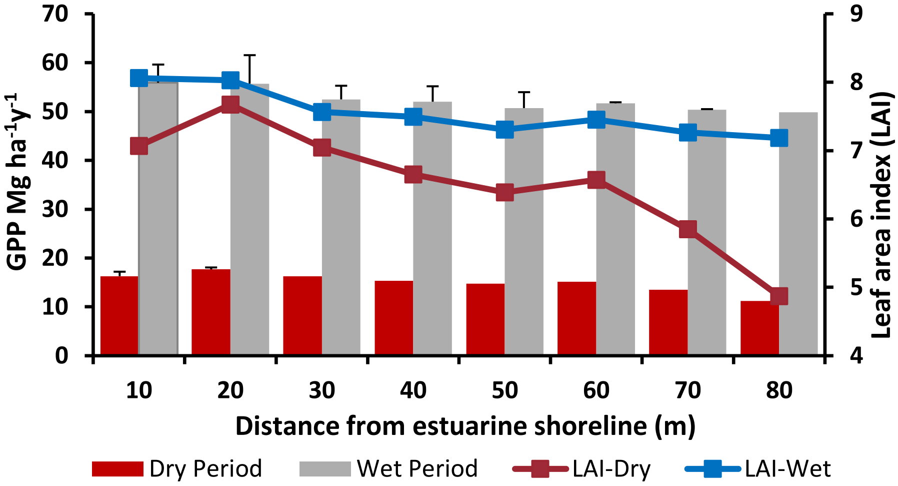
3. RESULTS

3.1 Gross primary productivity (GPP) of Negombo mangrove ecosystems

A statistically significant difference ($p>0.05$) was not observed between the values of photon flux density beneath the canopy (I), above the canopy (I_0), LAI and GPP recorded from the two study areas (Kadolkele and Wedikanda) in Negombo estuary within the same climatic period, thus data was pooled and averaged the values for Negombo estuary. GPP and LAI were revealed to be lower in dry period than in wet/rainy period of the year. Higher values of GPP and LAI were recorded at the study plots near the estuarine waterfront and it declined with distance towards the land (Fig 2).

3.2 Relationship between dry and wet seasons Gross Primary Productivity (GPP) at Negombo estuary

GPP data of wet period and corelated with dry period data and a linear curve was observed the most fitted for the data set and therefore, the relationship was derived with linear curve. A statistically significant positive correlation ($p<0.05$) and a high



coefficient of determination ($r^2=0.82$) with linear relationship was revealed between the GPP of dry and wet seasons in mangroves (Fig. 3).

Fig.2: Variation of GPP and LAI during wet/rainy and dry conditions of different distances from estuarine shoreline at Mangrove areas in Negombo estuary.

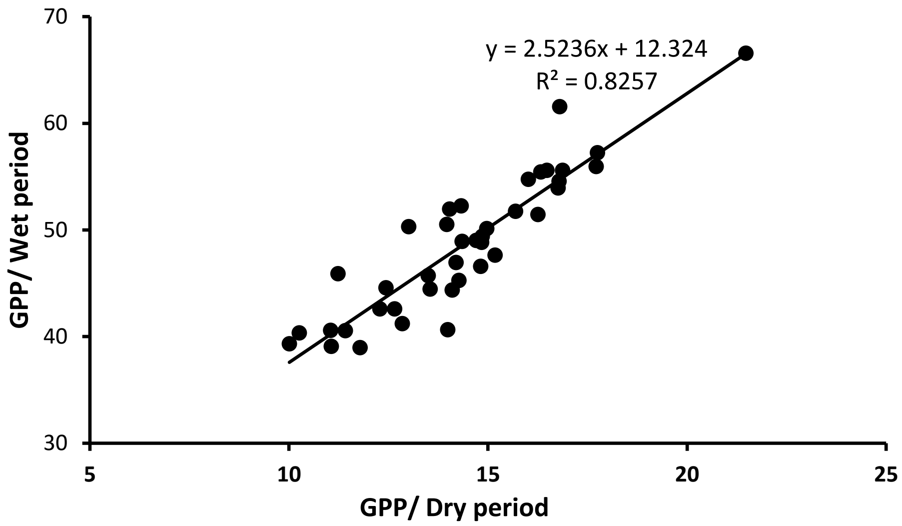


Fig. 3: Relationship between dry and wet seasons GPP at Negombo estuary

3.3 Gross primary productivity (GPP) of mangrove ecosystems in Sri Lanka

PAR (photosynthetically active radiation) data was used to calculate the LAI (leaf area index) followed by calculation of GPP of mangrove ecosystems in Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar lagoon and Batticaloa lagoon. Although, PAR data of Negombo estuary, was collected during a two-year period, the PAR data of other mangrove areas were collected once in dry period only, during same year. Using the relationship between wet and dry GPP of Negombo estuarine mangroves (Fig. 2), GPP of wet season of other study areas were estimated. Average annual GPP of study areas were estimated and number of rainy months was determined with the local rainfall data (section 2.6) was obtained from the nearest station of the Meteorological Department of Sri Lanka (Table 2).

Relatively a high GPP values were recorded in wet and intermediate zone mangroves. A clear variation of GPP was recorded between the two study areas, Chilaw (35.64 Mg ha^{-1} y^{-1}) and Rekawa (26.74 Mg ha^{-1} y^{-1}) with in the intermediate zone. The low GPP values were recorded in mangrove areas at dry zone (average 33.64 Mg ha^{-1} y^{-1}). Average annual GPP of mangrove ecosystems in Sri Lanka was calculated to be, 24.74 Mg ha^{-1} y^{-1} (Table 2).

Table 2: Estimated average values of the annual GPP (Mg $ha^{-1}y^{-1}$) at mangrove ecosystems of Negombo estuary, Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar lagoon and Batticaloa lagoon.

Study area	Climatic zone	Mean GPP at dry season	Mean GPP at wet/rain season	No.wet months	No. dry months	Estimated Average annual GPP
Negombo estuary	Wet zone	18.25 ± 0.37	38.02 ± 1.11	11	1	36.81 ± 1.04
Rekawa lagoon	Intermediate zone	15.14 ± 0.37	27.81 ± 0.39	11	1	26.74 ± 0.36
Chilaw lagoon		16.84 ± 0.19	37.25 ± 0.65	11	1	35.64 ± 0.61
Kala Oya estuary	Dry zone	11.80 ± 0.35	23.45 ± 1.17	10	2	20.53 ± 1.03
Malwathu Oya estuary		12.18 ± 0.29	21.65 ± 0.99	6	6	16.91 ± 0.64
Uppar lagoon		12.96 ± 0.46	20.85 ± 1.54	9	3	18.87 ± 1.27
Batticaloa lagoon		12.25 ± 0.50	19.50 ± 1.68	9	3	17.68 ± 1.38
Average		14.37 ± 0.42	27.00 ± 1.01			24.74 ± 1.26

3.4 Relationship between gross primary productivity (GPP) and annual rainfall

A positive correlation was revealed between estimated average annual GPP values and annual rain fall of the areas. Power curve was observed the most fit for the data set and therefore, the relationship was derived from power curve (Fig. 4).

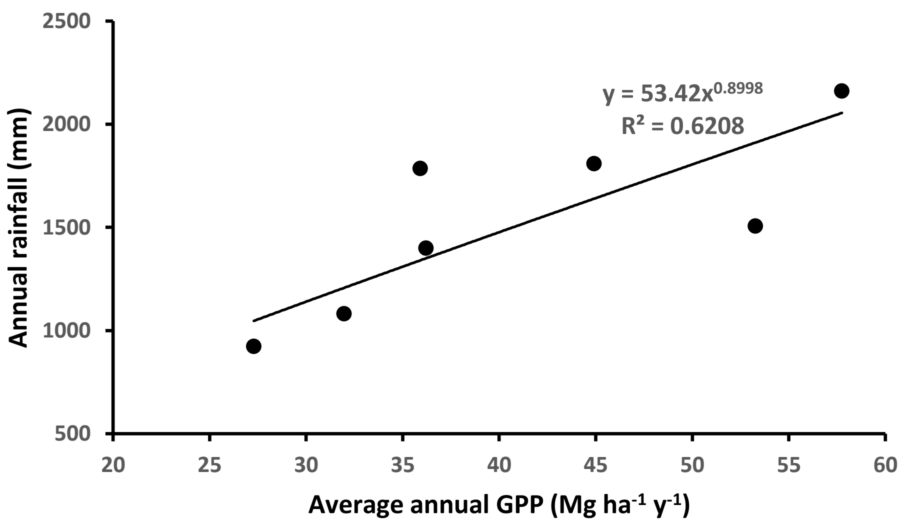


Figure 4: Relationship between average annual GPP of mangroves and annual rainfall of the area.

3.5 Mangrove vegetation structure and gross primary productivity (GPP)

Data on mangrove vegetation structure (CI) gathered from all seven study areas were corelated with the calculated GPP values for respective areas. A linear curve was observed the most fitted for the data set and therefore, the relationship was derived with linear curve. Therefore, a statistically significant positive correlation ($p<0.05$) and a high coefficient of determination ($r^2=0.709$) with linear relationship was revealed to occur between gross primary productivity and vegetation structural complexity in mangrove ecosystems (Fig.5).

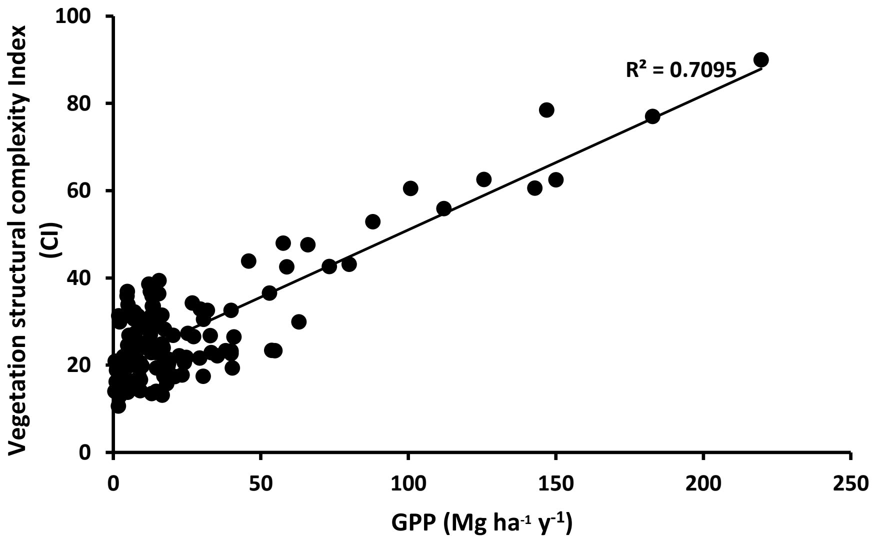


Fig. 5: Relationship between gross primary productivity vegetation complexity index of Wedikanda mangroves.

4. DISCUSSION

The higher values of potential GPP observed during and immediately after the raining season, at Kadolkele and Wedikanda mangrove areas at Negombo estuary, may be due to the enhanced nutrient inputs from surface and river runoff and decreased soil salinity (Gammanpila et al., 2009) that in turn may lead to low leaf fall in comparison to dry period, thus resulting a higher LAI. The availability of freshwater indicated an important factor for development and growth of mangroves. Freshwater supply has often been indicated by the ratio of rainfall to evapotranspiration (Barr et al., 2014). Under the humid conditions where the ratio exceeds 1, the mangroves grow abundantly and under the arid climates, where the ratio of rainfall to evapotranspiration falls below 1, the mangroves get stunted

(Kathiresan and Khan, 2010). High rainfall in humid conditions leaches out residual salts from mangrove soil and thus encourages growth of mangroves. In general mangrove vegetation is more luxuriant in lower salinities (Chen and Ye, 2014). Experimental evidence indicates that at high salinity, mangroves spend more energy to maintain water balance and ion concentration rather than for primary production and growth (Alongi, 2014). High salinities result in physiological responses similar to terrestrial plants that experience drought, as highly saline soils have low osmotic potential that constrain water relations of mangroves (Sparks, 2003; Artiola et al., 2019)

Photosynthetic capacity of mangrove leaves however depends on their location of the canopy as it affects the leaf morphology, anatomy and physiology. Based on the experimental evidence Farnsworth & Ellison, (1996), reported that the photosynthetic rate of sun leaves of *Rhizophora mangal*, which are smaller in size and occupy the upper parts of the canopy having a thick cuticle and tannin cells, are twice as that of shade leaves which occupy the lower strata of the canopy and thus are larger in size with a thin cuticle.

Leaf fall rates have been observed to be significantly greater during dry period than in the wet season (Pahalawattarachchi, 1995) which in turn reduces LAI and the GPP of the mangrove stand. In addition, reduction of leaf size has been observed to be an initial morphological reaction to environmental stress on plants (Parida and Das, 2005) and therefore relativity a high salinity exists during the months of low rainfall and it may cause stress on mangroves resulting lower GPP than recorded in rainy periods.

Rate of photosynthesis vary widely among the physical environmental factors as well as vegetation structural characteristics. Complexity index (CI) represents the vegetation structure of the mangrove stand, that contributes to functions of the mangrove ecosystem, revealed a strong positive relationship ($p>0.05$) with the GPP calculated for Negombo estuary ($r^2 = 0.802$) and similar relationships were reported by Jayakody et al., (2008) and Perera et al., (2010) for mangrove areas in Negombo estuary.

Estimated GPP values in the present study were revealed higher in both wet and dry periods than those reported by Jayakody et al., (2008), the only study on GPP of Sri Lankan mangroves that has been conducted in Negombo estuarine mangroves, during one wet and a dry period. On contrary to GPP values reported by Jayakody et al., (2008), i.e., 12.77 – 23.89 Mg $ha^{-1}y^{-1}$ during dry season and 20.81 -37.28 Mg $ha^{-1}y^{-1}$ during the wet season. Present study revealed the dry season and wet season GPP are to be 13.00 – 21.47 Mg $ha^{-1}y^{-1}$ and 44.45 – 66.56 Mg $ha^{-1}y^{-1}$ respectively.

Calderon et al., (2014) explain geomorphology and hydrology determined by local geology, sea-level change, tide, freshwater input, shoreline structure, watershed morphology, groundwater influence, natural disturbance regimes and climate, contribute to development of physico-chemical gradients which in turn govern the structure and function of the intertidal ecosystems. Many of the estuaries and lagoon in Sri Lanka can be categorized as riverine which receive continuous input of nutrient rich freshwaters through rivers and get mixed with saline waters resulting reduced salinity and this water inundates areas close to the shoreline most frequently than in the landward areas. High mangrove structural complexity, which is represented by high number of species, plant densities and heights, high leaf area indexes is observed with the mangrove areas close to the shoreline and it was revealed to decrease along the environmental gradient towards inland, thus GPP also declines along the water-land gradient in the estuary.

The GPP values for dry period of other six (6) mangrove areas in Sri Lanka, i.e., Chilaw lagoon, Rekawa lagoon, Kala Oya estuary, Malwathu Oya estuary, Uppar lagoon and Batticaloa lagoon, comparatively high value was resulted in Negombo Chilaw study areas than in others. High input of fresh water may be a potential reason for this situation where they located in wet and intermediate climatic zone, (mean annual rainfall 1750-2500 mm) while other estuaries/lagoons are situated in the dry zone of Sri Lanka which mean annual rainfall recorded lesser than that. Although Rekawa is located in the intermediate zone annual rainfall recorded 1082 mm which is lower than that of recoded annual rainfall in other dry zone mangrove areas.

Comparison of data on GPP of the present study with published estimates, reveal that they are relatively lower than that have been recorded by Clough and Dalhaus (1997), at Matang mangrove forest at Malaysia, where GPP was recorded to be 56 Mg $ha^{-1}y^{-1}$. Estimated GPP of 102.9 Mg $ha^{-1}y^{-1}$ has been reported from Kandelia candel forests in Okinawa Island, Japan (Suwa et al., 2006) and it is much higher than those values recorded by the present study. Only a very few studies have been dedicated to estimating mangrove GPP and even among them, no consideration has been given to the seasonal variations in climate that leads to changes in physiological traits of mangrove leaves. It was revealed that PAR data is highly variable with the climatic conditions (wet or dry) and therefore seasonal changes in photosynthesis and dark respiration rates of leaves are probably necessary for obtaining reliable estimates of annual canopy photosynthesis and respiration rates.

5. CONCLUSION

Estimation of the Leaf area index (LAI) and Gross Primary Productivity (GPP) of mangrove ecosystems located in different climatic zones in Sri Lanka and its relationship with rainfall and the vegetation structure were the main objectives of the study. Highest average values of LAI and GPP were recorded from the wet and the intermediate zone mangroves. Statistically significant positive linear relationship with high coefficient of determination (r^2>0.7) were revealed to occur between GPP values of wet and dry periods of mangroves and GPP with vegetation structural complexity. The average LAI of mangrove ecosystems in Sri Lanka therefore was 5.66, with a GPP of 40.92 Mg ha^{-1} y^{-1}. A positive correlation was recorded between estimated average annual gross primary productivity (GPP) values and annual rain fall of the study areas. Results revealed that LAI and GPP of mangroves is potentially driven by annual rainfall pattern among other factors, by climate.

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