BILINGUAL PUBLISHING GROUP

Journal of Botanical Research

https://journals.bilpubgroup.com/index.php/jbr

ARTICLE

Photosynthetic Electron Transport in the Liverwort *Conocephalum conicum* (Marchantiales)

Raymond J. Ritchie

Technology and Environment, Prince of Songkla University-Phuket, Phuket, Thailand

ABSTRACT

Photosynthetic Electron Transport Rate (ETR) of *Conocephalum conicum* (Snakeskin Liverwort) was measured using PAM technology modelled using the Waiting-in-Line model. Plants were grown in greenhouses which had irregular sunflecks of full sunlight and in a culture room under LED lights. Plants grown in the greenhouse had photosynthetic maxima about 1/3 to ½ of sunlight, but very low optimum light requirements when grown in a culture room under LED lights. Chl *a* content was ≈ 241 mg Chl *a* m^{-2} (Chl *b*/*a* ≈ 0.216). Mid-morning (10:30 solar time): Y_{max} ≈ 0.629, irradiance ½ point for Yield ≈ 231 µmol photon m^{-2} s^{-1}; E_{opt} ≈ 910 µmol photon m^{-2} s^{-1}. ETR_{max} ≈ 266 µmol e^{-} g^{-1} Chl *a* s^{-1}, photosynthetic efficiency (Alpha, α0) ≈ 0.794 e^{-} $photon^{-1}$ g^{-1} Chl *a*. Photoinhibition was significant at high irradiances. Photosynthesis was markedly diurnal: E_{opt} and ETR_{max} were substantially lower in the afternoon. Integrating Gross photosynthesis (Pg) over the course of the day Pg ≈ 39.6 gC g^{-1} Chl *a* d^{-1} under full sunlight and ≈ 29.6 gC g^{-1} Chl *a* d^{-1} in the shaded greenhouse. On a projected surface area basis daily Pg is ≈7.14 gC m^{-2} d^{-1}. The respiration rate was relatively low (≈2.23 µmol O_2 g^{-1} Chl *a* s^{-1}) so net photosynthesis is positive even at very low irradiances. Greenhouse gown plants had a conspicuous diurnal pattern of photosynthesis where optimum rates were found in midmorning and midday with a decrease in the afternoon. Plants grown under LED lights had a very low E_{opt} (≈90 µmol photon m^{-2} s^{-1}) and ETR_{max} (≈40 µmol g^{-1} Chl *a* s^{-1}). pH experiments indicate that it is capable of using HCO_3^- as a carbon source.

Keywords: Snakeskin Liverwort; *Conocephalum conicum*; PAM, Pulse Amplitude Modulation Fluorometry; Optimum Irradiance (E_{opt}); Maximum Photosynthetic Electron Transport Rate (ETR_{max}); Carbon Concentrating Mechanism (CCM)

*CORRESPONDING AUTHOR:

Raymond J. Ritchie, Technology and Environment, Prince of Songkla University-Phuket, Phuket, Thailand;
Email: Raymond.ritchie@alumni.sydney.edu.au

ARTICLE INFO

Received: 25 March 2024 | Revised: 7 April 2024 | Accepted: 11 April 2024 | Published Online: 10 July 2024
DOI: https://doi.org/10.30564/jbr.v6i3.9222

CITATION

Ritchie, R.J., 2024. Photosynthetic Electron Transport in the Liverwort *Conocephalum conicum* (Marchantiales). Journal of Botanical Research. 6(3): 1–17. DOI: https://doi.org/10.30564/jbr.v6i3.9222

1. Introduction

Despite their global distribution bryophyte photosynthetic physiology is not well understood, particularly liverworts living in tropical environments[1–3]. No Bryophyte appears to have C4 photosynthesis[4]. Photosynthetic Electron Transport Rate (ETR) has been very successfully measured in the tropical moss *Hyophila involuta* using PAM (Pulse Amplitude Modulation) fluorometric technology[5, 6]. The plants were growing outdoors in a heavily shaded habitat with irregular sunflecks of full sunlight[7]: a shared habitat for many liverworts and mosses[8]. Like in the case of crustose lichens[9], the flat geometry of thallose liverworts is particularly suitable for PAM techniques for measuring photosynthesis[7, 10–13]. Snakeskin liverwort (*Conocephalum conicum* (L.) Dum.) is of North American and Eurasian origin that is now distributed worldwide because it readily grows on the soil of pot-plants and so has been incidentally spread worldwide by the decorative plant industry[2]. It is frequently used in teaching and so is often found in university botanical teaching collections. The related species, *Marchantia sp.* has been used previously in PAM studies[14] and *Marchantia polymorpha* has also been used in PAM studies[15]. Marchantiales genera are widespread including Antarctica (*Marchantia berteroana*:[15]) as well as many other liverworts[3].

Desiccation tolerance is frequently noted in liverworts (*Dumortiera hirsute*, Marchantiales:[16]; rainforest epiphytic species[1]) but the duration and frequency of desiccation is also important[17]: a plant might be homiochlorophyllous (rapid recovery from desiccation with revivable chloroplasts) in the case of short term desiccation but poikilochlorophyllous (recovery over a longer time course because new chloroplast need to be manufactured) in the case of seasonal prolonged desiccation where the dormant cells of the plant are progressively destroyed over time. There is however, a great diversity in desiccation tolerance amongst mosses, liverworts and hornworts[3, 18]. Diurnality of photosynthesis, although known in bryophytes[6, 11], has largely been neglected even though the gametophyte of species like *Conocephalum conicum* and related *Marchantia* species do have air-pores analogous to stomata (ventilated liverworts). Studies of aquatic macrophytes using PAM data have also demonstrated diurnality in photosynthetic electron transport[19]. Photosynthetic data on the moss, *Hyophila involuta* using PAM (Pulse Amplitude Modulation) fluorometric technology[6] showed that it was able to use HCO_3^- as a carbon source consistent with it having a carbon concentrating mechanism (CCM) but Frangedakis et al.[20, 21] states that amongst the bryophytes a CCM is only well documented on molecular evidence in the hornwort, *Anthoceros agrestis* (Paton) Damsholt (Anthocerotales). CCM is not commonly reported in Bryophyte phyla (Moss, *Hyophila involuta*:[4, 6]; Bryophyta (Liverworts):[22–24]; Anthocerophyta (Hornworts):[25–27]. The three Bryophyta phyla are not very closely related and so comparisons of the physiology of the three different types of bryophytes need to be treated with caution[4, 28]. The bryophyta where a CCM mechanism has been identified experimentally were aquatic, not terrestrial (*Fontinalis antipyretica*:[23]; *Fontinalis antipyretica* and *Fissidens grandifrons*:[24]). Others have reported that most aquatic bryophytes were not bicarbonate users[29].

N-fixation is known to occur in liverworts by the activity of cyanobacterial symbionts[30]. Although cyanobacteria are present in *Conocephalum conicum* actual N-fixation of a magnitude to substantially contribute to the N-economy of the plants does not appear to have been demonstrated experimentally[20, 21]. The presence of N-fixing anoxygenic photosynthetic bacteria is not documented in liverworts[31]: they are widespread in plant associations but their presence is largely not given attention unless specifically looked for. Their presence might not be conspicuous and might appear only in culturing experiments on tissue extracts incubated anoxically.

This study is an investigation of the basic aspects of photosynthesis in the common liverwort *Conocephalum conicum,* including rapid light curves, to characterise its light saturation kinetics, diurnal responses of photosynthesis, its chlorophyll content, resistance to desiccation and its ability to use HCO_3^- as a carbon source as it is frequently found growing in semi-aquatic habitats. *Conocephalum conicum* has been dispersed to many parts of the world and so is now a cosmopolitan species. Here it used as a benchmark example of a liverwort that is readily available because it is used in typical introductory biology teaching.

2. Materials and Methods

2.1. Experimental Material

Conocephalum conicum (L.) Dum., Family Conocephalaceae, commonly known as Snakeskin Liverwort (**Figure 1**), is a common, originally Holarctic species that is now cosmopolitan largely because of accidental introductions as a consequence of the international ornamental plant trade [2]. Plants can be 20 cm long and up to 20 mm wide. It reproduces sexually as well as asexually by propagules formed in splash cups on the surface of the thallus. The specimens used in the present study were from the greenhouse collections of the Botany Dept., Biological Sciences, Prince of Songkla University - Hat Yai, Songkhla Province, Thailand (7°1′ N, 100°28′ E) and School of Life Science, The University of Sydney, NSW, Australia (33°52′ S, 151°13′ E).

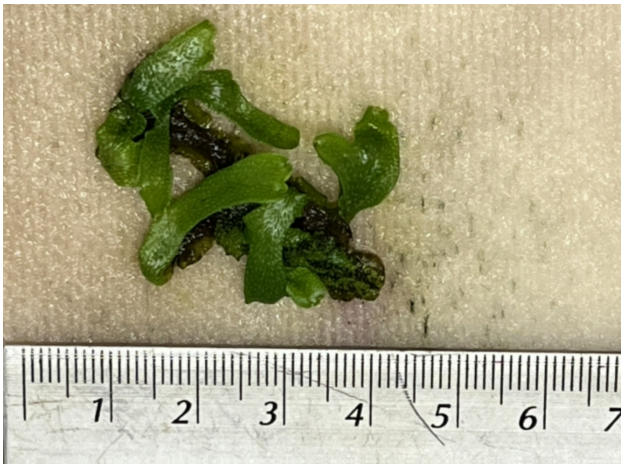

Figure 1. Photograph with cm scale of Conocephalum conicum from the material grown in the Botanical Science greenhouse at Prince of Songkla University-Hat Yai, Hat Yai, Thailand.

2.2. Culture Conditions

The pH experiments could not be practically conducted in the greenhouse. *Conocephalum conicum* was grown in plastic lunchboxes in an algal culture room over a period of about 3 weeks. Plants were regularly watered with a pondwater medium was based on a 5% dilution of Bg-11 medium [32] but with lower nitrate: 0.5 mol m^{-3} $NaNO_3$, 0.5 mol m^{-3} $NaHCO_3$, 200 µmol m^{-3} NaH_2PO_4, $MgSO_4$ and $CaCl_2$, micronutrients as for 5% Bg-11 medium. Irradiance was approximately 50 µmol photon m^{-2} s^{-1} 400–700 nm PAR (Quantum Meter, Model MQ200, Apogee Instruments, Logan, Utah, USA). These culture room conditions are similar to those used by Koide et al. [15] for *Marchantia polymorpha.* It was found that the photosynthesis vs. irradiance behaviour of the culture-room grown material was quite different to the greenhouse material.

2.3. Chemicals

Acetone $(CH_3)_2CO$ 99.5 AR/ACS was from LOBA Chemie PVT. LTD., Mumbai, India. 90% Acetone was neutralised with magnesium carbonate (≈100 mg/100 ml). DMSO (Dimethylsulphoxide, dimethyl sulfoxide, $(CH_3)_2SO$) was from WINNEX (Thailand) Co. Ltd., Bangkok, Thailand.

2.4. Scanning Dual Beam Spectrophotometer

A Shimadzu UV-1601 UV–visible double beam spectrophotometer (Shimadzu Corporation, Kyoto, Japan) was used for routine chlorophyll determinations using standard scanning settings (1 nm bandwidth and 1 nm sampling interval) Chl *a* and Chl *b/a* ratio were determined using the algorithms developed for 90% acetone or DMSO using 1 cm quartz cuvettes. The chlorophyll algorithms used are described in previous studies [6, 33–35].

2.5. Chlorophyll

Unlike the case of the moss *Hyophila involuta* (Ritchie and Sma-Air 2023), it was not difficult to extract chlorophylls from *Conocephalum conicum* in 90% acetone or DMSO (dimethyl sulphoxamine). Extracts were cleared by centrifuge at 5000 rpm (3914 rcf) in a standard swing-bucket bench centrifuge for 5 min (Hermle Z323K, Hermle Labortechnik, Wehingen, Germany) and the supernatant removed for spectroscopy. 850 nm was used as the standard blank for the Chl *a & b* equations because it is a better choice of blank than the more routinely used 750 nm [6, 35]. The possible presence of bacteriochlorophylls from symbiotic photosynthetic bacteria were specifically searched for on scans at 774 nm but no significant BChl *a* was detectable [31].

2.6. Preparation for Uniform Liverwort Disks for Chlorophyll Determinations

PAM Machines (Pulse Amplitude Modulation Fluorometers) measure the photosynthetic Electron Transport Rate (ETR) as mol e^- m^{-2} s^{-1} and so a Chlorophyll *a* per unit surface area determination is needed to convert them to mol

e^- g^{-1} Chl *a* s^{-1}. A 9.7 mm diameter cork-borer (projected surface area 73.90 × 10^{-6} m^2) was used to obtain a large set of disks of *Conocephalum conicum*. Based on a sample of 4 separate collections, making a total of 32 cork borings, the average Chl *a* content was 241 ± 16.34 mg Chl *a* m^{-2} with Chl *b*/*a* ≈ 0.216 ± 0.014 (4,32). This is within the range found in many different liverworts[8, 12, 17]. The chlorophyll *a* content of *Conocephalum conicum* found in the present study on a surface area basis is similar to that found previously in *Marchantia sp.*[10, 14] but the Chl *b* content and hence Chl *b*/*a* ratio was lower.

The PAM software calculates relative ETR (rETR) as μmol e^- m^{-2} s^{-1} (projected surface area) but if the absorptance ($Abt_{445\ nm}$) of the cut disks of *Conocephalum conicum* and the Chl *a* content of the disk (mg m^{-2}) were both known, the ETR could be recalculated as μmol e^- g^{-1} Chl *a* s^{-1}. Like other prostrate liverworts (*Dumortiera hirsute*:[17]), *Conocephalum conicum* has an excellent geometry for PAM experiments because Chl *a* per unit projected surface area is easily measured. Absorptance was measured experimentally using a RAT device (Reflectance-Absorptance-Transmission) which uses a 445 nm blue diode[6, 36]. *Conocephalum conicum* was nearly optically black at the 445 nm wavelengths used by the PAM machine used in the present study (Abt_{465nm} = 97.39 ± 0.994%, n = 24, reflectance ≈ 2.6 ± 0.994%). *Conocephalum conicum* had a much higher absorptance (in blue light) than for liverworts in white light[3].

2.7. PAM (Pulse Amplitude Modulation) Fluorometry

A portable chlorophyll fluorometer (Junior PAM) made under license by Gademann Instruments, Würzburg, Germany was used for the fluorometric measurements of photosynthesis: it uses WINCONTROL software (v2.08 and v2.13; Heinz Walz Gmbh, Effeltrich, Germany). It has a 1.5 mm-diameter optic fibre and a blue diode light source (445 ± 20 nm) with a simple highpass filter (>695 nm) to measure the PSII fluorescent emission by the plant[6]. The PAM parameters (Y, rETR, NPQ) were automatically calculated using the WINCONTROL software using the standard default settings for rapid light curves (default absorptance factor, AbtF = 0.84, PSI/PSII allocation factor = 0.5) to calculate the relative electron transport rate (rETR) (Ralph and Gademann 2005). The full protocol here is based on the most recent published version[6]. Rapid light curves have some statistical limitations because fluorescence measurements are measured in order of increasing irradiance: this is an unacknowledged inherent limitation of the Walz rapid light curve protocol[37, 38]. Yield (Y) was calculated by the WINCONTROL software. If Y is plotted against irradiance (*E*), it usually follows a simple exponential decay function of the form $Y_E = Y_{max}\ e^{-kY \times E}$, where Y_E is the Yield at PPFD irradiance (*E*) (μmol photon m^{-2} s^{-1}), Y_{max} is the maximum Yield at asymptotically zero irradiance and kY is an exponential constant. $E_{½\text{-}Y_{max}}$ is the irradiance where Yield is reduced to ½ of maximum the Y_{max} ($E_{½\text{-}Y_{max}} = -\ln 2/kY$).

Photosynthetic electron transport rate (ETR) is proportional to the product of the Yield at irradiance *E* (Y_E) × Irradiance (E). The Walz software uses a default absorptance of 0.84 and so calculates relative ETR (rETR): if absorptance (Abt) is measured experimentally, the actual ETR can be calculated. Experimentally measured Absorptance values (Abt_{465nm}) of plant material is often rather different to the default value of 0.84 and so ETR as calculated by the Walz software needs to be corrected for the actual absorptance ($ETR = rETR \times Abt_{465nm}/0.84$)[36]. Since the liverwort disks were essentially optically black under blue light (Abt_{465nm} = 97.39 ± 0.994%, n = 24) the actual ETR was about 16% higher than rETR (ETR = 1.159 ± 0.0118 × rETR). The electron source in oxygenic photosynthesis is water:

$$2H_2O \rightarrow 4H^+ + 4e^- + O_2 \text{ and}$$
$$\text{hence } 1\ \mu mol\ O_2\ m^{-2}s^{-1} \equiv 4\ \mu mol\ e^- m^{-2}\ s^{-1}$$

Photosynthetic Electron Transport Rate (ETR) is unaffected by photorespiration (unlike photosynthetic light reaction measurements based on O_2) and so is a *rough estimate* of gross photosynthesis (Pg). ETR is based on fluorescence measurements made with very short flashes of light and so fluorometrically measured ETR *inherently* measures photosynthetic activity under conditions where photorespiratory O_2 inhibition is minimised.

The Waiting-in-Line equation of the form $y = x \times e^{-x}$ is a good minimalist model for rapid light curves of ETR vs. Irradiance[6, 38]. A form of the Waiting-in-Line equation suitable for photosynthesis vs. irradiance is:

$$ETR = \frac{ETR_{max} \times E}{E_{opt}} \times e^{1-E/E_{opt}}$$

where, ETR is a measure of the photosynthetic Electron Transport Rate (μmol e^- m^{-2} s^{-1}), *E* is the experimental

irradiance (μmol photon m^{-2} s^{-1} 400–700 nm PPFD), E_{opt} is the calculated optimum irradiance and ETR_{max} is the calculated maximum photosynthetic Electron Transport Rate.

Importantly, the Waiting-in-Line model includes photoinhibition at high irradiance in a minimalist way: it follows from the experimental observation that Yield follows a simple exponential decay function ($y = e^{-x}$) and consequently the photosynthetic electron transport rate should follow the Waiting-in-Line equation because ETR would be proportional to the product of Yield × Irradiance ($y = x \times e^{-x}$)[39]. The maximum photosynthetic efficiency (α0) is the initial slope of the curve at E = 0 ($\alpha 0 = ETR_{max} \times e/E_{opt}$). Photosynthetic Electron Transport Rate (μmol e^- m^{-2} s^{-1}) and asymptotic Photosynthetic Efficiency (α0) (e^- $photon^{-1}$) were converted into μmol e^- g^{-1} Chl *a* s^{-1} and e^- g^{-1} Chl *a* $photon^{-1}$ using the known Chl *a* m^{-2} of *Conocephalum conicum* disks. Maximum photosynthetic efficiency (α0) can be expressed on either a surface area (e^- $photon^{-1}$) or Chl *a* basis (e^- g^{-1} Chl *a* $photon^{-1}$). The Waiting-in-Line model inherently predicts photoinhibition at high irradiances without having to introduce additional coefficients which greatly increase the difficulty in obtaining a satisfactory curve fit and the error-bars of the fitted parameters become very large[6, 39, 40].

Photochemical (qP) and Non-photochemical quenching (NPQ)[5], were calculated by the Walz software and have more to do with photoprotection mechanisms for PSI than as a stress indicator[41, 42]. qP can be fitted to a simple exponential decay curve with a zero irradiance value of unity (by definition) and a decay constant kqP. The shape of the curve is best visualised by quoting the ½-point for decay of qP (½ decay point for irradiance, $-\ln 2/kqP = E_{½\ decay\ point}$). NPQ is basically a waste heat index for PSII. NPQ vs. irradiance in most plants *can usually* be fitted to a simple exponential saturation curve of the form $NPQ = NPQ_{max} \times (1-e^{-kNPQ \times E})$ where, NPQ_{max} is the maximum NPQ and kNPQ is an exponential constant. The shape of the curve can be described by quoting the maximum NPQ (NPQ_{max}) and the irradiance at which ½ of the NPQ_{max} is achieved ($-\ln 2/kNPQ = E_{½\text{-}NPQ_{max}}$). The NPQ concept was developed for vascular plant systems and so might not quite fit Bryophytes. qP and NPQ are calculated from complicated equations that sometimes generate spurious negative values or zero values in the denominator. Spurious values are usually generated only at high irradiances. When the Walz software generates such spurious values it generates an error signal (recognisable error code numbers displayed by the Walz software).

Some photosynthetic organisms, although giving plausible Y and ETR results, may not give satisfactory NPQ data. We found that *Conocephalum conicum* typically gave plausible exponentially saturating NPQ curves, with a NPQ_{max} of about 1 to 2 (**Figure 2**), similar to vascular plants[38, 43, 44] and in previous studies on mosses (*Hyophila involuta*:[6]; *Marchantia*: Shimakawa et al.[14]; *Conocephalum conicum*:[13]). More complex fitting curves have been used to characterise NPQ such as logistic and Hill curves (vascular plant *Arabidopsis thaliana* and diatom *Nitzchia palea*:[41], however, the high variance of NPQ data might not justify more complex fitting models. It is prudent not to over-interpret NPQ.

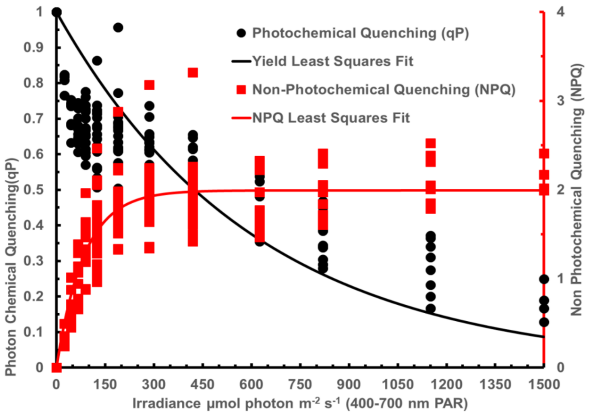

Figure 2. Photochemical quenching (qP) and Non-Photochemical Quenching (NPQ) of *Conocephalum conicum* plotted against irradiance in an XYY format. qP was calculated for the 10:30 h rapid light curves on presented in **Figure 3**. The tabulated data fits a simple exponential decay curve with a zero value of unity. NPQ½ point irradiance, 424 ± 53.8 μmol photon m^{-2} s^{-1}, r = 0.818, n = 20,180. Non-photochemical quenching (NPQ) was calculated from the rapid Light curve data used in **Figure 3**. NPQ_{max} = 1.995 ± 0.0732, $NPQ_{½\ point\ irradiance}$ 58.9 ± 8.11 μmol photon m^{-2} s^{-1}, r = 0.9026, n = 20, 180.

2.8. Estimates of Irradiance Under Full Sunlight and Shaded Conditions

The SMARTS algorithm and software were used to estimate representative daily irradiance in Hat Yai (Thailand) and Sydney, NSW, Australia[45, 46]. Times are Solar Time. This approach was recently used for modelling pho-

tosynthesis vs. field irradiance in an orchid [44], a littoral herb [47] and the moss *Hypophila involuta* [6]. The irradiance in the greenhouse at Sydney University was about 1/3 that of outdoors (≈600–700 μmol photons m^{-2} s^{-1} PAR), similar values were found in the greenhouse at PSU-Hat Yai in Thailand (400–700 nm quantum light meter MQ-200, Apogee Instruments, Logan, UT, USA).

2.9. Desiccation

Blue bead silica gel was used to desiccate *Conocephalum conicum* (Silica Gel Australia, Desicco Pty Ltd., Chatswood NSW 2067, Australia) as described by Marschall and Beckett [17]. Approximately 50 g of dry (blue) gel beads were place in a 125 ml glass bottle and gauze placed on top of it to separate it from the liverwort samples. The bottle was sealed and the liverwort left to dry out over 24 h in the culture room in the light. Plants were rehydrated with tapwater that had been aerated overnight. The plants were mounted on moistened gauze in sealed bottles in the culture room for the recovery experiments. Marschall and Beckett [17] used PAM fluorometry criteria to assess desiccation tolerance in the liverwort, *Dumorteira hirsute* but only described their results in qualitative terms.

2.10. Carbonate System

For the experiments investigating the effects of CO_2/HCO_3^- availability photosynthetic electron transport was measured at a range of pH following a similar protocol used for the moss *Hyophila involuta* [6]. A range of buffered artificial media were prepared by adding 20 mol m^{-3} NaH_2PO_4 adjusted with NaOH (pH 5, 6, 7, 7.5, 8, 9 and 10) to the pondwater culture medium (above). The equations of Vollenweider [48] and Golterman et al. [49] and the pK1 and pK2 values from Millero [50] were used to calculate the amounts of CO_2, HCO_3^- and CO_3^{2-} present for a given pH.

2.11. Oxygen Electrode Experiments

A Rank Brothers Oxygen Electrode (Rank Bros Ltd., Cambridge, CB25 9DA) was used to measure respiration of *Conocephalum conicum* in water. For 100% air saturation a small volume (100 μL) of water was placed in the chamber to prevent the Teflon membrane from drying out and a stirrer flea was used to circulate water for the air-saturation determination. The volume of the electrode chamber was measured experimentally as 3.12 mL. 0.5% Sodium dithionite was used as zero (methylene blue indicator) and O_2 saturation in water in air was from the tables of Garcia and Gordon [51]. Incubations were run for about 1 h (3600 s) at 25 °C. Respiration of the liverwort was measured in artificial pondwater described above. Oxygen fluxes were calculated as mol O_2 s^{-1} and Chl *a* assays were used to convert mol O_2 g^{-1} m^{-2} s^{-1} to mol O_2 g^{-1} Chl *a* s^{-1}. Rank-type O_2-electrodes have very poor optical geometry and so although excellent for respiration measurements are rather unsatisfactory for developing light curves.

2.12. Statistics

Zar [52] was used as the standard statistical reference text. Where two replication numbers are quoted for n (n = a, b) that means (a) separate experiments with (b) total number of data points. All data are quoted as means ±95% confidence limits. The Waiting-in-Line models for fitting rapid light curves were fitted using least squares fitting routines with asymptotic errors calculated by matrix inversion [6]. Upgraded versions are available upon request.

3. Results

Figure 3 shows Yield vs. Irradiance and ETR vs. Irradiance expressed on a Chl *a* basis in a XYY format. Yield vs. Irradiance was calculated for the 10:30 h rapid light curves on the *Conocephalum conicum* population kept in the Biological Sciences greenhouse at PSU-Hat Yai in Thailand. The curve can be fitted to a simple exponential decay curve. Five irradiance ranges were used in 9 increments. $Y_{max} \approx 0.629 \pm 0.033$, irradiance ½ point for Yield ≈ 231 ± 29.3 μmol photon m^{-2} s^{-1}, r = 0.8707, n = 20, 180. The photosynthetic electron transport rate (ETR) can be modelled using the Waiting-in-Line equation. ETR based upon the Yield at each irradiance, the irradiance and the Absorptance (Abt_{465nm}) in blue light were initially expressed on the basis of the projected surface area of the thallus. $E_{opt} \approx 910 \pm 47.5$ μmol photon m^{-2} s^{-1}, $ETR_{max} \approx 64.1 \pm 1.67$ μmol e^- m^{-2} s^{-1}, photosynthetic efficiency (Alpha, α0) ≈ 0.192 ± 0.011 e^- $photon^{-1}$. **Figure 3** shows Rapid light curves on *Conocephalum conicum* of ETR vs. irradiance from the yield data calculated on a Chl

a basis. Chl *a* content of *Conocephalum conicum* was ≈241 ± 16.34 mg Chl *a* m^{-2}. The change in scaling of ETR does not affect the optimum irradiance E_{opt} ≈ 911 ± 47.5 µmol photon m^{-2} s^{-1}, ETR_{max} ≈ 266 ± 6.91 µmol e^- g^{-1} Chl *a* s^{-1}), photosynthetic efficiency (Alpha, α0) ≈ 0.794 ± 0.046 e^- $photon^{-1}$ g^{-1} Chl *a*, r = 0.9782, n = 20, 180.

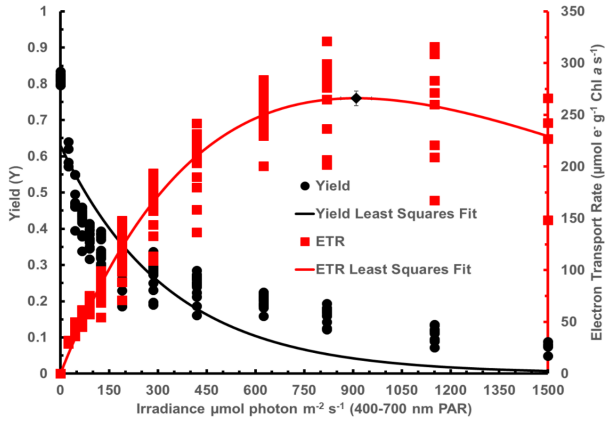

Figure 3. Yield vs. Irradiance and ETR vs. Irradiance presented in XYY format. Yield vs. Irradiance calculated for the 10:30 h rapid light curves on *Conocephalum conicum*. Five irradiance ranges were used in 9 increments. Y_{max} ≈ 0.629 ± 0.033, irradiance ½ point for Yield ≈ 231 ± 29.3 µmol photon m^{-2} s^{-1}, r = 0.8272, n = 20, 180. ETR vs. irradiance was calculated from the Yield data on a Chl *a* basis. Chl *a* content of *Conocephalum conicum* was ≈ 241 ± 16.34 mg Chl *a* m^{-2}. E_{opt} ≈ 911 ± 47.5 µmol photon m^{-2} s^{-1}, ETR_{max} ≈ 266 ± 6.91 µmol e^- g^{-1} Chl *a* s^{-1}, photosynthetic efficiency (Alpha, α0) ≈ 0.794 ± 0.046 e^- $photon^{-1}$ g^{-1} Chl *a*, r = 0.9782, n = 20, 180.

Figure 2 shows Photochemical Quenching (qP) calculated for the rapid light curves on *Conocephalum conicum* presented in **Figure 3**. The tabulated data fits a simple exponential decay curve with a zero value of unity. NPQ ½ point irradiance = 424 ± 53.8 µmol photon m^{-2} s^{-1}, r = 0.818. **Figure 2** also shows Non-Photochemical Quenching (NPQ) calculated for the 10:30 h rapid light curves on *Conocephalum conicum* presented in **Figure 2**. NPQ_{max} = 1.995 ± 0.0732 and NPQ ½ point irradiance was ≈58.9 ± 8.11 µmol photon m^{-2} s^{-1}. Note that the ½ point irradiances for Yield (**Figure 3**), and for qP and NPQ (**Figure 2**) were not similar.

Diurnal effects are commonly found in photosynthetic responses in plants. **Figure 4** shows the diurnality of Yield in *Conocephalum conicum* based on rapid light curves as described in **Figure 3** performed at 90 min intervals over a solar day. The rapid light curve protocol used a nominal zero and range of 8 irradiances from 90 to 1150 µmol photon m^{-2} s^{-1} and the curves were performed in 8 replicates. There was little difference in Maximum Yield (Y_{max}) over the course of the day (overall mean Y_{max} = 0.6385 ± 0.0220, n = 9,81). The half point of the decay of Yield with increasing irradiance ($E_{½pointYield}$) changed during the course of daylight. There was a morning and midday maximum followed by significantly lower half-points in the afternoon. **Figure 5** shows that as a consequence, there was a significant diurnality of photosynthesis in *Conocephalum conicum* based on rapid light curves as described in **Figure 3**. These curves were performed on a liverwort population maintained in a greenhouse at PSU-Hat Yai in Thailand because large amounts of material were available at Hat Yai but only limited amounts of material were available at Sydney University, Australia. Optimum irradiance (E_{opt}) and maximum Electron Transport Rates (ETR_{max}) are based on rapid light curves using 8 replicates at 90 min intervals starting at 6:00 Solar Time. Optimum irradiance (E_{opt}) was considerably higher (≈1000 µmol photon m^{-2} s^{-1}) which was about twice as high as for the Sydney University liverwort population (**Figure 3**). Diurnality occurs in both E_{opt} and ETR_{max} but is more pronounced in the case of ETR. E_{opt} was found to be higher from Solar Time dawn to about midday than in the afternoon. ETR_{max} was low at Solar Time dawn (despite having an E_{opt} similar to the plants measured in the morning phase) but rapidly increased as the morning progressed reaching a maximum from about 10:30 to midday. In the afternoon there was a significant drop in ETR_{max} and so photosynthesis was significantly depressed in the afternoon.

The respiration rate of *Conocephalum conicum* was measured using standard oxygen electrode techniques. One h incubations (3600 s) were used. The respiration rate of the liverwort was found to be 2.23 ± 0.704 µmol O_2 g^{-1} Chl *a* s^{-1} (n = 8). Combined with the estimates of gross photosynthesis (Pg) from the PAM data it was possible to estimate net photosynthesis (Pn).

Figure 6 shows the estimated Pg of *Conocephalum conicum* using E_{opt} and ETR_{max} data from **Figure 5** and irradiance over the course of a day (Solar Time) at Hat Yai, Thailand for 15 November 2023 calculated using the Waiting-in-Line Equation. The E_{opt} and ETR_{max} data from **Figure 5** were fitted to a 6th order polynomial to calculate E_{opt} and ETR_{max} at 15 min intervals from 6:00 solar time to 18:00 solar time. Irradiance was calculated using the SMARTS software. Pg was calculated as µmol O_2 g^{-1} Chl *a* s^{-1} ($4e^-$

≡ $1O_2$). The difference between Bangkok Standard Time (GMT + 7h) and local solar time (Hat Yai, Thailand: (7°1′ N, 100°28′ E) was calculated using an Equation of Time calculator and the latitude for 15 November 2023. *Conocephalum conicum* would have experienced significant photoinhibition during the middle of the day because in Hat Yai the irradiance reached 1965 µmol m^{-2} s^{-1} with early morning and late afternoon photosynthetic maxima at about 8:00 and 16:00h. Due to the change in the E_{opt} and ETR_{max} in the afternoon (**Figure 5**) there was a minimum at about 14:00 to 15:00. In the greenhouse, where the irradiance was about 1/3 of outdoors, the liverwort would have experienced near-optimal irradiance for much of the day which would have minimised bleaching and photoinhibition and so overall daily rates of photosynthesis would be similar to full sunlight. The respiratory rate of the liverwort was measured and is shown on **Figure 6** as mean ±95% confidence limits. The respiratory rate was quite low compared to the photosynthetic capacity of the liverwort and so net photosynthesis would have been positive even at very low irradiances. Löbs et al.[1] in their study of epiphytic liverworts in an Amazonian rainforest were concerned about night-time respiration of the liverworts but did not measure their respiratory rate experimentally. The very low respiratory rate of *Conocephalum conicum* found in this study shows that total daily night & day respiration was very small compared to photosynthesis. The exceptionally low respiration rate and hence high Pg/R ratio might be a significant survival strategy of *Conocephalum conicum*. The low respiration rate found in the present study does not agree with the generalisation that liverworts have high respiration rates[3] but does agree with the findings of Wang et al.[53].

Eight pieces of liverwort were prepared for a desiccation experiment using material brought to PSU-Phuket from PSU-Hat Yai. Control measurements were first made of the material using the PAM machine. The control Y_{max} was 0.7315 ± 0.0624 and the irradiance ½ point was 99 ± 15.4 µmol photon m^{-2} s^{-1}, r = 0.9347; the E_{opt} was 718 ± 126 µmol photon m^{-2} s^{-1} and ETR_{max} = 288 ± 13.7 µmol photon m^{-2} s^{-1}, r = 0.8001; NPQ_{max} = 1.597 ± 0.062, irradiance ½ point was 103 ± 15.4 µmol photon m^{-2} s^{-1}, r = 0.9572. After dehydration for 24 h, the liverworts were rehydrated with 1 ml of tapwater for 24 h in sealed tubes and photosynthetic activity measured using PAM fluorometry: no detectable Yield or ETR was measureable. This indicated no short term or homiochlorophyllous recovery. Plants were then left a further 3 days in changed tapwater and remeasured. There was no apparent longer term or poikilochlorophyllous recovery even after 3 days' rehydration.

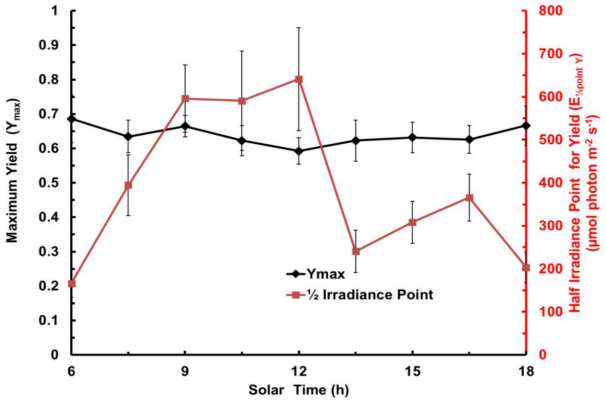

Figure 4. Diurnality of Yield in *Conocephalum conicum* based on rapid light curves as described in **Figure 3** performed at 90 min intervals over a solar day. The rapid light curve protocol used a range of 8 irradiances from 90 to 1150 µmol photon m^{-2} s^{-1} and were performed in 8 replicates. The curves were performed on a liverwort population maintained in a greenhouse at PSU-Hat Yai in Thailand. There was little difference in Maximum Yield (Y_{max}) over the course of the day (overall mean Y_{max} = 0.6385 ± 0.0220, n = 9, 81). The half point of the decay of Yield with increasing irradiance (E½ point Yield) changes during the course of daylight.

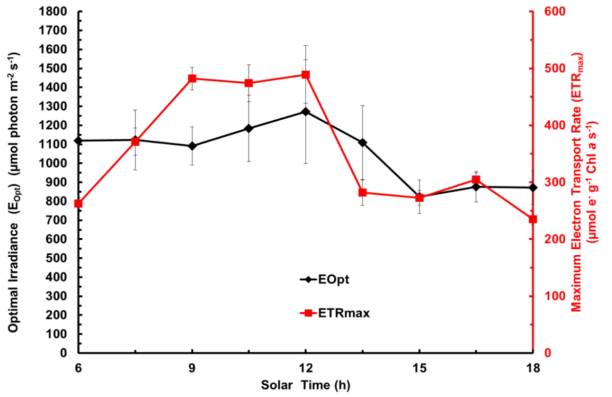

Figure 5. Diurnality of photosynthesis in *Conocephalum conicum* based on rapid light curves as described in **Figure 3** performed at 90 min intervals over a solar day. Optimum irradiance (E_{opt}) and maximum Electron Transport Rates (ETR_{max}) are based on rapid light curves using 8 replicates. As a consequence of the diurnality of the kinetics of the decay of Yield vs. irradiance shown in **Figure 4** diurnality occurs in both E_{opt} and ETR but more pronounced in the case of ETR_{max}. Photosynthesis was significantly depressed in the afternoon.

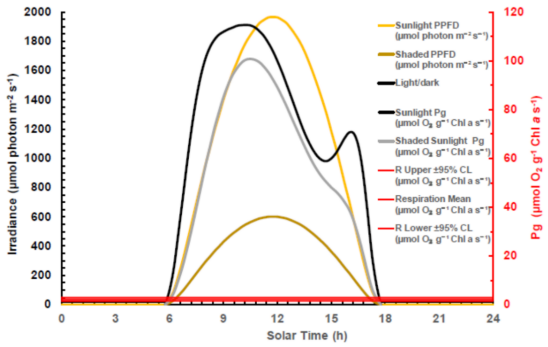

Figure 6. Estimated Gross Photosynthesis (Pg) of *Conocephalum conicum* using E_{opt} and ETR_{max} data from **Figure 5** and irradiance over the course of a day at PSU-Hat Yai on 13 to 16 November 2023 calculated using the Waiting-in-Line Equation. Pg calculated as $4e^- \equiv 1O_2$. The respiratory rate of the liverwort was measured using an oxygen electrode.

The pH experiments were run on material grown in a culture room for several weeks rather than in the greenhouse. The free CO_2 in solution calculated for total inorganic carbon of 0.5 mol m^{-3} was (in mmol m^{-3}): pH 5, $[CO_2]$ = 476; pH 6.02, $[CO_2]$ = 326; pH 7.00, $[CO_2]$ = 81.9; pH 7.52, $[CO_2]$ = 27.9; pH 8.03, $[CO_2]$ = 8.9; pH 9, $[CO_2]$ = 0.09; pH 10, $[CO_2]$ = 0.01. The pond water medium would be in approximate equilibrium with atmospheric CO_2 (atmospheric 427 ppm, 14.3 mmol m^{-3} CO_2) at pH 7.83. **Table 1** shows the results of rapid light curves conducted on *Conocephalum conicum* incubated for 2 h in a range of buffered pondwater from pH 5 to pH 10 in a culture room. Overall photosynthesis was conspicuously lower than found in the material grown in the greenhouse. Each experimental rapid light curve was repeated 8 times for each pH. ANOVA and the Student-Newman-Kuels test were used to calculate minimal significant ($p < 0.05$) differences (Zar 2014). Y_{max} was approximately constant (≈0.7) over the pH range although the rate of decay of Y_{max} as irradiance increased varied. The half-point irradiance for Yield was very low for plants incubated at pH 5. Optimum irradiance (E_{opt}) was very low at pH 5 but at higher pH was ≈100 µmol photon m^{-2} s^{-1}. ETR_{max} was very low at pH 5, reached a maximum at pH 6 but was relatively constant from pH 7 to 10 (≈40 µmol e^- g^{-1} Chl *a* s^{-1}). At pH 9 and 10 almost no free CO_2 would have been available and so the ETR results are consistent with *Conocephalum conicum* being able to use HCO_3^- as a carbon source. Photosynthetic efficiency (Alpha (α0) was remarkably constant and did not seem to be affected by pH ($p = 0.1910$, not significant, Overall α0 = 1.13 ± 0.0542 e^- g^{-1} Chl *a* $photon^{-1}$). Photochemical quenching (qP) followed at simple exponential decay function at all pH. qP was lowest at pH 5 and pH 10 but from pH 6 to 9 the qP ½ point was about 50 µmol photon m^{-2} s^{-1}. Maximum Non Photochemical Quenching (NPQ_{max}) was very low compared to *Conocephalum conicum* grown in the greenhouse (NPQ_{max} ≈ 0.4) and was very low at pH 10. The kinetics of the NPQ could not be resolved very accurately. **Table 1** shows that the photosynthetic characteristics of the material at pH 7, 7.5 and 8 were not greatly different and so the data could be combined into a single data set.

Table 1. Photosynthetic Parameters on Conocephalum conicum incubated in various pH.

	pH 5	**pH 6.02**	**pH 7**	**pH 7.52**	**pH 8.03**	**pH 9**	**pH 10**	**Tukey Test MSD**
Y_{max}	0.751 ± 0.025	0.710 ± 0.038	0.681 ± 0.044	0.735 ± 0.035	0.732 ± 0.028	0.690 ± 0.032	0.628 ± 0.043	0.0589
$Y_{½\ point}$ µmol photon m^{-2} s^{-1}	29.1 ± 2.01	65.2 ± 8.31	41.1 ± 5.79	50.6 ± 5.43	46.7 ± 3.52	54.6 ± 5.88	42.6 ± 6.36	9.30
E_{opt} µmol photon m^{-2} s^{-1}	51.7 ± 6.85	129 ± 15.5	85.1 ± 15.1	95.6 ± 11.3	85.3 ± 9.85	104 ± 12.4	83.1 ± 16.1	21.1
ETR_{max} µmol e^- g^{-1} Chl *a* s^{-1}	23.7 ± 2.20	54.4 ± 4.16	32.4 ± 3.81	42.3 ± 3.31	35.9 ± 2.75	43.6 ± 3.41	30.6 ± 3.93	5.64
Alpha (α0) e^- g^{-1} Chl *a* $photon^{-1}$	1.25 ± 0.202	1.15 ± 0.164	1.03 ± 0.220	1.20 ± 0.171	1.14 ± 0.158	1.14 ± 0.163	1.00 ± 0.232	0.312
$qP_{½\ point}$ µmol photon m^{-2} s^{-1}	30.9 ± 2.54	63.5 ± 7.75	39.5 ± 4.74	51.1 ± 5.36	43.7 ± 3.73	54.4 ± 5.75	39.0 ± 9.71	9.48
NPQ_{max}	0.314 ± 0.036	0.382 ± 0.028	0.361 ± 0.099	0.380 ± 0.046	0.406 ± 0.035	0.374 ± 0.022	0.074 ± 0.054	0.0804
$NPQ_{½\ point}$ µmol photon m^{-2} s^{-1}	19.3 ± 7.23	37.1 ± 7.85	53.6 ± 32.7	37.1 ± 12.4	29.2 ± 7.64	23.8 ± 4.61	130 ± 150	91.1

Figure 7 shows the combined Yield and ETR data (pH 7, 7.5 & 8) for the culture room material and the curve fitting for a simple exponential decay curve for the yield data and the Waiting-in-Line model for the ETR data. Comparison with the greenhouse-grown material (**Figure 3**) shows that the material acclimated to the culture room with its very low irradiance had a different Yield curve and E_{opt} and ETR_{max}: $Y_{max} \approx 0.715$, irradiance ½ point for Yield ≈ 44.8 µmol photon m^{-2} s^{-1}. ETR vs. irradiance was calculated from the Yield data on a Chl *a* basis: $E_{opt} \approx 89.1$ µmol photon m^{-2} s^{-1}, $ETR_{max} \approx 36.9$ (µmol e^- g^{-1} Chl *a* s^{-1}), photosynthetic efficiency (Alpha, α0) ≈ 1.125 (e^- photon^{-1} g^{-1} Chl *a*).

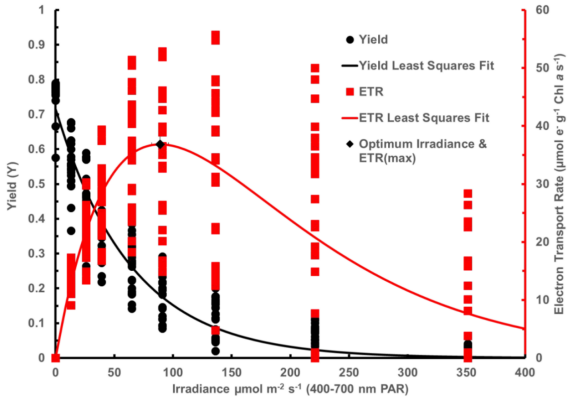

Figure 7. Yield and ETR curves for the culture-room grown material. The rapid light curve characteristics are very different to those of the greenhouse-grown material (**Figure 3**). $Y_{max} \approx 0.715$, irradiance ½ point for Yield ≈ 44.8 µmol photon m^{-2} s^{-1}. ETR vs. irradiance was calculated from the Yield data on a Chl *a* basis: E_{opt} ≈ 89.1 µmol photon m^{-2} s^{-1}, $ETR_{max} \approx 36.9$ (µmol e^- g^{-1} Chl *a* s^{-1}), photosynthetic efficiency (Alpha, α0) ≈ 1.125 (e^- photon^{-1} g^{-1} Chl *a*).

4. Discussion

The results of the rapid light curves show that the Waiting-in-Line model fits the data quite well (**Figure 3**). The Waiting-in-Line model is a very good fit to actual photosynthesis vs. irradiance curves and in particular models photoinhibition using a minimalist model compared to the simple exponential saturation model which needs to be revised to account for photoinhibition[6, 13, 23, 39, 40, 44, 53, 54]. Plants growing in high light conditions generally have very high optimum irradiances ($E_{opt} \approx$ 800 to 1200 µmol photon m^{-2} s^{-1}, or about ½ full sunlight), for example pineapple[55], water lilies[56], crustose lichens on palm trees[9] and epiphytic ferns on palm trees[43]. Plants growing in a sunfleck environment often have optimal irradiances higher than might be expected based on mean irradiances, apparently giving them the ability to cope with intermittent high irradiances (this study on *Conocephalum conicum;* the moss *Hyophila involuta*:[6] and the terrestrial alga *Trentepohlia* sp.:[57]). Low optimum irradiances are generally found in organisms living in consistently low irradiances (the endolithic alga *Chlorococcum*:[58]. *Conocephalum conicum* grown in a culture room with a very low irradiance for the pH experiments in the present study (**Table 1**) had very low optimum irradiance (E_{opt}) compared to those grown in the green houses (**Figures 3**, **4**, **5** and **6**) and **Supplementary Figures S1 and S2**. The very different rapid light curves found in the three different light regimes show that *Conocephalum conicum* is capable of acclimation to a wide range of light regimes: careful attention needs to be paid to the conditions under which the material used in a study was grown. It can be a sun or shade plant depending on how it is grown (**Figure 3** vs. **Figure 7**)[8].

Figure 3 shows that a simple exponential decay model is suitable for modelling Yield and the Waiting-in-Line model can be used to model ETR of *Conocephalum conicum*. Hao and Chu[12] measured Yield in a variety of liverworts using PAM technology but did not perform rapid light curves that would have given much more information on photosynthesis of the plants. As in the case of the moss *Hyophila involuta*[6] we found that *Conocephalum conicum* to be optically black at 445 nm ($Abt_{445nm} \approx 0.98$, hence ETR ≈ 1.16 × rETR): the default value of 0.84 (AbtF) used in many plant studies is thus misleading. As pointed out by Ritchie and Runcie[9], the commonly used default absorptance value of 0.84 is actually derived from studies using white light not monochromatic blue or red light and so for blue-diode based PAM fluorometry can be very misleading. The PAM data shown in **Figure 3** is based on routine measurements made at 10:30 (Solar Time) based on the previous experience with the moss *Hyophila involuta* where it was found that there was a strong diurnal effect on photosynthesis[6]. The measurement of rapid light curves over the course of the day confirmed that there was a strong diurnal effect on photosynthesis of *Conocephalum conicum* (see below). Diurnality of photosynthetic electron transport is also found in a variety of aquatic plants using PAM methods[19].

For most physiological purposes ETR on a Chl *a* basis

is usually quoted (**Figure 3**) but there are situations where photosynthesis on a surface area basis is useful, particularly in primary productivity studies and so are quoted in the results used to prepare **Figure 3**[3, 53, 59]. Unfortunately, measurements based on biomass such as the modelling used by Nikolić et al.[59] are difficult to convert into surface area or g^{-1} Chl *a* bases. Furthermore, their model used a simple exponential saturation model for photosynthesis vs. irradiance with an unrealistically low saturation point of about 200 µmol photon m^{-2} s^{-1}, well below that found in the present study or in other studies[53]. Models are only as good as their data input. The ETR_{max} on a surface area basis was estimated to be ≈64.1 ± 1.67 µmol e^- m^{-2} s^{-1}: since an ETR of 4 µmol e^- m^{-2} s^{-1} is *approximately* equal to a gross photosynthetic rate (Pg) of 1 µmol O_2 m^{-2} s^{-1}, then the ETR_{max} found in the present study for *Conocephalum conicum* was Pg_{max} ≈ 16 ± 0.42 µmol O_2 m^{-2} s^{-1} or in terms of theoretical maximum carbon fixation Pg_{max} ≈ 192 ± 5.01 µg C m^{-2} s^{-1}. These estimates are much higher than averages for liverworts presented by Perera-Castro et al.[3].

Measurements of Photochemical Quenching (qP) and Non-Photochemical Quenching found in the present study (**Figure 2**) were comparable to those found in *Marchantia* material[14, 15]. **Figure 2** shows non-photochemical quenching (NPQ) of *Conocephalum conicum* derived from the same rapid light curves used to prepare **Figure 3**. The NPQ data for *Conocephalum conicum* had a maximum (NPQ_{max}) of about 2 and fitted a simple exponential saturation curve quite well, which is entirely consistent with typical values found in vascular plants[12, 60] on a variety of mosses, in our previous study on the moss *Hyophila involuta*[6] and in *Riella helicophylla*[11], but is much higher than typically found in algae (usually « 0.5:[9, 39, 56, 57]). The ½ irradiance points for Yield, qP and NPQ are not similar (**Figures 2** and **3**) but are significantly different. The three different ½ points reflect different aspects of the photosynthetic physiology of the liverwort.

The shape of the ETR vs. Irradiance curves found for *Conocephalum conicum* in the present study and for the moss *Hyophila involuta*[6] were typical Waiting- in-Line curves showing an optimum irradiance and photoinhibition at higher irradiances. However, the two populations of *Conocephalum conicum* used in the present study in Thailand (Hat Yai) had significant differences in optimal irradiance (**Figures 3**, **4** and **5**) in comparison to the Sydney University population (**Supplementary Figures S1 and S2**). The Sydney University population had a significantly lower optimum irradiance and ETR (E_{opt} ≈ 520 ± 68 µmol photon m^{-2} s^{-1}, ETR_{max} ≈ 27.8 ± 1.74 µmol e^- m^{-2} s^{-1}; ETR_{max} ≈ 115 ± 7.2 µmol e^- g^{-1} Chl *a* s^{-1} even though the midday irradiances inside the respective greenhouses were comparable. NPQ was very similar in both populations. **Figure 7** shows that the light curve characteristics of the Hat Yai plants were quite different when acclimated to the very low irradiance in a culture room situation.

Proctor and Bates[40] working on a wide variety of Bryophyte species from various British habitats found a very wide range of differently-shaped ETR vs. Irradiance curves. Some showed a simple exponential saturation model with no apparent photoinhibition whereas in others photoinhibition was apparent at higher irradiances. Often the simple exponential saturation model is used for modelling photosynthesis in bryophytes[53] without checking for significant photoinhibition. It was expected in the present study that *Conocephalum conicum* growing in a shaded greenhouse would be a shade plant with an optimum irradiance of about 300 µmol photon m^{-2} s^{-1} or less[8], but that expectation was contrary to other studies on the organism growing in field situations[13, 14]. **Figure 3** shows that greenhouse-grown *Conocephalum conicum* had an optimum irradiance of about 1000 µmol photon m^{-2} s^{-1} which was the range of "sun plant responses" with very high optimum irradiances and little or no apparent photoinhibition except at very high irradiances. On the other hand, the Hat Yah material when acclimated to a culture room irradiance regime (**Table 1** and **Figure 7**) had optimum irradiances of only about 100 µmol photon m^{-2} s^{-1}. The C3 littoral sun plant *Launaea sarmentosa*[35] and very highly irradiance tolerant species such as Water Lilies, Pineapples, Oil Palm have optimum irradiances of about 1000 µmol photon m^{-2} s^{-1} which is about ½ tropical sunlight[13, 54–56]. Chen et al.[13] had also found that field-grown *Conocephalum conicum* was tolerant of high irradiances and was not a shade plant. Shimakawa et al.[14] also found very high optimum irradiances in their field-grown *Marchantia* material but the range of irradiances they used did not extend into the range where photoinhibition would have been noticeable. Wang et al.[53] based on many species of bryophytes from a North American forest situation found optimal irradiances of about 400 µmol photon m^{-2}

s^{-1} but did not report photoinhibition. Choice of the range of irradiances used can have critical effects on what model seems to best fit the data.

Observations of the diurnal effects on Yield are interesting (**Figure 4**). Diurnal effects on Yield and other PAM parameters are not often reported but it would be expected that the fluorescence of photosynthetic cells would vary during the day if looked for[61]. There was little (if any) diurnal effect on Y_{max} but the shape of the Yield vs. Irradiance curves changed significantly over the course of the day. Combined with the estimates of the Optimum irradiance (E_{opt}) and ETR_{max} in **Figure 5** and the Waiting-in-Line equation it was possible to make an estimate of the daily carbon fixation of a mat of *Conocephalum conicum*[6, 47, 56]. **Figure 6** shows estimated gross photosynthesis of *Conocephalum conicum* during the course of a daily cycle under full sunlight condition (Hat Yai, Thailand) and under shaded conditions. The diurnal curve for this liverwort does not show strong midday inhibition as found previously in many plants because E_{opt} and ETR_{max} changed during the course of the day (**Figure 5**) (*Ananas comosus*:[55]; *Nymphaea caerulea*:[56]; *Davallia angustata*:[43]; *Trentepohlia* sp:[57]; *Launaea sarmentosa*:[47]). Substantial midday inhibition was found in the moss *Hyophila involuta*[6]. Full sunlight (1965 µmol m^{-2} s^{-1}) in this tropical moss was sufficient to result in significant (≈50%) photoinhibition during the middle of the day with conspicuous early morning (8:00) and late afternoon (16:00) peaks in photosynthesis. Under the shaded conditions of the greenhouse the liverwort would have been able to achieve high rates photosynthesis for much of the day with little photoinhibition. Similar results were found for the *Vanda sp*. orchid[44] and a littoral herb *Launaea sarmentosa*[47]. Integrating Pg over the course of the day Pg is about 3.30 mol C g^{-1} Chl *a* d^{-1} or 39.6 gC g^{-1} Chl *a* d^{-1} under full sunlight and about 2.47 mol C g^{-1} Chl *a* d^{-1} or 29.6 gC g^{-1} Chl *a* d^{-1} in the shaded greenhouse. Primary production expressed on a surface area basis is often of importance in ecological studies[3]. On a projected surface area basis daily Pg is about 0.79 mol C m^{-2} d^{-1} or 9.5 gC m^{-2} d^{-1} under full sunlight or about 0.60 mol C m^{-2} d^{-1} or 7.14 gC m^{-2} d^{-1} in the shaded greenhouse. The relative error of these estimates of daily Pg would be about ±13% but are high productivity estimates. The total daily Pg of *Conocephalum conicum* is almost as high under a greenhouse shaded condition as in full sunlight (**Figure 6**). Estimates of the net assimilation rate in the present study are higher than those reported by Perera-Castro et al.[3]: the estimates of Pg are higher and the respiration rate of *Conocephalum conicum* was found to be very low, contrary to the generalisations of Perera-Castro et al.[3].

Conocephalum conicum was growing in a shaded environment and so it was naturally expected that the plant would have very low saturating irradiances. However, **Figures 3**, **4**, **5** and **6** show that the optimum irradiance was about 1000 µmol photon m^{-2} s^{-1} PPFD or about ½ of full tropical sunlight for the Hat Yai, Thailand population growing in a greenhouse. This result is in agreement with Shimakawa et al.[14] working on *Marchantia sp.* and Chen et al.[13] (*Conocephalum conicum*). The saturating irradiances found in the present study were those that would be expected of a sun-type plant not a shade plant. Naturally shaded habitats, unlike shaded greenhouses, are likely to intermittently and suddenly exposed to sunlight-level light intensities by sunflecks even though *median* irradiances may be quite low[6, 57]. Even in Antarctica, mosses and liverworts can be intermittently exposed to irradiances up to in excess of 2000 µmol photon m^{-2} s^{-1}[16]. On the other hand, Waite and Sack[62] found saturating irradiances of only about 100 to 200 µmol photon m^{-2} s^{-1} in the maritime tropical forest mosses they studied in Hawaii but do not appear to have suspected diurnal effects because they do not specify the solar times at which they did their field measurements. Wang et al.[53] found an optimum irradiance of about 400 µmol photon m^{-2} s^{-1} in forest bryophytes but did not report diurnal effects. The high optimum irradiance (E_{opt}) of *Conocephalum conicum* resulted in high photosynthetic efficiencies at relatively high irradiance allowing it to more fully exploit transient sunflecks and early morning sunshine where it was being grown (**Figures 4**, **5** and **6**). A high optimum irradiance found in both populations of *Conocephalum conicum* used in this study (**Figures 3**, **4**, **5** and **6**, **Supplementary Material** for Sydney, Australia) has some advantages in a *sunfleck environment* where many bryophytes live[6]. The form of the Waiting-in-line equation ($y = x \times e^{-x}$) predicts values greater than 50% of the maximum at x = 0.23 and 2.67, hence if the E_{opt} of a plant is 520 µmol photon m^{-2} s^{-1} as found in the Sydney, Australia part of the study, the model predicts >50% of photosynthetic maxima in the irradiance range from 120 to 1388

μmol photon m^{-2} s^{-1}. For the Hat Yai population with an E_{opt} in the morning of about 1000 μmol photon m^{-2} s^{-1}, the liverworts would be able to perform photosynthesis at 50% of the maximum rate at 230 μmol photon m^{-2} s^{-1} and even in full equatorial sunlight (≈2200 μmol photon m^{-2} s^{-1}) ETR would be 66% of ETR_{max}. The Hat Yai *Conocephalum conicum* liverwort population showed a significant difference in both E_{opt} and ETR_{max} in the morning and afternoon with higher E_{opt} and ETR_{max} in the morning compared to the afternoon (**Figures 5** and **6**). However, the diurnal variation in ETR_{max} is greater than for E_{opt} and so the two photosynthetic parameters are not directly proportional to one another over the course of the day (**Figure 5**). This is particularly apparent for the dawn (6:00) rapid light curves where it was found that E_{opt} was as high as found during the other morning determinations, but ETR_{max} was low. The resultant diurnal curve for photosynthesis (**Figure 6**) is conspicuously asymmetrical. The respiratory rate of the liverwort was measured using standard oxygen electrode methods and was found to be quite low (≈2 μmol g^{-1} Chl *a* s^{-1}) compared to estimates of Pg (**Figure 6**) and was also low compared to that recently found in a moss (*Hypophila involuta:* [6]). The respiratory rates of *Conocephalum conicum* (**Figure 6**) are exceptionally low: a very low background respiration is an advantage in a marginal habitat cf[3]. Wang et al.[53] also found very low respiratory rates and hence very high Pg/R ratios in their study of forest bryophytes contrary to the conclusions drawn by Perera-Castro et al.[3].

There appears to be a substantial difference in the irradiance physiology of plants exposed to *continuous* low irradiance to those that live in sunfleck environments where the *median* irradiance might be quite low but are intermittently exposed to high irradiances. Thus, light saturation characteristics can be quite different for plants growth in an environment with a low median irradiance but occasionally exposed to sunlight light intensities compared to those grown in a culture room environment with constant but low irradiance (**Table 1** and Koide et al.[15]). Perhaps it is the variability of irradiance rather than irradiance intensity that proves to be fatal. Even *Zea mays*, which is a classic C4 sun plant, has very complex responses to variable irradiance environments simulating a sunfleck environment[63].

Unlike our previous findings on the moss, *Hypophila involuta*[6] at least the strain of *Conocephalum conicum* used in the present study was not desiccation tolerant. Plants were desiccated and rehydrated and photosynthetic electron transport measured after 24 h. There was no apparent fluorescence Yield and zero ETR. After 72 h there was no apparent delayed recovery. The plant was thus neither homiochlorophyllous (rapid desiccation recovery) or poikilochlorophyllous (recovery over several days). Teeri[22] and Vitt et al.[18] noted that members of the order Marchantiales, which includes *Conocephalum conicum* are not generally desiccation tolerant. The Antarctic liverwort *Marchantia berteroana*[16] is an exception in being tolerant of desiccation and predictably enough also freezing but the liverwort, *Dumorteira hirsuta*, studied by Marschall and Beckett[8] showed more limited desiccation tolerance.

The experiment on the effect of pH upon photosynthesis (**Table 1**) is a classic Steeman Nielsen experiment[64] where it is inferred that if an aquatic plant is able to photosynthesise under alkaline conditions where no free CO_2 is available then it is concluded that the plant is able to use HCO_3^- as a carbon source[23, 24, 29, 64]. *Conocephalum conicum* was easily able to photosynthesise under conditions where there would be negligible free CO_2 available (**Table 1**) and so fits the criteria for being able to use bicarbonate as an inorganic carbon source[4, 64]. An incidental outcome of the pH experiment arose from using culture room grown material whereas the rest of the project was done on green-house grown material. The optimum irradiance of the culture-room-grown material was only about 100 μmol photon m^{-2} s^{-1} (about 5% of sunlight) and ETR_{max} was only about 40 μmol g^{-1} Chl *a* s^{-1} (**Table 1**, **Figure 7**): contrast with the greenhouse results (**Figures 3**, **5** and **6**) and the **Supplementary material** from the Sydney University greenhouse. *Conocephalum conicum* can acclimate fixed carbon at very low irradiances such as in a typical algal culture room but with substantial changes in photosynthetic characteristics.

Supplementary Materials

The supporting information can be downloaded at https://journals.bilpubgroup.com/files/Supplementary.docx.

Funding

There was no specific funding for this project but the Faculty of Environment and Technology of Prince of Songkla

University-Phuket and the faculty of Science at Prince of Songkla University Hat Yai provided access to the facilities for the project as part of their policies of promoting environmental programs in Southern Thailand.

Institutional Review Board Statement

There are no ethical issues arising from the material used in the paper. No collection permits were required for the Sydney University or PSU-Hat Yai material used in the project.

Informed Consent Statement

Not applicable.

Data Availability

The datasets generated during and/or analysed during the current study are available from the author on reasonable request. The EXCEL files for the curve-fitting routines are also available upon request.

Acknowledgements

The liverwort material used in this paper were identified and provided for the study by Sahut CHANTANAORRAPINT, PhD, PSU Herbarium, Division of Biological Science, Faculty of Science, Prince of Songkla University in Hat Yai, Songkhla, 90112 Thailand. his interest and expertise were much appreciated.

Conflicts of Interest

The author declares no competing interests in this project. The author declares no conflicts of interest for this paper.

References

[1] Löbs, N., Walter, D., Barbosa, C.G.G., et al., 2020. Microclimatic conditions and water content fluctuations experienced by epiphytic bryophytes in an Amazonian rain forest. Biogeosciences. 17(21), 5399–5416. DOI: https://doi.org/10.5194/bg-17-5399-2020

[2] Lee, G.E., Gradstein, S.R., 2021. Guide to the Genera of Liverworts and Hornworts of Malaysia. Hattori Botanical Laboratory and Kokusai Bunkensha: Tokyo, Japan. 236p.

[3] Perera-Castro, A.V., González-Rodríguez, Á.M., Fernández-Marín, B., 2022. When time is not of the essence: constraints to the carbon balance of bryophytes. Journal of Experimental Botany. 73(13), 4562–4575. DOI: https://doi.org/10.1093/jxb/erac104

[4] Raven, J.A., Colmer, T.D., 2016. Life at the boundary: photosynthesis at the soil–fluid interface. A synthesis focusing on mosses: Table 1. Journal of Experimental Botany. 67(6), 1613–1623. DOI: https://doi.org/10.1093/jxb/erw012

[5] Rout, G.R., Das, A.B., (Eds.), 2013. Molecular Stress Physiology of Plants. Springer India. Springer New Delhi: New Delhi, India. DOI: https://doi.org/10.1007/978-81-322-0807-5

[6] Ritchie, R.J., Sma-Air, S., 2023. Photosynthetic Electron Transport in a Tropical Moss *Hyophila involuta*. The Bryologist. 126(1), 52-68. DOI: https://doi.org/10.1639/0007-2745-126.1.052

[7] Ihle, C., Laasch, H., 1996. Inhibition of Photosystem II by UV-B Radiation and the Conditions for Recovery in the Liverwort Conocephalum conicum Dum. Botanica Acta. 109(3), 199–205. DOI: https://doi.org/10.1111/j.1438-8677.1996.tb00564.x

[8] Marschall, M., Proctor, M.C.F., 2004. Are Bryophytes Shade Plants? Photosynthetic Light Responses and Proportions of Chlorophyll a, Chlorophyll b and Total Carotenoids. Annals of Botany. 94(4), 593–603. DOI: https://doi.org/10.1093/aob/mch178

[9] Ritchie, R.J., 2014. Photosynthesis in an Encrusting Lichen (Dirinaria picta(Sw.) Schaer.ex Clem., Physiaceae) and its Symbiont, Trebouxiasp., Using Pulse Amplitude Modulation Fluorometry. International Journal of Plant Sciences. 175(4), 450–466. DOI: https://doi.org/10.1086/675575

[10] Rao, K.R., Kumar, N.R., Reddy, A.N., 1979. Studies of Photosynthesis in Some Liverworts. The Bryologist. 82(2), 286. DOI: https://doi.org/10.2307/3242088

[11] Conde-Álvarez, R.M., Pérez-Rodríguez, E., Altamirano, M., et al., 2002. Photosynthetic performance and pigment content in the aquatic liverwort Riella helicophylla under natural solar irradiance and solar irradiance without ultraviolet light. Aquatic Botany. 73, 47–61. DOI: https://doi.org/10.1016/S0304-3770(02)00007-4

[12] Hao, J., Chu, L.M., 2021. Short-term detrimental impacts of increasing temperature and photosynthetically active radiation on the ecophysiology of selected bryophytes in Hong Kong, southern China. Global Ecology and Conservation. 31, e01868. DOI: https://doi.org/10.1016/j.gecco.2021.e01868

[13] Chen, C.-I., Lin, K.-H., Huang, M.-Y., et al., 2023. Photo-protection and photo-inhibition during light in-

duction in Barbula indica and Conocephalum conicum under different light gradients. Photosynthesis Research. 159(2–3), 191–202. DOI: https://doi.org/10.1007/s11120-023-01030-0

[14] Shimakawa, G., Ishizaki, K., Tsukamoto, S., et al., 2017. The Liverwort, Marchantia, Drives Alternative Electron Flow Using a Flavodiiron Protein to Protect PSI. Plant Physiology. 173(3), 1636–1647. DOI: https://doi.org/10.1104/pp.16.01038

[15] Koide, E., Suetsugu, N., Iwano, M., et al., 2019. Regulation of Photosynthetic Carbohydrate Metabolism by a Raf-Like Kinase in the Liverwort Marchantia polymorpha. Plant and Cell Physiology. 61(3), 631–643. DOI: https://doi.org/10.1093/pcp/pcz232

[16] Marschall, M., Beckett, R.P., 2005. Photosynthetic responses in the inducible mechanisms of desiccation tolerance of a liverwort and a moss. Acta Biological Szegediensis. 49, 155–156.

[17] Davey, M.C., 1997. Effects of physical factors on photosynthesis by the Antarctic liverwort Marchantia berteroana. Polar Biology. 17(3), 219–227. DOI: https://doi.org/10.1007/s003000050125

[18] Vitt, D.H., Crandall-Stotler, B., Wood, A., 2014. Bryophytes: survival in a dry world through tolerance and avoidance. In: Rajakaruna, N., Boyd, R., Harris, T., (Eds.). Plant ecology and evolution in harsh environments. Nova Science: New York, NY, USA. pp. 267–295.

[19] Chotikarn, P., Pramneechote, P., Sinutok, S., 2022. Photosynthetic Responses of Freshwater Macrophytes to the Daily Light Cycle in Songkhla Lagoon. Plants. 11(21), 2806. DOI: https://doi.org/10.3390/plants11212806

[20] Frangedakis, E., Marron, A.O., Waller, M., et al., 2023. What can hornworts teach us? Frontiers in Plant Science. 14. DOI: https://doi.org/10.3389/fpls.2023.1108027

[21] Frangedakis, E., Shimamura, M., Villarreal, J.C., et al., 2020. The hornworts: morphology, evolution and development. New Phytologist. 229(2), 735–754. DOI: https://doi.org/10.1111/nph.16874

[22] Teeri, J. A., 1981. Stable Carbon Isotope Analysis of Mosses and Lichens Growing in Xeric and Moist Habitats. The Bryologist. 84(1), 82. DOI: https://doi.org/10.2307/3242982

[23] MABERLY, S. C., 1985. PHOTOSYNTHESIS BY FONTINALIS ANTIPYRETICA. New Phytologist. 100(2), 127–140. DOI: https://doi.org/10.1111/j.1469-8137.1985.tb02765.x

[24] PEÑUELAS, J., 1985. HCO_3^- as an Exogenous Carbon Source for Aquatic Bryophytes *Fontinalis antipyretica* and *Fissidens grandifrons*. Journal of Experimental Botany. 36(3), 441–448. DOI: https://doi.org/10.1093/jxb/36.3.441

[25] Smith, E.C., Griffiths, H., 2000. The role of carbonic anhydrase in photosynthesis and the activity of the carbon-concentrating-mechanism in bryophytes of the class Anthocerotae. New Phytologist. 145(1), 29–37. DOI: https://doi.org/10.1046/j.1469-8137.2000.00559.x

[26] Hanson, D., Andrews, T. J., Badger, M.R., 2002. Variability of the pyrenoid-based CO_2 concentrating mechanism in hornworts (Anthocerotophyta). Functional Plant Biology. 29(3), 407. DOI: https://doi.org/10.1071/pp01210

[27] Villarreal, J.C., Renner, S.S., 2012. Hornwort pyrenoids, carbon-concentrating structures, evolved and were lost at least five times during the last 100 million years. Proceedings of the National Academy of Sciences. 109(46), 18873–18878. DOI: https://doi.org/10.1073/pnas.1213498109

[28] Morris, J.L., Puttick, M.N., Clark, J.W., et al., 2018. The timescale of early land plant evolution. Proceedings of the National Academy of Sciences. 115(10). DOI: https://doi.org/10.1073/pnas.1719588115

[29] BAIN, J.T., PROCTOR, M.C.F., 1980. THE REQUIREMENT OF AQUATIC BRYOPHYTES FOR FREE CO_2 AS AN INORGANIC CARBON SOURCE: SOME EXPERIMENTAL EVIDENCE. New Phytologist. 86(4), 393–400. DOI: https://doi.org/10.1111/j.1469-8137.1980.tb01680.x

[30] Adams, D.G., Duggan, P.S., 2008. Cyanobacteria-bryophyte symbioses. Journal of Experimental Botany. 59, 1047–1058. DOI: https://doi.org/10.1093/job/ern005

[31] Glime, J.M., 2022. Bacterial effects on bryophytes. In 'Bryophyte Ecology Chapt. 19-1. Volume 2. Interactions.' Ebook 19-1-1. p. 94. Sponsored by Michigan Technological University and the International Association of Bryologists. Available from: http://digitalcommons.mtu.edu/bryophyte-ecology/ (cited 12 January 2023).

[32] Nichols, H.W., 1973. Growth Media - freshwater. In ' Handbook of Phycological methods: culture methods and growth measurements' (Ed JR Stein) Chapter 1 pp. 7 - 24. Cambridge University Press: Cambridge, UK.

[33] Jeffrey, S.W., Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and phytoplankton. Biochemie und Physiologie der Pflanzen. 167, 191–194. DOI: https://doi.org/10.1016/S0015-3796(17)30778-3

[34] Ritchie, R.J., 2006. Consistent Sets of Spectrophotometric Chlorophyll Equations for Acetone, Methanol and Ethanol Solvents. Photosynthesis Research. 89(1), 27–41. DOI: https://doi.org/10.1007/s11120-006-9065-9

[35] Ritchie, R.J., Sma-Air, S., Phongphattarawat, S., 2021. Using DMSO for chlorophyll spectroscopy. Journal of Applied Phycology. 33(4), 2047–2055. DOI: https://doi.org/10.1007/s10811-021-02438-8

[36] Ritchie, R.J., Runcie, J.W., 2014. A portable reflectance-absorptance-transmittance meter for photosynthetic work on vascular plant leaves. Photosynthetica. 52(4), 614–626. DOI: https://doi.org/10.1007/s11099-014-0069-y

[37] Potvin, C., Lechowicz, M.J., Tardif, S., 1990. The Statistical Analysis of Ecophysiological Response Curves Obtained from Experiments Involving Repeated Measures. Ecology. 71(4), 1389–1400. DOI: https://doi.org/10.2307/1938276

[38] Ralph, P.J., Gademann, R., 2005. Rapid light curves: A powerful tool to assess photosynthetic activity. Aquatic Botany. 82(3), 222–237. DOI: https://doi.org/10.1016/j.aquabot.2005.02.006

[39] Ritchie, R.J., 2008. Fitting light saturation curves measured using modulated fluorometry. Photosynthesis Research. 96(3), 201–215. DOI: https://doi.org/10.1007/s11120-008-9300-7

[40] Proctor, M.C.F., Bates, J.W., 2018. Chlorophyll-fluorescence measurements in bryophytes: evidence for three main types of light-curve response. Journal of Bryology. 40(1), 1–11. DOI: https://doi.org/10.1080/03736687.2017.1407280

[41] Serôdio, J., Lavaud, J., 2011. A model for describing the light response of the nonphotochemical quenching of chlorophyll fluorescence. Photosynthesis Research. 108(1), 61–76. DOI: https://doi.org/10.1007/s11120-011-9654-0

[42] Alboresi, A., Storti, M., Morosinotto, T., 2018. Balancing protection and efficiency in the regulation of photosynthetic electron transport across plant evolution. New Phytologist. 221(1), 105–109. DOI: https://doi.org/10.1111/nph.15372

[43] Quinnell, R., Howell, D., Ritchie, R.J., 2017. Photosynthesis of an epiphytic resurrection fern Davallia angustata (Wall .ex Hook. & Grev.). Australian Journal of Botany. 65(4), 348. DOI: https://doi.org/10.1071/bt16222

[44] Sma-Air, S., Ritchie, R.J., 2020. Photosynthesis in a Vanda sp orchid with Photosynthetic Roots. Journal of Plant Physiology. 251, 153187. DOI: https://doi.org/10.1016/j.jplph.2020.153187

[45] Ritchie, R.J., 2010. Modelling photosynthetic photon flux density and maximum potential gross photosynthesis. Photosynthetica. 48(4), 596–609. DOI: https://doi.org/10.1007/s11099-010-0077-5

[46] Larkum, A.W.D., Ritchie, R.J., Raven, J.A., 2018. Living off the Sun: chlorophylls, bacteriochlorophylls and rhodopsins. Photosynthetica. 56(SPECIAL ISSUE), 11–43. DOI: https://doi.org/10.1007/s11099-018-0792-x

[47] Ritchie, R.J., Sma-Air, S., Limsathapornkul, N., et al., 2021. Photosynthetic electron transport rate (ETR) in the littoral herb Launaea sarmentosa known as mole crab in Thailand. Photosynthesis Research. 150(1–3), 327–341. DOI: https://doi.org/10.1007/s11120-021-00826-2

[48] Vollenweider, R.A., 1974. Primary production in aquatic environments. IBP Handbook No 12, pp. 54–59. Blackwell Scientific Publ.: London, UK. 242p.

[49] Golterman, H.L., Clymo, R.S., Ohnstad, M.A.M., 1978. Methods for physical and chemical analysis of fresh waters, 2nd ed. IBP Handbook No 8, pp. 58–64, 186–194. Blackwell Scientific Publ.: Oxford, UK. 231p.

[50] Millero, F.J., 1979. The thermodynamics of the carbonate system in seawater. Geochimica et Cosmochimica Acta. 43, 1651–1661. DOI: https://doi.org/10.1016/0016-7037(79)90184-4

[51] Garcia, H.E., Gordon, L.I., 1992. Oxygen solubility in seawater: Better fitting equations. Limnology and Oceanography. 37(6), 1307–1312. DOI: https://doi.org/10.4319/lo.1992.37.6.1307

[52] Zar, J.H., 2014. Biostatistical Analysis, 5th ed. Pearson New International Edition Pearson: Edinburgh Gate, Harlow, UK. 761p.

[53] Wang, Z., Liu, X., Bao, W., 2015. Higher photosynthetic capacity and different functional trait scaling relationships in erect bryophytes compared with prostrate species. Oecologia. 180(2), 359–369. DOI: https://doi.org/10.1007/s00442-015-3484-2

[54] Apichatmeta, K., Sudsiri, C.J., Ritchie, R.J., 2017. Photosynthesis of Oil Palm (*Elaeis guineensis*). Scientia Horticulturae. 214, 34–40. DOI: https://doi.org/10.1016/j.scienta.2016.11.013

[55] Ritchie, R.J., Bunthawin, S., 2010. Photosynthesis in Pineapple (*Ananas comosus comosus* [L.] Merr) Measured Using PAM (Pulse Amplitude Modulation) Fluorometry. Tropical Plant Biology. 3(4), 193–203. DOI: https://doi.org/10.1007/s12042-010-9057-y

[56] Ritchie, R.J., 2012. Photosynthesis in the Blue Water Lily (*Nymphaea caerulea* Saligny) Using Pulse Amplitude Modulation Fluorometry. International Journal of Plant Sciences. 173(2), 124–136. DOI: https://doi.org/10.1086/663168

[57] Ritchie, R.J., Heemboo, M., 2021. *Trentepohlia* sp., a terrestrial chlorophyte growing on galvanised iron lamp posts. Phycologia. 60(1), 48–61. DOI: https://doi.org/10.1080/00318884.2020.1851008

[58] Ritchie, R.J., Sma-Air, S., 2022. Photosynthesis of an endolithic Chlorococcum alga (Chlorophyta, Chlorococcaceae) from travertine calcium carbonate rocks of a tropical limestone Spring. Applied Phycology. 3(1), 1–15. DOI: https://doi.org/10.1080/26388081.2021.2023631

[59] Nikolić, N., Zotz, G., Bader, M.Y., 2024. Modelling the carbon balance in bryophytes and lichens: Presentation of PoiCarb 1.0. a new model for explaining distribution patterns and predicting climate-change effects. American Journal of Botany. 111(1). DOI: https://doi.org/10.1002/ajb2.16266

[60] Sello, S., Meneghesso, A., Alboresi, A., et al., 2019. Plant biodiversity and regulation of photosynthesis in the natural environment. Planta. 249(4), 1217–1228. DOI: https://doi.org/10.1007/s00425-018-03077-z

[61] Franco, A.C., Herzog, B., Hubner, C., et al., 1999. Diurnal changes in chlorophyll a fluorescence, CO_2-exchange and organic acid decarboxylation in the tropical CAM tree Clusia hilariana. Tree Physiology. 19(10), 635–644. DOI: https://doi.org/10.1093/treephys/19.10.635

[62] Waite, M., Sack, L., 2009. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. New Phytologist. 185(1), 156–172. DOI: https://doi.org/10.1111/j.1469-8137.2009.03061.x

[63] Wu, H.-Y., Qiao, M.-Y., Zhang, Y.-J., et al., 2022. Photosynthetic mechanism of maize yield under fluctuating light environments in the field. Plant Physiology. 191(2), 957–973. DOI: https://doi.org/10.1093/plphys/kiac542

[64] Steeman Nielsen, E., 1947. Photosynthesis of aquatic plants with special reference to carbon sources (Dansk botanisk archiv). Munksgaard: Denmark. Volume 12, pp. 5–71.