Photosynthetic Rates in Mangroves

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***Abstract*—**Generally mangrove forests have high productivity and provide habitat for many species. Pulse Amplitude Modulation fluorometry (PAM) methods are a revolutionary way of measuring photosynthesis in plants based on PSII fluorescence. Mangroves growing in Paklok (Phuket**)** such as *Avicennia alba* (L.), *Rhizophora mucronata* and *Bruguiera cylindrica* are all C3 plants. Photosynthesis of common mangroves growing in the Phuket area was characterized using PAM (Pulse Amplitude Modulation) Fluorometry (Blue diode based). We have found that *Rhizophora* sp. has photosynthetic rates (P_{max}) of ≈ 102 μmol mgChl $a^{-1}h^{-1}$. *Avicennia* has higher photosynthetic rates (P_{max}) of ≈ 183 μmol mg Chl a^{-1} h^{-1}. *Bruguiera* sp. has a relatively low Pg_{max} ≈ 51 μmol mgChl $a^{-1}h^{-1}$. Photosynthetic efficiency (α) and non-photochemical quenching were also measured. The results of the photosynthesis studies will be used to make it possible to estimate carbon-fixation of mangroves. Estimates of photosynthesis will be valuable in assessing the productivity of mangroves stands.

***Keywords*—**Light Curves, Mangroves, Photosynthesis, Pulse Amplitude Modulation fluorometry (PAM).

I. Introduction

COASTAL environments refer to various kinds of natural habitats such as muddy areas, sandy substrates, rocky beaches, mangrove forest, submerged aquatic vegetation and coral reefs. They provide food, shelter, and breeding grounds for terrestrial and marine species [1].

It is important to be able to measure the level of environment stress on mangrove plants. Measurement of photosystem II fluorescence is a convenient way of estimating photosynthetic activity of plants in particular stress physiology. Basically plant cells using Chlorophyll *a* as their primary photosynthetic pigment strongly absorb light at the blue (430 nm) and red (680 nm) peaks of *in vivo* Chlorophyll *a* absorption. Some of this absorbed light is used to power the light reactions of photosynthesis and some is re-emitted as waste heat and some is re-emitted as fluorescent light with a peak at about 730 nm. Hence, plants appear bright red in the Far-Red/NIR part of the spectrum (> 700 nm to 800 nm). This infrared glow of vegetation is used as a basis for monitoring vegetation using satellite and aerial photometric methods. Pulse Amplitude Modulation fluorometry (PAM) methods are a revolutionary way of measuring photosynthesis in plants based on PSII fluorescence [2,3,4] which can be used to monitor photosynthetic activity of a wide variety of photosynthetic organisms including green algae such as *Chlorella* and diatoms [4,5] as well as vascular plants such as orchids, pineapple and water lilies [6,7]**.**

Mangroves such as *Rhizophora* sp., *Avicennia* sp., *Bruguiera* sp. and the mangrove Palm (*Nipa fructans*) are all C3 plants and so interpretation of PAM measurements on these plants should be straightforward. Photosynthetic rates, as measured by leaf stomatal conductance and leaf chlorophyll fluorescence induction, were tested as indicators of salinity stress in seedlings of the red mangrove, *Rhizophora mangle*, grown under five different salinity levels: 0, 15, 30, 45, and 60 parts per thousand [8]. Photosynthetic gas exchange (measured by stomatal conductance), as well as the light reaction of photosynthesis (measured by chlorophyll fluorescence) were found to decrease as salinity increased. The use of leaf stomatal conductance and chlorophyll fluorescence as a measure of photosynthesis has allowed rapid and reliable quantification of the known stressor, salinity, in seedlings of *R. mangle*. These non-destructive *in-vivo* techniques were found to be rapid and reliable for monitoring photosynthetic stress, an important physiological parameter determining survival and growth of mangrove plants. PAM methods are the most rapid techniques for monitoring photosynthesis in forestry management and mangrove restoration projects to assess plant condition [9].

II. Methodology

Suitable mangrove areas are readily accessible on the eastern coast of Phuket, Thailand. We selected a seagrass and mangrove reserve on the East Coast as a suitable field site: located at Paklok, Phuket, Thailand (8°0'49" N, 98°24'33"E).

We have characterised photosynthesis of three mangrove species growing in the Phuket area using PAM (Pulse Amplitude Modulation) Fluorometry (Blue diode based). PAM Fluorometry can measure photosynthetic quantum yield (Y), electron transport rate (ETR), optimum light (Eopt), maximum gross photosynthesis (Pg_{max}), photosynthetic efficiency (α) and photochemical and non-photochemical quenching (qN and NPQ) characteristics of the plants. Light saturation curve measurements were made on the adaxial surfaces with a Junior-PAM portable chlorophyll fluorometer

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(Gademann Instruments, Wurzburg, Germany) fitted with a 1.5-mm-diameter optic fiber and a blue diode (485-640 nm) light source. PAM parameters (Y, rETR, qN, and NPQ) were calculated with the WinControl software (ver. 2.13) [10]. Quantum yield of photosystem II (PSII) electron transport (Y or Φ) s calculated as $(Fm_0 - F)/Fm_0$. In this research we sampled a total of 16 replicates in the laboratory (seedlings in sea water). We studied three mangrove species: *Rhizophora mucronata*, *Avicennia alba* and *Bruguiera cylindrica*. We found that all three species were very sensitive to wounding and leaves rapidly shut down if cut from the plants. Leaves still attached to the plants were used in this study.

F is the light-adapted fluorescence when a saturating light pulse of about 2000 to 2500 (or higher) μmol m^{-2} s^{-1} PPFD for 700 ms duration is superimposed on the prevailing environmental irradiance level [10]. Electron transport rate (ETR) through PSII can be calculated as 0.5×0.84×PPFD×Y assuming that 84% of incidental light is absorbed by leaves (Absorptance, Abt) [11] and that photons are equally distributed between PSII and PSI (0.5). We have a RAT (Reflectance/Absorptance/Transmission) machine which can experimentally measure Absorptance and so we were able to use actual Abt values rather than the assumed value of 0.84 [12]. Absorptances of all three species in blue light are very much higher than 0.84.

Since four electrons move through PSII for each O_2 produced the conversion factor for Pg from ETR is to divide by 4. The ETR of plants is calculated on a surface area basis (mol m^{-2} s^{-1} or mol m^{-2} h^{-1}). If the Chlorophyll a content of the leaves is also known it is possible to recalculate ETR and hence Pg as mol mgChl a^{-1} h^{-1}. Chl a was determined on disks of mangrove leaf (97 mm) cut with a cork borer, then extracted in hot ethanol and Chl *a* estimated by spectroscopy [13].

Plots of Photosynthesis vs. irradiance follow a saturation/inhibition curve called the Waiting-in-Line (W-in-L) model. A form of the W-in-L saturation model suitable for modelling photosynthesis with experimentally determinable constants that are easily recognisable on a graphical representation of the data is [4,5]

$$Pg = \frac{Pg_{\max} \times E}{E_{opt}} \times e^{1-E/Eopt} \qquad (1)$$

where, *Pg* is gross photosynthesis,

Pg_{max} is the maximum gross photosynthesis,

E is the Irradiance (μmol m^{-2} s^{-1} 400 – 700 nm PPFD),

E_{opt} is the optimum irradiance.

Non-Photochemical quenching measured as qN and NPQ increases as irradiance increases and can usually be described as a simple exponential saturation curve [4,5]. Thus for NPQ,

$$\mathrm{NPQ} = \mathrm{NPQ}_{\max}\left(1 - e^{k_{NPQ} E}\right) \qquad (2)$$

where, NPQ is non-photochemical quenching,

k_{NPQ} is a constant,

E is the irradiaance.

III. Results and Discussion

Table 1 shows to the absorptances of mangrove leaves measured using the RAT machine (blue light and white light). The absorptances for blue light were used for the ETR determinations using the PAM machine because the Junior PAM uses a blue-diode light source. In all three mangroves the absorptances are about 99% in the case of blue light and so the default value of 84% used in most PAM studies of photosynthesis seriously *underestimates* photosynthesis in mangroves. For example, ETR estimates calculated on *Avicennia* using the PAM machine in default mode needed to be corrected by multiplying by a factor of 99.7/84 to obtain the true ETR. Some types of PAM machine use a white light source (quartz halogen). The absorptances of *Avicennia* and *Rhizophora* in white light is also well above the default value of 84%. The absorptance in white light for *Bruguiera* however is close to the default value. The RAT results show that it is important to be able to measure absorptances of leaves experimentally rather than use default values [12].

TABLE I
TABLE OF ABSORPTANCE OF MANGROVE

Species	Absorptance (%)	
	Blue light	White light
Avicennia alba	99.7 ± 0.1	93.4 ± 0.5
Rhizophora mucronata	99.2 ± 0.3	94.1 ± 1.0
Bruguiera cylindrica	98.8 ± 0.6	85.5 ± 0.8

Photosynthesis of *Avicennia* sp. on a leaf surface area basis has an Optimum Irradiance of about 859 ± 102 μmol photons m^{-2} s^{-1} (Fig. 1) This about 41% of full sunlight. This is typical of a “sun plant” and Maximum photosynthesis (Pg_{max}) is about 56.97 ± 4.08μmol m^{-2} s^{-1}. This is a high value for a higher plant. The maximum photosynthetic Efficiency (Alpha, α) is about 0.180 ± 0.0250. This means that at zero irradiance (the instantaneous slope of Equation 1 at zero irradiance) 18% of photons are used for photosynthesis. The fit to data is very good (r = 0.714) and the relative errors of the fitted parameters are low (RE ≈ ±4.6 to 7.6%).

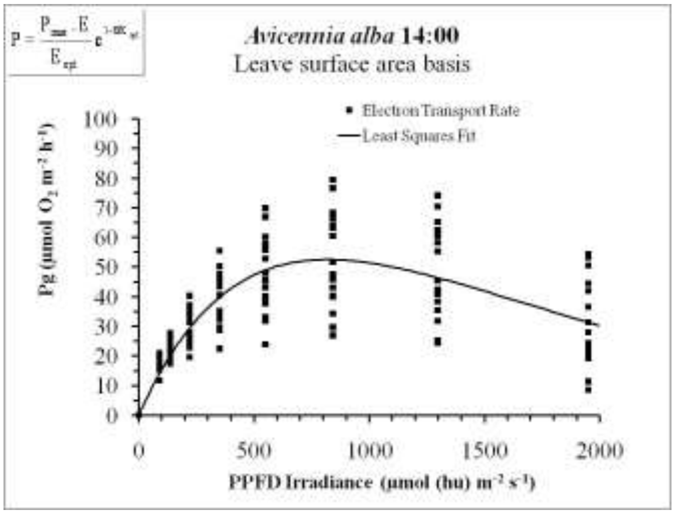

Fig. 1

Recalculating the results of the PAM experiments on a Chlorophyll *a* basis the Optimum Irradiance is not changed (Eopt = 614 ± 33 µmol photons m^{-2} s^{-1}) because the conversion to a chlorophyll a basis only changes the Y-axis scale (Fig. 2). P_{max} is about 183±8.5 µmol mgChl a^{-1} h^{-1}. This is a high value for a higher plant. Fit to data is very good (r = 0.8861) and the relative errors of the fitted parameters are low (RE ≈ ±3.7 to 5.4%).

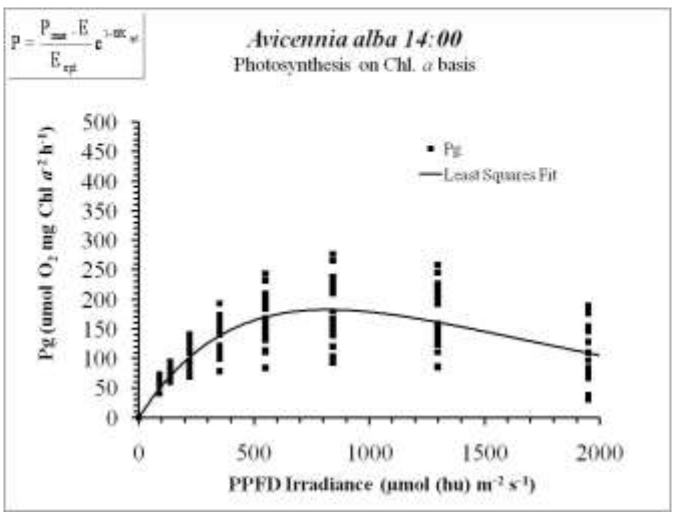

Fig. 2

Fig. 3 shows the PAM results for *Rhizophora mucronata* on a leaf surface area basis. The Optimum Irradiance is about 820 ± 62 µmol photons m^{-2} s^{-1}. This about 39% of full sunlight and so *Rhizophora* also behaves like a sun plant. The Maximum photosynthesis (P_{max}) is about 52.5 ± 2.44 µmol m^{-2} s^{-1}. The maximum photosynthetic Efficiency (Alpha, α) is 0.174 ± 0.0155. This means that at the maximum 17% of photons are used for photosynthesis. The theoretical maximum would be 25%. The fit to the data is very good (r = 0.8443) and the relative errors of the fitted parameters are low (RE ≈ ±4.6 to 7.6%).

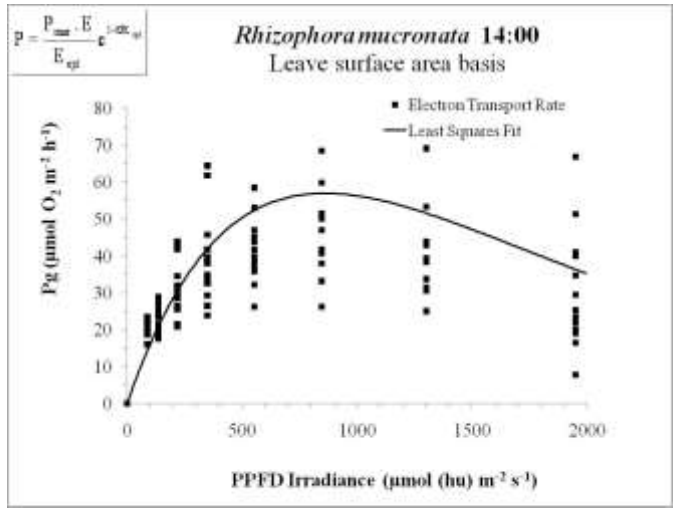

Fig. 3

On a Chlorophyll *a* basis the Optimum Irradiance is unchanged (about 820 ± 62 µmol photons m^{-2} s^{-1}). Maximum photosynthesis (P_{max}) is about 102± 3.8 µmol mg Chl a^{-1} h^{-1}. Fit to data is unchanged (r = 0.8443) by the new scaling.

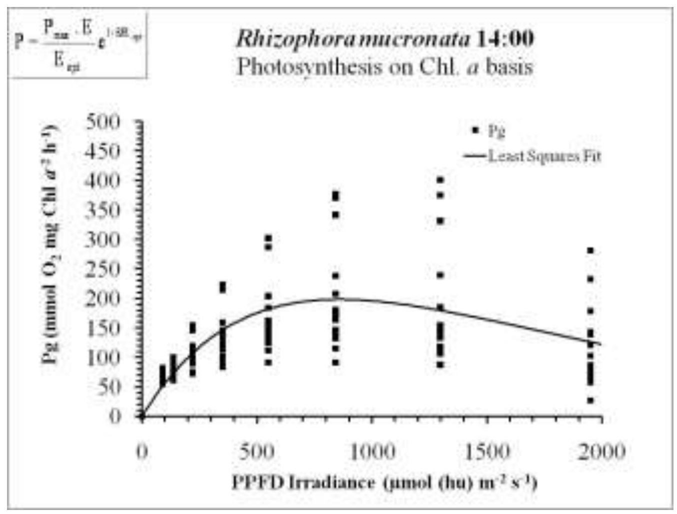

Fig. 4

In *Bruguiera cylindrica* the Optimum Irradiance is about 376 ± 31 µmol photons m^{-2} s^{-1} (Fig. 5). While still typical of a "sun plant" it is conspicuously lower than in *Avicennia* & *Rhizophora*. Maximum photosynthesis (P_{max}) is about 14.6 ± 0.77 µmol m^{-2} s^{-1}.The maximum photosynthetic Efficiency (Alpha, α) is 0.105 ± 0.0103. These mean that at the maximum efficiency of use of irradiance is only 10% of photons are used for photosynthesis. Fit to data is very good (r = 0.8631) and the relative errors of the fitted parameters are low (RE ≈ 5.3 to 8.2%).

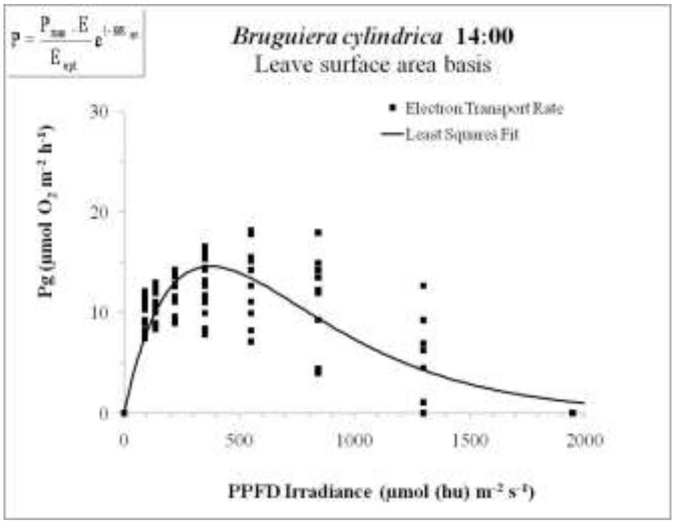

Fig. 5

On a Chlorophyll *a* basis the Optimum Irradiance remains unchanged (Fig. 6). Maximum photosynthesis (P_{max}) is about 50.78± 2.7 µmol mg Chl a^{-1} h^{-1}.

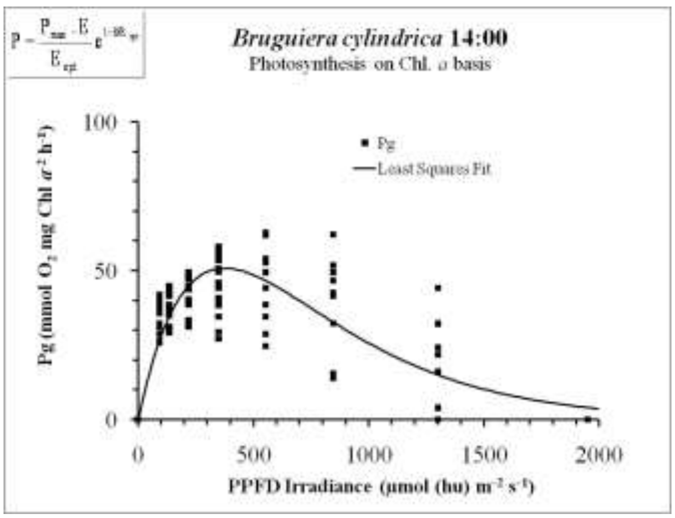

Fig. 6

Figures 7 and 8 show the non-photochemical quenching results for *Bruguiera* where non-photochemical quenching is expressed as qN and NPQ [4,5]. Both qN and NPQ show classical simple exponential saturation curves with a qNmax of about 0.751 ± 0.183 and NPQmax of 1.473 ± 0.0928. In most vascular plants NPQ is greater than qN. The half saturation irradiance is about 170 µmol photons m^{-2} s^{-1} and for NPQ it is about 318 µmol quanta m^{-2} s^{-1}.

The results for *Avicennia* and *Rhizophora* were comparable and are presented in Table 2. The qN and NPQ values of the mangroves are very similar and qNmax < NPQmax. The qN and NPQ of mangroves are typical of vascular plants [3,4,5,6,8].

The importance of qN and NPQ is that they reflect the state of the proton motive force across the thylakoid membranes of the chloroplasts and are sensitive to nutrient deficiencies and herbicides.

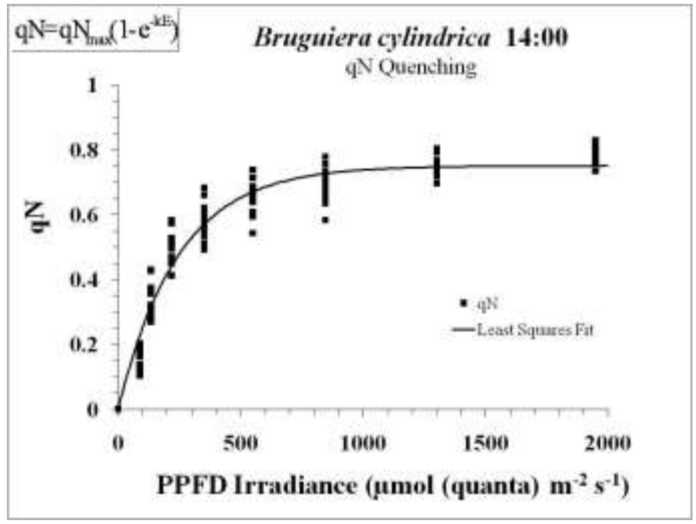

Fig. 7

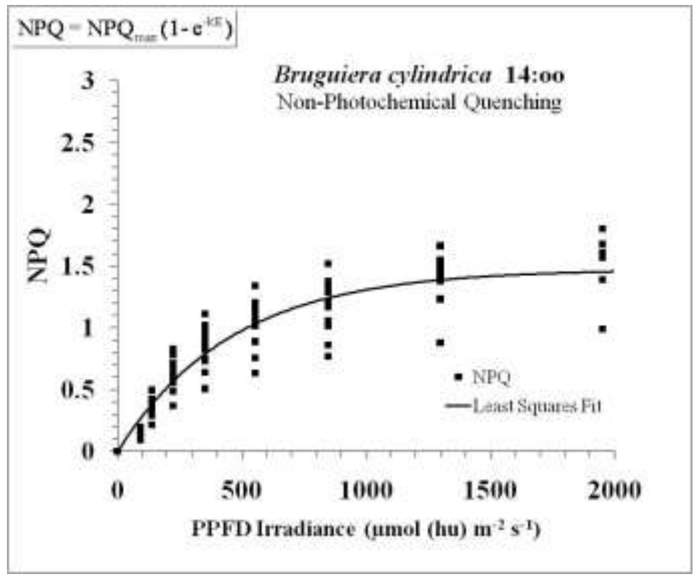

Fig. 8

TABLE II
TABLE OF NON-PHOTOCHEMICAL QUENCHING OF MANGROVES.

Species	qN		NPQ	
	qNmax	kqN	NPQmax	kNPQ
Avicennia	0.859 ±0.0239	0.00714 ±0.000754	1.545 ±0.104	0.00366 ±0.000749
Rhizophora	0.805 ±0.0342	0.00571 ±0.000863	1.598 ±0.123	0.00315 ±0.000713
Bruguiera	0.751 ±0.183	0.00407 ±0.00029	1.473 ±0.0928	0.00218 ±0.000308

IV. CONCLUSION

- It is important to be able to estimate absorptances of leaves experimentally for PAM studies because many types of leaves have absorptances quite different to the commonly used default value of 84%. The higher Abt results in higher estimates of Gross photosynthesis (Pg).

- Gross photosynthesis was estimated as mol m^{-2} s^{-1} (leaf area basis for productivity studies) and mol mg Chl a^{-1} h^{-1} (for interspecies comparisons).
- *Avicennia* and *Rhizophora* are adapted to very high irradiance and have high photosynthetic efficiencies.
- *Bruguiera* saturates at much lower irradiance, has a lower photosynthetic rate both on a surface area and Chl *a* basis and a lower Photosynthesis efficiency.
- Non-photochemical quenching characteristics of *Avicennia*, *Rhizophora* and *Bruguiera* are closely similar and typical of vascular plants.

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