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REGULAR PAPER – ECOLOGY/ECOPHYSIOLOGY/ENVIRONMENTAL BIOLOGY

Laboratory and field measurements of water relations, photosynthetic parameters, and hydration traits in macrolichens in a tropical lower montane rainforest in Thailand

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Abstract
Ecophysiological studies of lichens in tropical Asia are rare, and additional studies can increase the understanding of lichen life in this region. The main aim of this study was to observe the relationships between water availability and photosynthetic parameters, as well as hydration trait parameters, in macrolichens during the rainy and dry seasons in a tropical forest. A total of 11 lichen species growing in a lower montane rainforest in Thailand were collected and studied. The results clearly showed that the specific thallus mass (STM), net photosynthetic rate (Pn), the potential quantum yield of primary photochemistry (Fv/Fm), chlorophyll content, and carotenoid content of almost all lichens were lower in the dry season than in the rainy season. Field measurements in the dry season revealed that only the foliose chlorolichen *Parmotrema tinctorum* was metabolically active and exhibited slight carbon assimilation. In the rainy season, all lichens started their photosynthesis in the early morning, reached maximal values, declined, and ceased when the thalli desiccated. The photosynthetically active period of the lichens was approximately 2–3 h in the morning, and the activities of the cyanolichens ended approximately 30 min after the chlorolichens. The hydration trait parameters, including the STM, maximal water content (WC_{max}), and water holding capacity (WHC), were greater in the cyanolichens. In addition, the maximal Pn (Pn_{max}) and optimal water content (WC_{opt}) for Pn were also greater in the cyanolichens, but the maximal Fv/Fm (Fv/Fm_{max}) was lower. The cyanolichens compensated for their inability to use humid air to restore photosynthesis by having higher water content and storage, higher photosynthetic rates, and longer photosynthetically active periods. This study provides additional insights into lichen ecophysiology in tropical forests that can be useful for lichen conservation.

Keywords Chlorolichen · CO_2 gas exchange · Cyanolichen · Ecophysiology · Photosystem II · Poikilohydric organism · Water stress

Introduction

Lichens are obligate symbiotic organisms between fungi and algae and/or cyanobacteria (Nash 2008a). They can assimilate carbon via photosynthesis, which is carried out by photosynthetic partners called photobionts (Friedl and Budel 2008; Sanders and Masumoto 2021). Approximately 7–10% of photobionts are contained within a lichen thallus (Ahmadjian 1993; Green et al. 2008). Most lichens (85%) have green algae as primary photobionts and are called chlorolichens. About 10% of them have cyanobacteria as primary photobionts and are called cyanolichens (Friedl and Budel 2008; Honegger 2007). Three major growth forms commonly known from lichens include crustose, foliose, and fruticose. The foliose and fruticose forms are macrolichens, while the crustose form is a microlichen (Bergamini et al. 2007). Lichens are poikilohydric organisms whose thallus water content tends to reach equilibrium with the water status of the environment (Green et al. 2011; Kranner et al. 2008). Its metabolism depends on the thallus water content, which is active when hydrated and inactive when

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desiccated (Lange et al. 1999, 2007; Leisner et al. 1996). On a clear sky day, lichens absorb water at night and photosynthesize in the early morning (Lange 2003a). They are then in a dormant state when the thalli desiccate, which accounts for a major part of the day (Lange et al. 2007; Zotz et al. 2003). Cyanolichens need liquid water to activate or reactivate photosynthesis, while chlorolichens can use water vapor alone (Lange et al. 1986). Suboptimal water content, both low and high, can depress photosynthetic rates in lichens (Lakatos et al. 2006; Lange and Green 1996; Zotz et al. 2003). The forms of available water, i.e., rain, dew, and humid air, are drivers of the morphology, function and spatial distribution of epiphytic lichens (Gauslaa 2014). Most lichens adapt and tolerate extreme environments, such as cold, hot, and drought (Green et al. 2011; Kranner et al. 2008); however, they are sensitive to air pollution (Nash 2008b). It is very interesting to know how lichens adapt their physiology to the environment to achieve survival and distribution in ecosystems.

Several abiotic factors can influence the growth, survival, and distribution of lichens, of which the key factors are water availability (Honegger 2007; Lange et al. 2004, 2007), light intensity (Green et al. 1997; Paoli et al. 2010; Piccotto and Tretiach 2010; Pintado and Sancho 2002), temperature (Lange 2002; Lange et al. 1994), CO_2 concentration (Lange 2002; Lange and Green 2008; Nash et al. 1983), and chemical pollutants (Boonpeng et al. 2023; Nash 2008b; Paoli et al. 2015; Sujetovienė et al. 2020). Ecophysiological studies in lichens have been intensively performed in temperate and polar regions (Gauslaa and Arsenault 2020; Green et al. 2008; Kappen et al. 1998; Kershaw 1985; Lange and Green 2008; Mkhize et al. 2022; Palmqvist et al. 2008; Phinney et al. 2018). The polar regions have cold and dry climates, lichens are under snow and ice for months during winter, and they are adapted to this extreme environment. The temperate regions are warmer and more humid, most lichens are abundant in these regions due to their favorable environment. The tropical regions are hot and humid, lichens in these regions are adapted to high temperatures and rainfall events. Fewer studies have been conducted in the tropical regions of Central and South America (Lakatos et al. 2012; Lange et al. 2000, 2004; Zotz et al. 1998, 2003). This field of study is very scarce in tropical Asia (Phaengphech et al. 2019; Wang et al. 2022). Therefore, it is important to add additional studies in this region.

Thailand is a tropical country in Southeast Asia with relatively high biodiversity. Buaruang et al. (2017) reported that 1,292 lichen species were present in Thailand. Taxonomic studies in the country are continuous, and new species are regularly discovered. However, ecophysiological studies that help to understand lichen life in nature are rare. Previous studies were conducted in dry evergreen forests and tropical rain forests, approximately 700 to 850 m above sea level (asl) (Boonpeng et al. 2014; Phaengphech et al. 2019; Poajaroen and Boonpragob 2013). The proposed study was performed in another area, lichens, forest types, and elevations, during the rainy and dry seasons. The main objectives of this study were (i) to study the relationship between water availability and the photosynthetic rate and the potential quantum yield of primary photochemistry in macrolichens, (ii) to observe photosynthetic pigments and hydration trait parameters in lichens during the rainy and dry seasons, and (iii) to measure CO_2 gas exchange, chlorophyll fluorescence, and water status in lichen thalli under natural conditions. We tested the following hypotheses: (i) the CO_2 gas exchange and photosystem II (PSII) efficiency of lichens are influenced by the water status of lichen thalli and by the season; (ii) the photosynthetic pigments and hydration trait parameters of lichens are species-specific, and higher values can be observed in cyanolichens than in chlorolichens due to their higher water requirements and greater growth in shaded habitats; and (iii) drought stress during the dry season strongly affects carbon assimilation in lichens, especially in cyanolichens. The results of this study can increase the body of fundamental knowledge on the ecophysiology of tropical lichens, especially in tropical Asia.

Materials and methods

Research site and experimental lichens

This research was conducted on a lower montane rainforest in Phu Hin Rong Kla National Park, Phitsanulok Province, Thailand. The park terrain is complex, with an elevation of approximately 290 to 1,820 m asl. There are 3 forest types that cover the area, namely, the dry dipterocarp forest in the lower part of the park (below 900 m asl), the lower mountain rainforest, and the lower mountain coniferous forest in the higher part of the mountain (above 900 m asl). The climatic conditions recorded in 2022 at a station near the park office (17°0’12.40"N 100°59’40.95"E, 1,170 m asl) by the park staff showed that the cumulative annual rainfall was 1,713 mm. The driest period was found to be from December to February, in which the amount of rainfall was less than 1 mm per month. Rain of more than 48 mm per month was found to occur from March to November, during which the highest rain amount occurred in August (586 mm). The highest temperature ranged from 21.6 (January) to 33.3 (July) °C, and the lowest temperature ranged from 15.5 (January) to 20.2 (June) °C.

A total of 11 macrolichen species were selected for this study (Table 1). Most of them (7 species) are foliose (*Coccocarpia palmicola* (Spreng.) Arv. & D. J. Galloway;

Table 1 Description of eleven studied macrolichens collected from the lower montane rainforest in Phu Hin Rong Kla National Park, Thailand

No.	Lichen species	Growth form	Thallus structure	Primary photobiont	Group	Substrate	Habitat
1	*Cladonia arbuscula*	Fruticose	Heteromerous	Green alga	Chlorolichen	Rock	Zone B, 1,300 m asl., high light exposure
2	*Cladonia rappii*	Fruticose	Heteromerous	Green alga	Chlorolichen	Rock	Zone B, 1,300 m asl., high light exposure
3	*Coccocarpia palmicola*	Foliose	Heteromerous	Cyanobacterium	Cyanolichen	Bark	Zone C, 1,104 m asl., low-medium light exposure
4	*Leptogium furfuraceum*	Foliose	Homoiomerous	Cyanobacterium	Cyanolichen	Bark	Zone C, 1,104 m asl., low-medium light exposure
5	*Leptogium marginellum*	Foliose	Homoiomerous	Cyanobacterium	Cyanolichen	Bark	Zone B, 1,300 m asl., low light exposure
6	*Parmelinella wallichiana*	Foliose	Heteromerous	Green alga	Chlorolichen	Rock	Zone B, 1,300 m asl., low-medium light exposure
7	*Parmotrema reticulatum*	Foliose	Heteromerous	Green alga	Chlorolichen	Bark	Zone A, 1,492 m asl., medium light exposure
8	*Parmotrema sancti-angelii*	Foliose	Heteromerous	Green alga	Chlorolichen	Bark	Zone C, 1,104 m asl., medium-high light exposure
9	*Parmotrema tinctorum*	Foliose	Heteromerous	Green alga	Chlorolichen	Bark	Zone C, 1,104 m asl., medium-high light exposure
10	*Ramalina farinacea*	Fruticose	Heteromerous	Green alga	Chlorolichen	Bark	Zone A, 1,492 m asl., medium light exposure
11	*Usnea undulata*	Fruticose	Heteromerous	Green alga	Chlorolichen	Bark	Zone B, 1,300 m asl., high light exposure

Leptogium furfuraceum (Harm.) Sierk, *Leptogium marginellum* (Sw.) Gray; *Parmelinella wallichiana* (Taylor) Elix & Hale; *Parmotrema reticulatum* (Taylor) M. Choisy; *Parmotrema sancti-angelii* (Lynge) Hale; *Parmotrema tinctorum* (Despr. ex Nyl.) Hale), and the remaining 4 species were fruticose (*Cladonia arbuscula* (Wallr.) Flot.; *Cladonia rappii* A. Evans; *Ramalina farinacea* (L.) Ach., and *Usnea undulata* Stirt.). Eight species were chlorolichens (*C. arbuscula*, *C. rappii*, *P. wallichiana*, *P. reticulatum*, *P. sancti-angelii*, *P. tinctorum*, *R. farinacea*, and *U. undulata*), while 3 species were cyanolichens (*C. palmicola*, *L. furfuraceum*, and *L. marginellum*). These lichens were collected from three zones. Zone A was located at Phu Lom Lo (16°58’56.05"N 101° 4’3.36"E, 1,492 m asl), approximately 8.15 km from the park office. Zone B was located near Pha Chu Thong (16°59’16.06"N 100°59’39.71"E, 1,300 m asl), approximately 1.77 km from the park office. Zone C was located at Lan Hin Teak (17° 0’26.21"N 100°59’21.15"E, 1,104 m asl), approximately 700 m from the park office. This study was performed during the dry (January 2023) and rainy (June 2023) seasons in the local area.

Laboratory measurements

Mass and area

The dry mass (DM) and area (A) of each lichen species were studied for several thallus fragments (50−100 pieces per season) of various sizes (0.5−10 cm^2). These fragments were obtained from 15−20 intact thalli of each species. All the fragments were placed in a desiccator for approximately 15 h until a constant weight was reached, after which the samples were weighed under relatively dry conditions (air relative humidity less than 30%) using a three-digit portable digital balance (EJ-303, A&D, Tokyo, Japan). Subsequently, each fragment was drawn under a plastic transparent sheet and scanned, and the area was measured using the ImageJ computer program (NIH, NY, USA). The specific thallus mass (STM) was calculated by STM = DM/A, and the specific thallus area (STA) was calculated by STA = A/DM. The STMs and STAs of this study were calculated from desiccated thallus areas, while previous studies used hydrated thallus areas (Eriksson et al. 2018; Esseen et al. 2017; Gauslaa and Arsenault 2020). However, the STMs and STAs of this study can be compared among the studies lichens because those were calculated by the similar method.

Water content and storage

The water content (WC) of each lichen thallus was calculated from the actual fresh weight (FW) and the desiccator-dry weight (DW) as follows: $WC = ((FW - DW)/DW) \times 100$. The results are expressed as the percentage of thallus desiccator-dry weight (% DW). This water content was considered as a total water content (external WC + internal WC). The water storage capacity of each lichen species was estimated by the water holding capacity (WHC). Five different thalli from each species ($n = 5$) were soaked in deionized water overnight for approximately 17 h and then shaken and weighed. The WHC was calculated as WHC = (WC_{17}

$_h$ − DW)/A, where DW is the desiccator-dry weight and A is the thallus area. The maximal water content (WC_{max}) of each lichen species was obtained from the highest number of WC observed from all laboratory and field measurements in all seasons of that species.

Photosynthetic pigment content

Thalli of each lichen species were placed in a desiccator for approximately 15 h until a constant weight was reached. Each thallus was cut into small fragments of approximately 2−3 mm^2. Pigment extraction was adapted from the procedures of Barnes et al. (1992), Boonpragob (2002) and Boonpeng et al. (2023). Approximately 300 mg of each lichen desiccator-dry weight sample was placed in a test tube. The sample was immersed in 5 mL of dimethyl sulfoxide (DMSO), which contained 2.5 mg mL^{-1} polyvinylpyrrolidone (PVP) that helped to prevent chlorophyll degradation during the extraction process, and then incubated in a hot air oven at 65 °C for 45 min in darkness. After that, the extract was allowed to cool to ambient temperature, and another 5 mL of DMSO was added and left in the dark for ca. 15 h. The optical density of the extract solution was measured at wavelengths of 480, 649 and 665 nm with a spectrophotometer (GENESYS 10 S UV–Vis spectrophotometer, Thermo Fisher Scientific, Inc., MA, USA) to determine the chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (TChl), and total carotenoid (TCar) content by using the equations of Wellburn (1994). Three measurements were performed on each sample, and an arithmetic mean was calculated. Five samples ($n = 5$) were measured for each species and each season.

CO_2 gas exchange and water relations

For CO_2 gas exchange measurements in laboratory, three intact thalli from each lichen species were combined and used as a sample for observing the response of the CO_2 gas exchange rate to the thallus water content. Each sample was submerged in deionized water under activated light ca. 80−100 µmol m^{-2} s^{-1} for approximately 2 h to obtain a saturated thallus water content. The samples were subsequently removed, shaken, weighed, and placed in a conifer chamber connected to a portable LI-6400 infrared gas analyzer (IRGA, LI-COR, NE, USA). The CO_2 gas exchange rate and water content of each sample were measured approximately every 5 min from fully hydrated thalli to fully desiccated thalli. These measurements were performed in a controlled temperature room (25 ± 2 °C) under a photosynthetic photon flux density (PPFD) of approximately 350 µmol m^{-2} s^{-1} and ambient CO_2 ranging from 410−450 ppm, and the IRGA used an open system with an air flow rate of 500 µmol s^{-1}. Six records were performed for each measurement, and an arithmetic mean was calculated.

Chlorophyll fluorescence and water balance

For chlorophyll fluorescence measurements in laboratory, the lichen samples were immersed in deionized water in darkness for approximately 2 h to obtain a saturated thallus water content. The lichen samples were dark-adapted for at least 2 h before measurement. The chlorophyll fluorescence parameter Fv/Fm = (Fm − Fo)/Fm, which indicates the maximal efficiency of PSII (Jensen and Kricke 2002; Maxwell and Johnson 2000; Murchie and Lawson 2013), was measured under dark-adapted conditions in a controlled temperature room of ca. 25 ± 2 °C using a MINI-PAM pulse amplitude modulated fluorometer (Heinz Walz GmbH, Effeltrich, Germany) that applied a saturating light pulse of ca. 4,000−5,000 µmol m^{-2} s^{-1} for 0.8 s. The measurements were performed approximately every 5 min from fully hydrated thalli to fully desiccated thalli. Five different complete thalli were measured from each species, and an arithmetic mean was calculated.

Field measurements

For field measurements, CO_2 gas exchange, chlorophyll fluorescence, and thallus water content were measured for four representative lichen species, namely, *P. tinctorum*, *L. furfuraceum*, *L. marginellum*, and *U. undulata*. This study was carried out under quasinatural conditions at a study site in Zone C (Lan Hin Teak) (17° 0’23.94"N 100°59’24.96"E, 1,124 m asl) and was performed in the dry (16−17 January 2023) and rainy (11 June 2023) seasons. The intact thalli of the lichens were detached from their substrate, cleaned by removing extraneous materials, and exposed to natural environmental conditions overnight at the study site. In the next early morning, CO_2 gas exchange, chlorophyll fluorescence, and thallus water content were measured approximately every 30 min, from approximately 6.00 a.m. to 12.30 p.m. CO_2 gas exchange was measured from the combination of three complete thalli from each species using a conifer chamber that was connected to a portable LI-6400 infrared gas analyzer (IRGA, LI-COR, NE, USA) with an open system and an air flow rate of 500 µmol s^{-1} and ambient CO_2 ranging from 400−440 ppm. Net photosynthetic rate (Pn) and respiration (R) were measured and recorded. Chlorophyll fluorescence was measured from five different complete thalli of each species using a MINI-PAM pulse amplitude modulated fluorometer (Heinz Walz GmbH, Effeltrich, Germany) that applied a saturating light pulse of ca. 4,000−5,000 µmol m^{-2} s^{-1} for 0.8 s. The chlorophyll fluorescence parameters ΦPSII = (Fm’ − F)/Fm’, and ETR (electron transport rate) = ΦPSII × PAR × 0.84 × 0.5. Thallus water content was measured immediately after finishing CO_2 gas exchange or chlorophyll fluorescence measurements. Microclimatic conditions, including light (PPFD) intensity, relative air humidity (RH), and air temperature, were recorded every 1 s during the field measurements using an LI-1400 Datalogger (LI-COR, NE, USA).

Statistical analysis

The normality of the data was tested using the Shapiro–Wilk test ($P < 0.05$), and the homogeneity of variance was tested using Levene's test ($P < 0.05$). The significance of the differences among the WHC dataset and the photosynthetic pigment content data were examined using one-way analysis of variance (one-way ANOVA) with Tukey's test for post hoc comparisons. Response curves of Pn and Fv/Fm to WC were fitted using nonlinear regressions provided in SigmaPlot 14.0 computer software (Systat Software, Inc., CA, USA).

Results

Morphology and water storage

The dry masses of all lichens were strongly positively correlated with their thallus areas ($P < 0.001$). The STM was calculated to determine the thallus mass of each lichen in a similar area. The STMs of 4 out of the 5 studied lichens that were measured in both seasons, were greater in the rainy season than in the dry season, except for *U. undulata*, which was slightly lower in the rainy season (Table 2). This indicates that the thallus mass of lichens growing in the rainy season was greater than that of lichens growing in the dry season. In the rainy season, the STM values ranged from 12.9 to 22.9 mg cm^{-2}, based on the species studies in this season, the lowest STM was found from the foliose chlorolichen *P. reticulatum* and the highest was from the foliose cyanolichen *L. furfuraceum*. However, during the dry season, the STMs ranged from 11.4 to 21.2 mg cm^{-2}, based on the species studies in this season, the lowest value was found for the foliose chlorolichen *P. tinctorum*, and the highest value was observed for the foliose cyanolichen *C. palmicola*. Considering data in the rainy season, the STMs of both cyanolichens were approximately 1.3 to 1.6 times greater than that of all chlorolichens.

The STA was calculated to determine the thallus area of each lichen with a similar mass. Due to the greater masses in the rainy season, the STAs of almost all lichens that were measured in both seasons showed lower STAs in the rainy season than in the dry season. The values in the rainy season ranged from 48 to 82 cm^2 g^{-1}, based on the species studies in this season, the lowest STA was found from the foliose cyanolichen *C. palmicola* and the highest STA was from the foliose chlorolichen *P. reticulatum*. However, during the dry season, the STAs ranged from 56 to 91 cm^2 g^{-1}, based on the species studies in this season, the lowest STA was found in the foliose cyanolichen *C. palmicola*, and the highest STA was observed in the foliose chlorolichen *P. tinctorum*. Considering data in the rainy season, the STA of all chlorolichens was approximately 0.6 times greater than that of both cyanolichens.

The WC_{max} in all lichens from all seasons ranged from 220 to 1,197% DW, of which the lowest WC_{max} was found for the foliose chlorolichen *P. reticulatum*, and the highest WC_{max} was observed for the gelatinous foliose cyanolichen *L. furfuraceum*. The WC_{max} values of the cyanolichens (1,052–1,197% DW) were approximately 3 to 4 times greater than those of the chlorolichens (220–351% DW). Among the chlorolichens, all the fruticose lichens (271–351% DW) had higher WC_{max} values than did the foliose lichens (220–264% DW).

The WHCs of all lichens in the rainy season ranged from 20 to 254 mg H_2O cm^{-2}, of which the lowest WHC was found for the foliose chlorolichen *P. tinctorum*, and the highest WHC was observed for the gelatinous foliose cyanolichen *L. furfuraceum*. Like that of WC_{max}, the WHC of the cyanolichens (131−254 mg H_2O cm^{-2}) was significantly greater than that of the chlorolichens (20−49 mg H_2O cm^{-2}). Most fruticose chlorolichens (41−49 mg H_2O cm^{-2}) had significantly greater WHCs than did the foliose chlorolichens (20–28 mg H_2O cm^{-2}), except for *U. undulata*, which had a value close to that of the foliose chlorolichens (27 mg H_2O cm^{-2}).

Photosynthetic pigments across species and seasons

The Chl a, Chl b and TChl levels in all lichens that were measured in both seasons, in the rainy season were greater than those in the dry season (Table 3), except for the Chl a in *C. rappii*, which was comparable between the rainy and dry seasons. Based on the species studies in each season, Chl a concentrations ranged from 0.33 (*C. rappii*) to 1.25 (*C. palmicola*) mg g^{-1} in the rainy season and from 0.27 (*P. sancti-angelii*) to 0.86 (*C. palmicola*) mg g^{-1} in the dry season, and the difference between the rainy and dry seasons was 0.9 to 3.6 times. Chl b concentrations in the chlorolichens ranged from 0.22 (*C. arbuscula*) to 0.44 (*R. farinacea*) mg g^{-1} in the rainy season and from 0.11 (*U. undulata*) to 0.20 (*P. tinctorum*) mg g^{-1} in the dry season, and the difference between the rainy and dry seasons was 1.6 to 3.3 times. TChl in the chlorolichens ranged from 0.58

Table 3 Photosynthetic pigment contents, including chlorophyll a (Chl a), chlorophyll b (Chl a), total chlorophyll (TChl), and total carotenoid (TCar) contents, of ten studied macrolichens collected in the rainy and dry seasons from the lower montane rainforest in Phu Hin Rong Kla National Park

Lichen species	Chl a (mg g^{-1})		Chl b (mg g^{-1})		TChl (mg g^{-1})		TCar (mg g^{-1})	
	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry
Parmelinella wallichiana	0.85 ± 0.07 fg	-	0.41 ± 0.03f	-	1.26 ± 0.10de	-	0.42 ± 0.01 h	-
Parmotrema reticulatum	0.75 ± 0.07ef	-	0.31 ± 0.02de	-	1.07 ± 0.09d	-	0.29 ± 0.02ef	-
Parmotrema sancti-angelii	0.96 ± 0.06 g	0.27 ± 0.06a	0.40 ± 0.06ef	0.15 ± 0.02ab	1.36 ± 0.12e	0.42 ± 0.08a	0.29 ± 0.01ef	0.20 ± 0.03bcd
Parmotrema tinctorum	0.90 ± 0.14 fg	0.53 ± 0.25 cd	0.39 ± 0.09ef	0.20 ± 0.08abc	1.28 ± 0.23de	0.73 ± 0.33bc	0.26 ± 0.03de	0.20 ± 0.04abc
Cladonia arbuscula	0.50 ± 0.05bcd	-	0.22 ± 0.01bcd	-	0.72 ± 0.07bc	-	0.24 ± 0.02cde	-
Cladonia rappii	0.33 ± 0.05ab	0.36 ± 0.02abc	0.26 ± 0.01 cd	0.16 ± 0.01abc	0.58 ± 0.04abc	0.51 ± 0.02abc	0.32 ± 0.02 fg	0.15 ± 0.01a
Ramalina farinacea	1.00 ± 0.01 g	0.62 ± 0.12de	0.44 ± 0.05f	0.15 ± 0.04ab	1.44 ± 0.06e	0.77 ± 0.15c	0.24 ± 0.00cde	0.16 ± 0.04ab
Usnea undulata	0.94 ± 0.02 fg	0.44 ± 0.02abcd	0.36 ± 0.03ef	0.11 ± 0.01a	1.30 ± 0.05de	0.55 ± 0.03abc	0.25 ± 0.01cde	0.18 ± 0.00ab
Coccocarpia palmicola	1.25 ± 0.04 h	0.86 ± 0.04 fg	Absence	Absence	-	-	0.36 ± 0.03 g	0.30 ± 0.02ef
Leptogium furfuraceum	0.34 ± 0.05abc	-	Absence	-	-	-	0.27 ± 0.03ef	-

Note Different letters on each parameter in both seasons indicate statistically significant differences by One-way ANOVA with the Tukey test at $P<0.05$, $n=5$. The hyphen (-) indicates that the data was not measured. The Chl a, b, TChl and TCar of *P. wallichiana*, *P. reticulatum*, *C. arbuscula*, and *L. furfuraceum* in the dry season were not measured because the samples were not collected

(*C. rappii*) to 1.44 (*R. farinacea*) mg g^{-1} in the rainy season and from 0.42 (*P. sancti-angelii*) to 0.77 (*R. farinacea*) mg g^{-1} in the dry season, and the difference between the rainy and dry seasons was 1.1 to 3.2 times. The TCar values in all lichens were significantly greater in the rainy season (1.2−2.1 times) than in the dry season. The concentrations ranged from 0.24 to 0.42 mg g^{-1} in the rainy season and from 0.15 to 0.30 mg g^{-1} in the dry season. The highest TCar value in the rainy season was found for the foliose chlorolichen *P. wallichiana*, and the lowest value was found for the fruticose chlorolichen *C. arbuscula*.

Response of CO_2 gas exchange to water content

The Pn of all lichens in all seasons was slightly negative at a thallus water content of approximately zero, after which the Pn gradually increased with increasing thallus water content and reached the maximal Pn (Pn_{max}) at the optimal water content (WC_{opt}). The Pn of most lichens, especially in the rainy season, decreased when the WC exceeded the WC_{opt}, and the WC in this state was considered to indicate suprasaturation (Fig. 1; Table 2). However, the decrease in the Pn at suprasaturation in the fruticose chlorolichen *C. rappii* and *U. undulata* was not clear from this experiment. The Pn values of 3 out of the 4 lichens that were measured in both seasons, in the rainy season were obviously greater than those in the dry season, although the lichens received adequate water. In addition, the Pn values of the lichens in the dry season did not seem to decrease or slightly decrease at suprasaturation. The Pn in the fruticose chlorolichen *R. farinacea* was similar between the rainy and dry seasons.

Based on the species studies in each season, the Pn_{max} of all lichens in the rainy season ranged from 2.0 (*C. rappii*) to 22.1 (*C. palmicola*) nmol CO_2 g^{-1} s^{-1}, while those in the dry season ranged from 7.0 (*U. undulata*) to 12.8 (*P. tinctorum*) nmol CO_2 g^{-1} s^{-1}. The average Pn_{max} from the lichens in the rainy season (avg. 13.9 nmol CO_2 g^{-1} s^{-1}) was greater than that from the same species in the dry season (avg. 9.0 nmol CO_2 g^{-1} s^{-1}). In the rainy season, the Pn_{max} of the cyanolichens (18.2–22.1 nmol CO_2 g^{-1} s^{-1}) was greater than that of the foliose chlorolichens (14.8–21.3

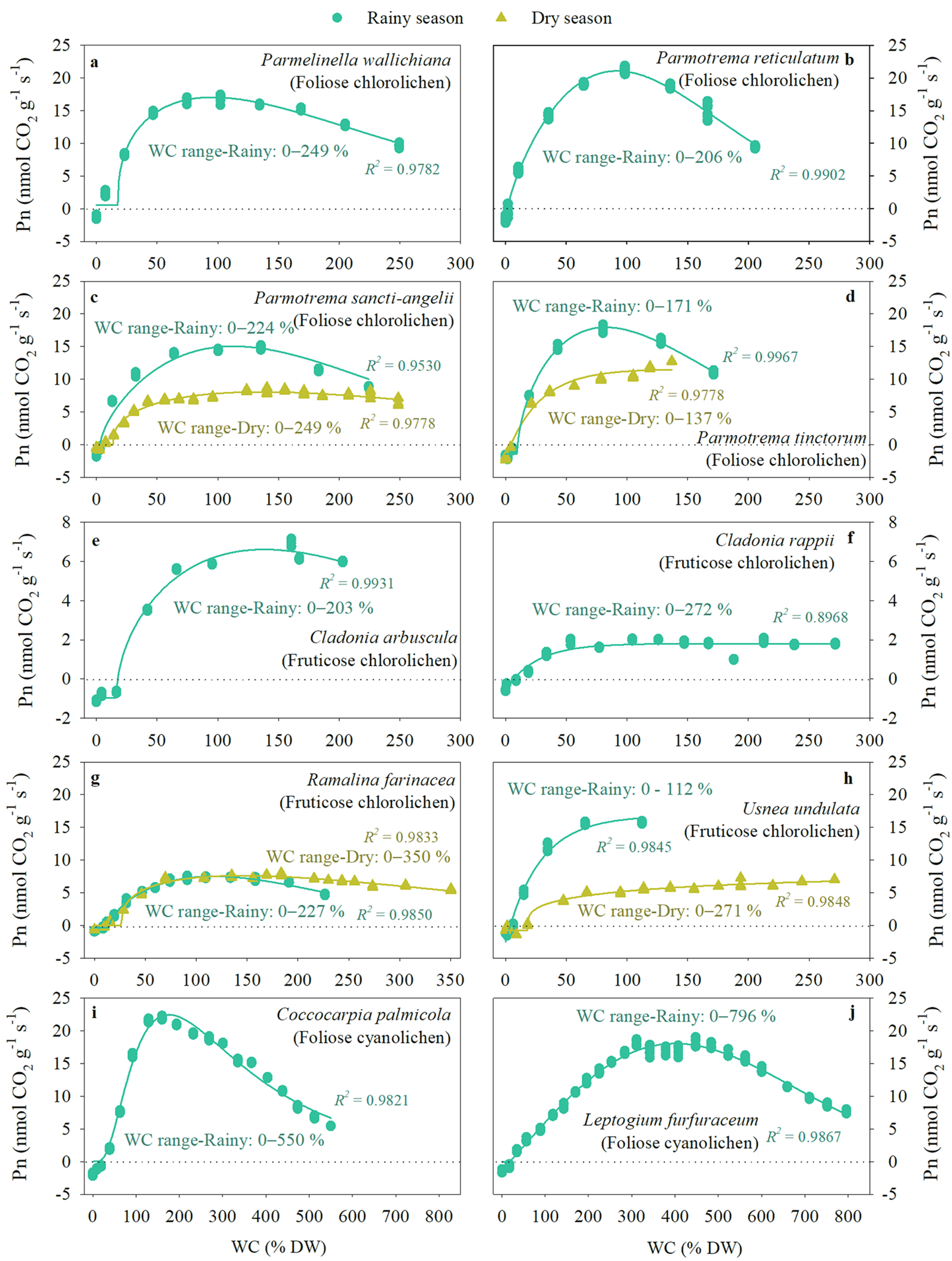

Fig. 1 Response curves of net photosynthetic rate (Pn) to thallus water content (WC) in ten studied macrolichens collected in the rainy and dry seasons from the lower montane rainforest in Phu Hin Rong Kla National Park

nmol CO_2 g^{-1} s^{-1}) and the fruticose chlorolichens (2.0–15.6 nmol CO_2 g^{-1} s^{-1}).

Based on the species studies in each season, the WC_{opt} of all lichens in the rainy season ranged from ca. 80 (*P. tinctorum*) to 311 (*L. furfuraceum*) % DW, while those in the dry season ranged from ca. 137 (*P. tinctorum*) to 271 (*U. undulata*) % DW. The average WC_{opt} from the lichens in the rainy season (avg. 109% DW) was lower than that from the same species in the dry season (avg. 187% DW). In the rainy season, the WC_{opt} of the cyanolichens (160–311% DW) was greater than that of the fruticose chlorolichens (104–161% DW) and the foliose chlorolichens (80–136% DW). The ranges of WC for which the Pn was equal to or greater than 80% of the Pn_{max} for each species are also shown in Table 2.

Response of the maximal efficiency of PSII to water content

The maximal efficiency of PSII in the lichens was estimated using the chlorophyll fluorescence parameter Fv/Fm. A value of 0 indicates that the lichens were metabolically inactive. This value was observed for all fully desiccated thalli (Fig. 2). There were two patterns of response curves for the Fv/Fm to the thallus water content. In patterns type I, the Fv/Fm increased with increasing WC, reached the maximal Fv/Fm (Fv/Fm_{max}) and then stabilized. This type was observed for all 8 chlorolichens in both seasons. In patterns type II, the Fv/Fm increased with increasing WC, reached the Fv/Fm_{max}, and then decreased at higher WCs. This type was found in both cyanolichens (*C. palmicola* and *L. furfuraceum*). The Fv/Fm in most lichens was greater in the rainy season, except for that in the fruticose chlorolichen *C. rappii*, which showed similar values in both seasons, and that in the foliose cyanolichen *C. palmicola* was slightly greater in the dry season.

As shown in Table 2 and based on the species studies in each season, the Fv/Fm_{max} of all lichens in the rainy season ranged from 0.43 (*L. furfuraceum*) to 0.68 (*U. undulata*), while those in the dry season ranged from 0.47 (*P. tinctorum*) to 0.67 (*C. rappii*). The average Fv/Fm_{max} of the lichens in the rainy season (avg. 0.62) was greater than that of the lichens from the same species in the dry season (avg. 0.54). In the rainy season, the Fv/Fm_{max} of all the chlorolichens (0.52−0.68) was greater than that of the cyanolichens (0.43−0.48). Among the chlorolichens, the difference in the Fv/Fm value between the foliose and fruticose was not clear.

Based on the species studies in each season, the WC_{opt} for Fv/Fm of all lichens in the rainy season ranged from ca. 30 (*C. rappii*) to 146 (*C. palmicola*) % DW, while those in the dry season ranged from ca. 31 (*U. undulata*) to 115 (*C. palmicola*) % DW. The WC_{opts} for Fv/Fm of most lichens in the rainy season were slightly greater than those in the dry season. Although the highest WC_{opt} for Fv/Fm was found for the cyanolichen *C. palmicola*, the value for another cyanolichen, *L. furfuraceum*, was within the range of chlorolichens. The WC_{opt} for Fv/Fm from the same species and season was lower than the WC_{opt} for Pn of approximately 9 to 273% DW.

Field measurements of CO_2 gas exchange and chlorophyll fluorescence

The microclimatic conditions at the field measurement site in the rainy and dry seasons are shown in Fig. 3. The PPFD intensity fluctuated during the rainy and dry seasons, with peak intensities of 1,854 and 1,395 µmol m^{-2} s^{-1}, respectively. The average air temperature in the rainy season was 23.9 °C, ranging from 19.8 to 30.6 °C. However, the average temperature in the dry season was 19.1 °C, ranging from 14.1 to 30.7 °C, which was 4.8 °C lower than that in the rainy season. The average air relative humidity in the rainy season was 69%, ranging from 46 to 83%. The average value in the dry season was 48%, ranging from 20 to 77%, which was 21% lower than that in the rainy season.

Field measurements of CO_2 gas exchange and chlorophyll fluorescence were performed on four representative lichens. The lichen *P. tinctorum* was representative of foliose chlorolichens, *U. undulata* was representative of fruticose chlorolichens, and *L. furfuraceum* and *L. marginellum* were representative of foliose cyanolichens. Different species were collected and measured in the cyanolichens because insufficient samples of *L. marginellum* were collected during the rainy season. The lichens absorbed water from water vapor, mist/fog, and dew from night to early morning. The highest WC in each lichen was found in the early morning. In the rainy season, the largest WC was observed for the foliose cyanolichen *L. furfuraceum* (357% DW), followed by the foliose chlorolichen *P. tinctorum* (183% DW) and the fruticose chlorolichen *U. undulata* (124% DW) (Fig. 4e, k, q; Table 4). Photosynthesis began in the hydrated lichen thalli in the early morning after they received sunlight. The Pn gradually increased and reached the maximal values of 38.9 (*L. furfuraceum*), 22.2 (*P. tinctorum*) and 17.8 (*U. undulata*) nmol CO_2 g^{-1} s^{-1} at approximately 7.18 a.m. to 7.26 a.m. The Pn subsequently decreased with decreasing WC, and carbon fixation ceased when the thalli desiccated at approximately 8.52 a.m. to 9.26 a.m. (Fig. 4f, l, r; Table 4). The photosynthetic process in the cyanolichen was approximately 30 min longer than that in the chlorolichens. After that, the lichens were in a dormant state for the remainder of the time of measurement. The WC in the lichen thalli according to the chlorophyll fluorescence measurements was also highest in the foliose cyanolichen *L. furfuraceum* (458% DW), followed by the foliose chlorolichen *P. tinctorum* (180% DW) and the fruticose chlorolichen *U. undulata* (101% DW) (Fig. 5d, j, p; Table 4). The response curves of the ETR were similar to the Pn curves. When hydrated, the ETR increased with increasing PPFD, reached the maximal values of 111 (*L. furfuraceum*), 73 (*P. tinctorum*) and 66 (*U. undulata*) and decreased with decreasing WC (Fig. 5e, k, q; Table 4). FPSII indicates the actual quantum yield of

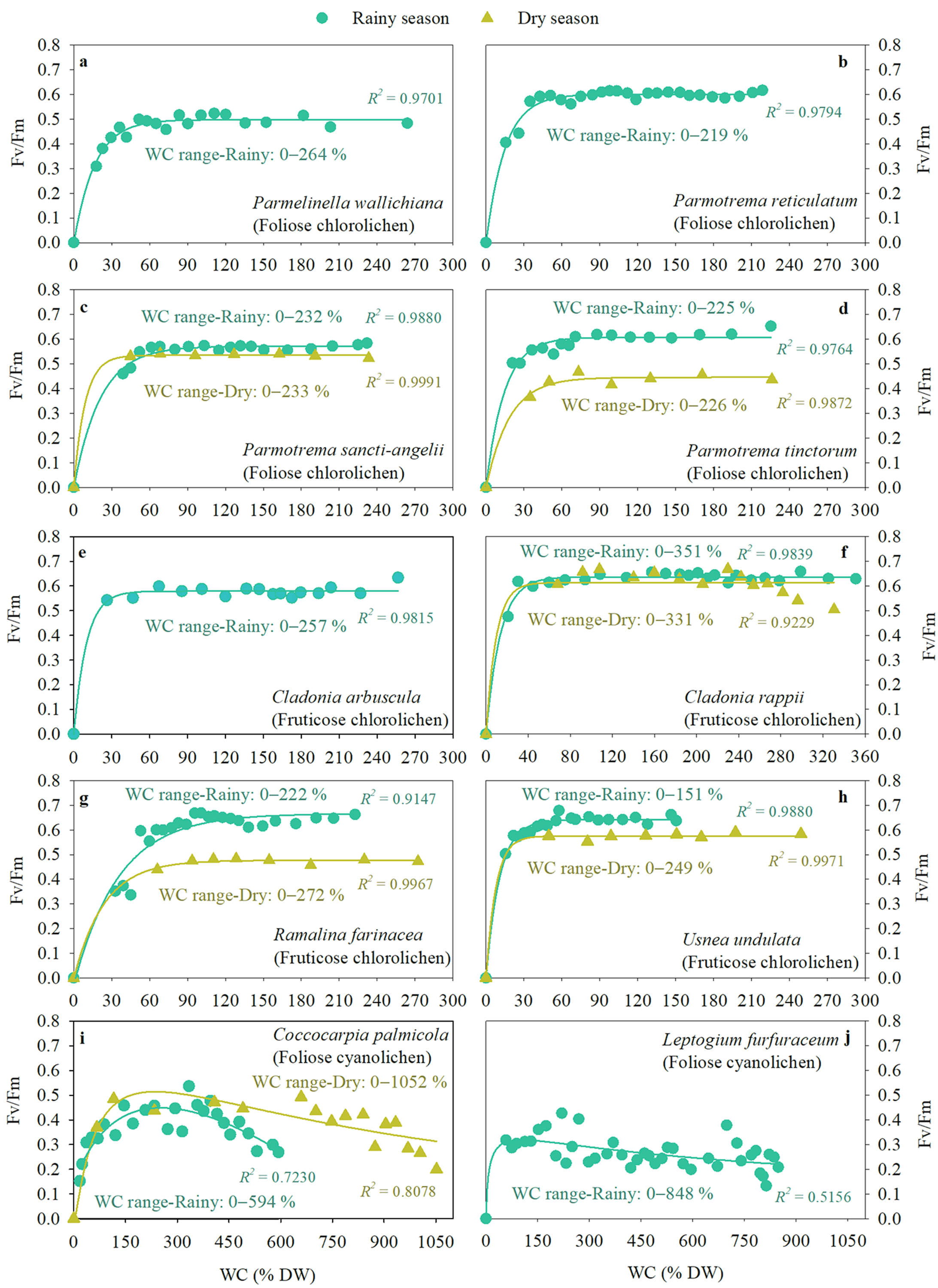

Fig. 2 Response curves of the maximal efficiency of PSII (Fv/Fm) on thallus water content (WC) in ten studied macrolichens collected in the rainy and dry seasons from the lower montane rainforest in Phu Hin Rong Kla National Park

PSII when photosynthesis occurs. These parameters in all lichens were greatest at the beginning of the measurement when the thalli were hydrated and had the lowest PPFD intensity. The highest values of 0.64, 0.68, and 0.62 were detected for *L. furfuraceum*, *P. tinctorum*, and *U. undulata*, respectively. FPSII decreased with increasing thallus desiccation and light intensity and reached a value of 0 when the thalli were fully desiccated at approximately 8.17 a.m. to

Table 2 Ecophysiological parameters from the laboratory measurements, including the specific thallus mass (STM), specific thallus area (STA), water holding capacity (WHC), maximal and optimal water content (WC_{max}, WC_{opt}), maximal net photosynthetic rate (Pn_{max}), and highest value of the maximal efficiency of PSII (Fv/Fm_{max}), of ten studied macrolichens collected in the rainy and dry seasons from the lower montane rainforest in Phu Hin Rong Kla National Park

Lichen species	STM (mg cm^{-2})		STA (cm^2 g^{-1})		WC_{max} (% DW)	WHC (mg H_2O cm^{-2})	Pn_{max} (nmol CO_2 g^{-1} s^{-1})		(µmol CO_2 m^{-2} s^{-1})		WC_{opt} for Pn (% DW)		WC at the Pn ≥ 80% of Pn_{max} (% DW)		Fv/Fm_{max}		WC_{opt} for Fv/Fm (% DW)	
	Rainy	Dry	Rainy	Dry	All season	Rainy	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry
Parmelinella wallichiana	14.3	-	74	-	264	22 ± 2a	16.8	-	2.4	-	102	-	47–169	-	0.52	-	52	-
Parmotrema reticulatum	12.9	-	82	-	220	26 ± 3a	21.3	-	2.7	-	98	-	64–136	-	0.62	-	35	-
Parmotrema sancti-angelii	16.8	12.8	66	85	249	28 ± 1a	14.8	8.4	2.4	1.4	136	155	64–136	56–226	0.58	0.54	52	45
Parmotrema tinctorum	16.9	11.4	66	91	226	20 ± 2a	17.8	12.8	2.7	1.9	80	137	43–128	105–137	0.65	0.47	71	50
Cladonia arbuscula	16.9	-	61	-	289	42 ± 5b	6.9	-	1.2	-	161	-	95–203	-	0.63	-	67	-
Cladonia rappii	17.2	16	62	66	351	49 ± 6b	2.0	-	0.34	-	104	-	54–272	-	0.66	0.67	30	68
Ramalina farinacea	14.8	-	72	-	350	41 ± 4b	7.3	7.8	1.1	1.2	109	184	74–191	70–256	0.67	0.48	65	66
Usnea undulata	14.2	15	81	75	271	27 ± 3a	15.6	7.0	2.2	1.0	112	271	66–112	136–271	0.68	0.59	41	31
Coccocarpia palmicola	22.8	21.2	48	56	1,052	131 ± 9c	22.1	-	5.0	-	160	-	129–301	-	0.48	0.49	146	115
Leptogium furfuraceum	22.9	-	49	-	1,197	254 ± 13d	18.2	-	4.2	-	311	-	253–562	-	0.43	-	38	-

Note The different letters on the WHC dataset indicate statistically significant differences by One-way ANOVA with the Tukey test at $P < 0.05$, $n = 5$. The hyphen (-) indicates that the data was not measured or not reported. The STM, STA, Pn and Fv/Fm of *P. wallichiana*, *P. reticulatum*, *C. arbuscula*, and *L. furfuraceum* in the dry season were not measured because the samples were not collected. The STM and STA of *R. farinacea* in the dry season were measured but not reported due to insufficient samples that provided unreliable data. The Pn of *C. rappii* and *C. palmicola* in the dry season was measured but not reported because of an instrumental error

9.14 a.m. (Fig. 5f, l, r; Table 4). A FPSII value of 0 indicated inactive thalli, and the lichens were in a dormant state. The active period was longer in the cyanolichen than in the chlorolichens by approximately 30 min.

Unlike those in the rainy season, most lichen thalli in the dry season were inactive during the time of measurement. This was because of the very low thallus water content, which was 19–21, 18–22, and 14–18% DW in *L. marginellum*, *P. tinctorum*, and *U. undulata*, respectively. Only the foliose chlorolichen *P. tinctorum* was slightly active and could photosynthesize during the time of measurement. However, its Pn was low, with a peak value of 2.3 nmol CO_2 g^{-1} s^{-1} occurring at approximately 7.50 a.m., and photosynthesis ended at approximately 9.51 a.m. The highest Pn found in the dry season was 9.7 times lower than that in the rainy season.

Discussion

The ecophysiological parameters of the lichens in this study varied across species and seasons. The hydration trait parameters (STM, WC_{max}, and WHC) were obviously greater in the cyanolichens than in the chlorolichens (Table 2). This could be explained by the greater water absorption and storage of cyanobacterial photobionts due to the presence of gelatinous sheaths (Gauslaa and Coxson 2011; Wan and Ellis 2020). In addition, the cyanolichen *C. palmicola* has tomentum at the lower thallus surface that could help to store water. The maximal water content found in *C. Palmicola* in this study (1,052% DW) was greater than that found in the same species in cool and damp forests in Canada (616% DW) (Gauslaa and Arsenault 2020) but was close to that found in the temperate rainforest in New Zealand (1,175% DW) (Lange et al. 1993). The higher WHC in the cyanolichens than in the chlorolichens could compensate for their inability to use humid air to restore photosynthesis (Gauslaa and Coxson 2011). Strongly significant positive correlations were observed among the STM, WC_{max}, and WHC obtained from all the species in the rainy season (Pearson's correlation: STM vs. WC_{max}, $R = 0.910$, $P = 0.0003$; STM vs. WHC, $R = 0.850$, $P = 0.0018$; WC_{max} vs. WHC, $R = 0.951$, $P = 0.0000$). This finding provides additional evidence confirming that STM is a significant hydration trait in lichens. It is a driver of water storage and the water economy in lichens (Eriksson et al. 2018; Esseen et al. 2017; Gauslaa and Arsenault 2020; Longinotti et al. 2017; Phinney et al. 2019). A higher WHC can prolong photosynthetically active periods in lichens (Gauslaa et al. 2017). The STMs of almost all lichens were lower in the dry season than in the rainy season. This was probably due to the effect of drought stress, and the lichens adapted to the limited water availability. A

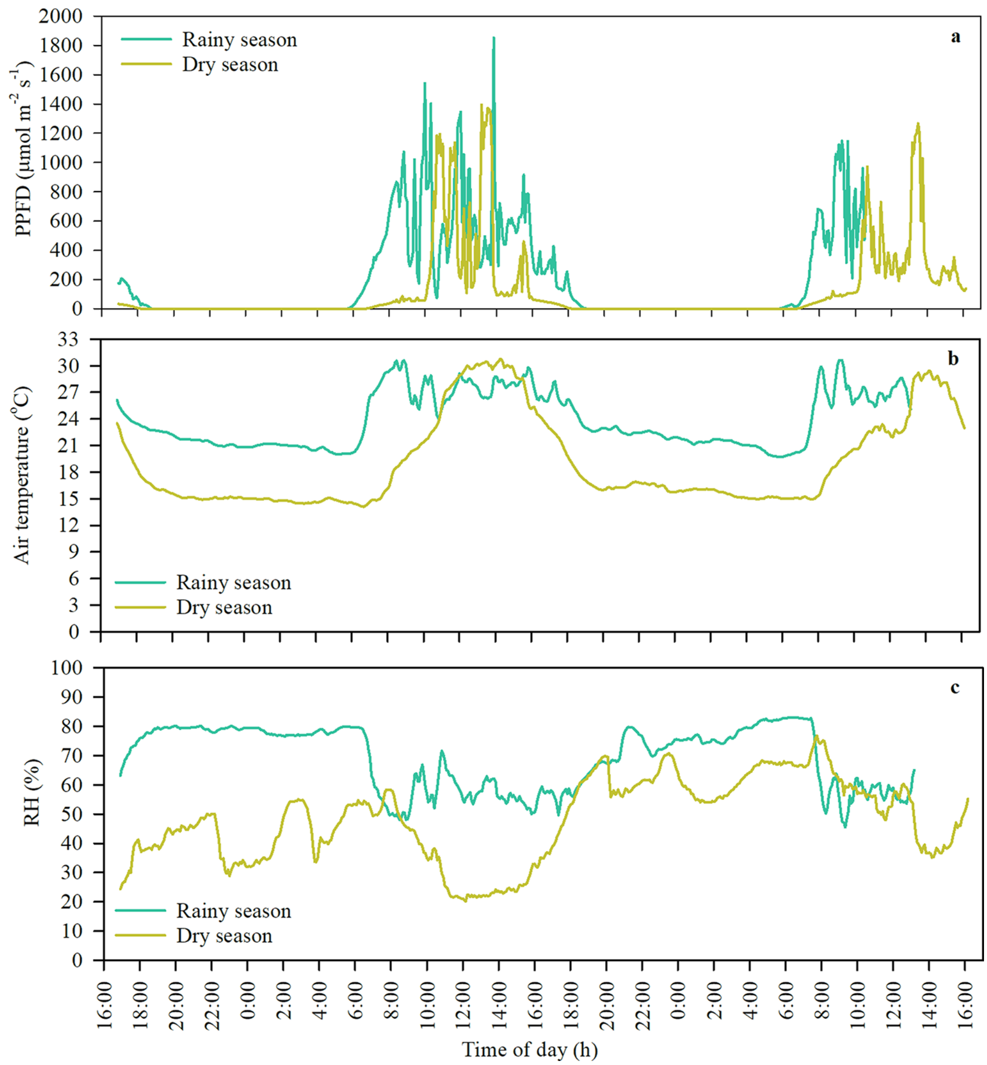

Fig. 3 Microclimatic conditions, including the photosynthetic photon flux density (PPFD, **a**), air temperature (**b**) and relative air humidity (RH, **c**), in the dry (January 15–17, 2023) and rainy (June 10–12, 2023) seasons at the field measurement site (17° 0'23.94"N 100°59'24.96"E, 1,124 m asl) in Phu Hin Rong Kla National Park

higher STM in cyanolichens than in chlorolichens indicates that they need more water, which is provided by rain and dew (Gauslaa and Arsenault 2020). Generally, cyanolichens need liquid water to activate or reactivate their photosynthesis, while chlorolichens can use water vapor alone (Lange et al. 1986). The STA was the opposite of the STM and was additionally calculated to create fundamental information for the biomonitoring of air pollutants. In that field, the S/V ratio (surface/volume ratio) or S/M ratio (surface/mass ratio) was used. This is frequently used to explain the capacity of lichens to accumulate air pollutants. Normally, a higher STA (S/V, S/M) indicates a greater capacity for interception and accumulation of deposited air pollutants (Garty and Garty-Spitz 2015).

Higher Chl a, Chl b, TChl and TCar contents were detected in almost all lichens during the rainy season (Table 3). This also indicates the effects of drought stress (Boonpeng et al. 2014; Paoli et al. 2010). Chl b was absent in cyanolichens, according to previous studies (Gauslaa et al. 2019; Liu et al. 2019). The photosynthetic pigments in lichens are species- and site-specific (Green et al. 1997; Piccotto and Tretiach 2010). Previous studies reported that, compared with those of chlorolichens, higher chlorophyll contents could be found in cyanolichens (Green et al. 1997; Lange et al. 2004). This finding was consistent with the findings of the present study, in which the highest Chl a were observed in the cyanolichen *C. palmicola*. However, that from the gelatinous cyanolichen *L. furfuraceum* were the lowest. A study in the tropical lower montane rainforest in Panama revealed that the chlorophyll contents of the three different species of the lichen genus *Leptogium* ranged from 0.96 to 1.71 mg g^{-1} (Lange et al. 2000), while the Chl a content in the lichen *L. furfuraceum* in this study was 0.34 mg g^{-1}, which was 2.8–5.0 times lower. This might be because of the species and site specificity of the strains, but additional studies should be performed to confirm these results. Light exposure is also a key factor influencing the pigment contents of lichens (Paoli et al. 2010; Piccotto and Tretiach

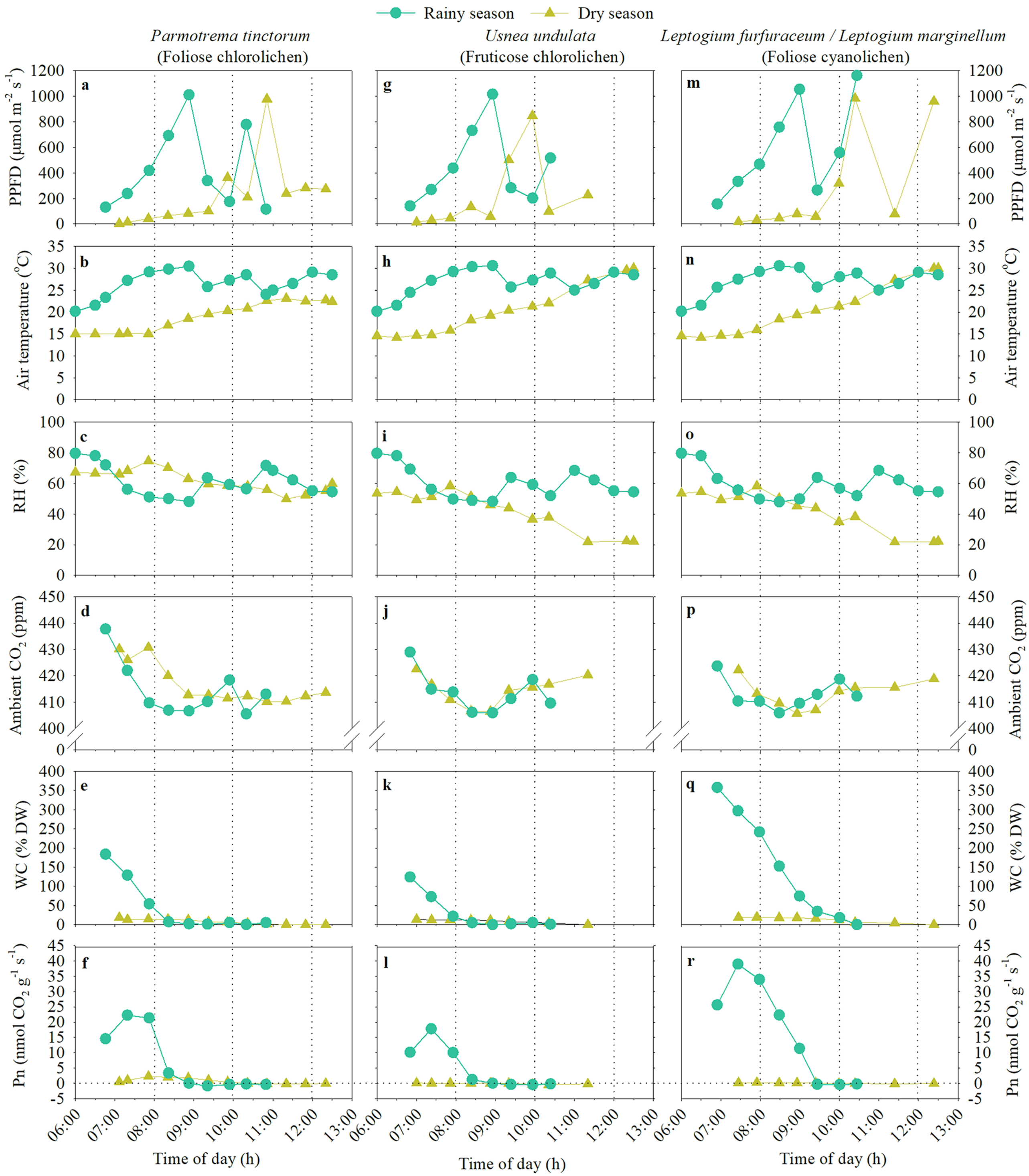

Fig. 4 Diurnal response of net photosynthetic rate (Pn) and thallus water content (WC) in the studied lichens under quasinatural conditions in Phu Hin Rong Kla National Park (17° 0'23.94"N 100°59'24.96"E, 1,124 m asl) and the microclimatic conditions during the measurement, including the photosynthetic photon flux density (PPFD) and air temperature, relative air humidity (RH) and ambient CO_2 concentration. The Pn and WC in the dry season were measured for *Leptogium marginellum* and *Usnea undulata* on January 16, 2023 and for *Parmotrema tinctorum* on January 17, 2023, while those in the rainy season were measured for *Leptogium furfuraceum*, *Parmotrema tinctorum* and *Usnea undulata* on June 11, 2023

Table 4 Significant parameters from the field measurements, including net photosynthetic rate (Pn), water content (WC), relative air humidity (RH), photosynthetic photon flux density (PPFD), and air temperature, actual quantum yield of photosystem II (FPSII) and electron transport rate (ETR) in the studied lichens in the rainy and dry seasons from the lower montane rainforest in Phu Hin Rong Kla National Park

Parameter	Unit	Lichen					
		Parmotrema tinctorum		*Usnea undulata*		*Leptogium furfuraceum*	*Leptogium marginellum*
		Foliose chlorolichen		Fruticose chlorolichen		Foliose cyanolichen	
		Rainy	Dry	Rainy	Dry	Rainy	Dry
CO_2 gas exchange measurement							
The highest Pn	nmol CO_2 g^{-1} s^{-1}	22.2	2.3	17.8	Around zero	38.9	Around zero
The highest WC	% DW	183	18	124	14	357	19
WC at the highest Pn	% DW	128	14	73	N/A	297	N/A
RH at the highest Pn	%	56	75	56	N/A	56	N/A
PPFD at the highest Pn	µmol m^{-2} s^{-1}	238	42	269	N/A	333	N/A
Air temperature at the highest Pn	°C	27.2	15.1	27.2	N/A	27.5	N/A
Ambient CO_2 at the highest Pn	ppm	422	431	415	N/A	410	N/A
Time at the highest Pn	a.m.	7.18	7.50	7.22	N/A	7.26	N/A
Time at the Pn ceased	a.m.	8.52	9.51	8.55	N/A	9.26	N/A
Chlorophyll fluorescence measurement*							
The highest FPSII		0.68	0.48	0.62	0	0.64	0
The highest ETR		73	4.5	66	0	111	0
The highest WC	% DW	180	22	101	18	458	21
Time at the FPSII was zero	a.m.	8.41	9.29	8.17	N/A	9.14	N/A

Note * Chlorophyll fluorescence was measured from different lichen thalli of the CO_2 gas exchange measurement, N/A = data was not available

2010). Shaded thalli had higher contents than sunny thalli of the same species (Legaz et al. 1986). This study revealed that the chlorophyll contents of the fruticose chlorolichens *C. arbuscula* and *C. rappii* growing in open and sunny habitats were lower than those of the other species that were exposed to lower light intensities. This difference might also be species-specific; future studies should determine the differences in pigment content between shade and sun thalli of the same species.

Under controlled laboratory conditions, the Pn values of most lichens gradually increased with increasing thallus water content, reached maximal values, and declined during suprasaturation (Fig. 1). The decrease in the Pn at suprasaturation was due to the increasing diffusion resistance of CO_2 to photobiont cells (Lange et al. 1993; Lange and Green 1996; Lange and Tenhunen 1981). Water molecules cause fungal cell turgor and fill the intercellular space between fungal hyphae, limiting the transfer of CO_2 to photobiont cells and resulting in lower assimilation rates. This phenomenon was not clear in the fruticose *C. rappii* or *U. undulata*. These lichens have 3D structures, and the thalli are shrubby and pendent, which might help them repel unnecessary water. However, this assumption needs to be confirmed by additional studies. The fruticose *C. arbuscula* and *R. farinacea* also showed slight decreases in the Pn at suprasaturation. A large decrease in the Pn was found in the foliose lichens, especially in the cyanolichens, whose Pn decreased by approximately 58−75% of their Pn_{max}. The Pn of most lichens was lower in the dry season, although they received sufficient water. This may be the physiological adaptation of the lichens to drought. The Pn of lichens in the dry season slightly decreased during suprasaturation. This physiological adaptation is beneficial for carbon fixation in lichens during rain events, which sometimes occur during the dry season. In the rainy season, the Pn_{max} and WC_{opt} varied across species. The lowest average Pn_{max} was found for the fruticose lichens, and the highest average value was observed for the cyanolichens. This difference may be characteristic of cyanolichens and chlorolichens. Green et al. (1993) reported that the green algal photobiont had a large photosynthetic advantage when the thallus water content was low, while the cyanobacterial photobiont was advantageous when the thallus water content was very high (Green et al. 2002). The cyanolichens had a greater WC_{opt} than did the chlorolichens. This could be explained by the gelatinous sheathes of cyanobacterial photobionts possibly acting as filters that slowly passed through water to the photobiont cell. This result also showed that lichens in the dry season require more water to reach the maximal Pn, which might be the acclimation to the limiting water availability during the drought period.

The maximal performance of PSII in the lichens could be estimated from the Fv/Fm parameter (Maxwell and Johnson 2000). The Fv/Fm of all the chlorolichens was zero when the thalli were desiccated, after which the value increased with increasing hydration, reached the maximal values, and

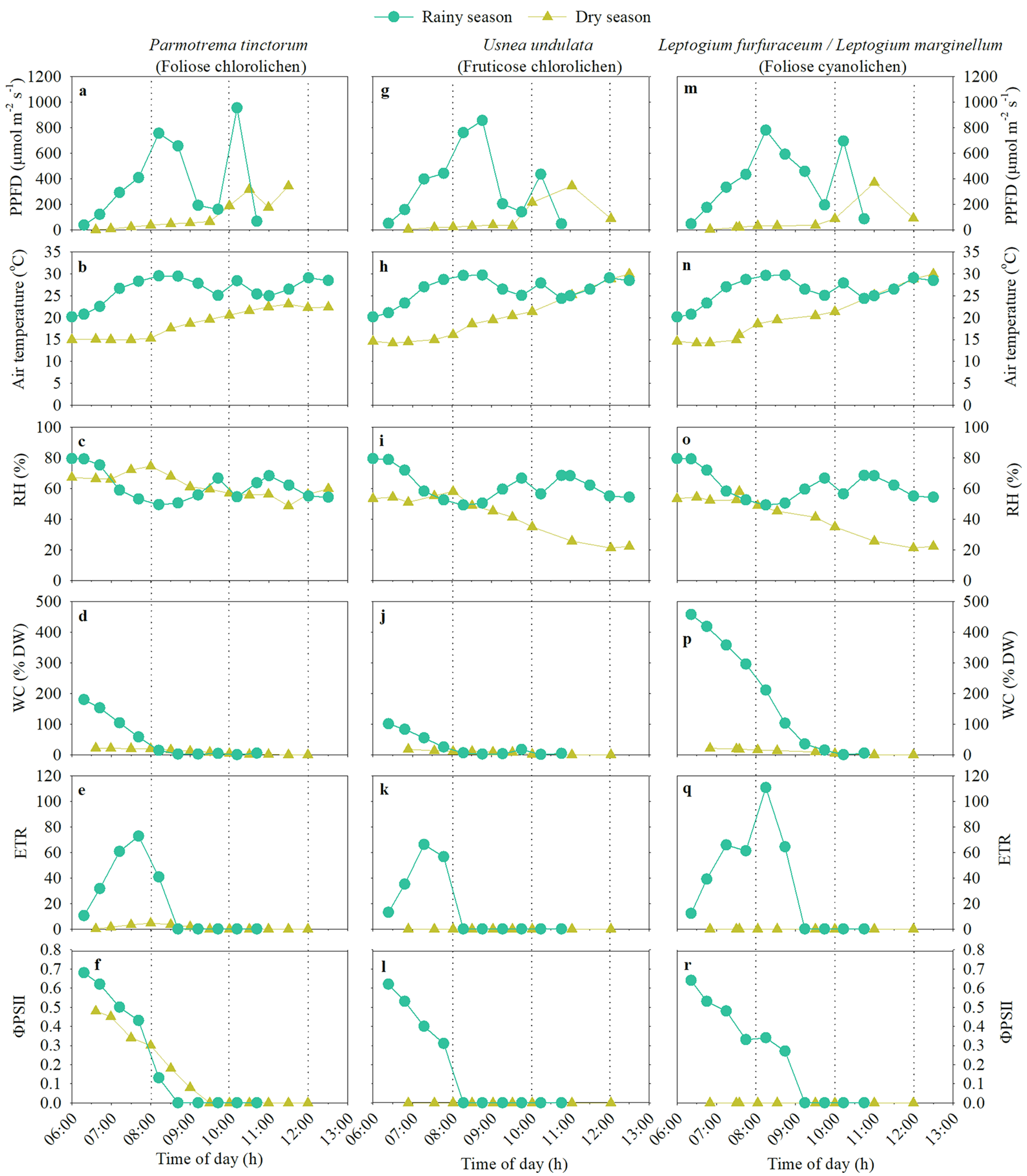

Fig. 5 Diurnal response of chlorophyll fluorescence parameters, including the actual quantum yield of photosystem II (FPSII) and electron transport rate (ETR), as well as thallus water content (WC) in the studied lichens under quasinatural conditions in Phu Hin Rong Kla National Park (17° 0'23.94"N 100°59'24.96"E, 1,124 m asl) and the microclimatic conditions during the measurement, including the photosynthetic photon flux density (PPFD), air temperature, and relative air humidity (RH). The FPSII, ETR and WC in the dry season were measured for *Leptogium marginellum* and *Usnea undulata* on January 16, 2023 and for *Parmotrema tinctorum* on January 17, 2023, while those in the rainy season were measured for *Leptogium furfuraceum*, *Parmotrema tinctorum* and *Usnea undulata* on June 11, 2023

was stable (Fig. 2a-h). This response curve was probably the typical type of response of PSII efficiency to the hydration state in chlorolichens (Lange et al. 1989; Miloš et al. 2018). However, the Fv/Fm in the cyanolichens decreased after reaching the maximal values (Fig. 2i-j), which was similar to the findings of studies in the cyanolichens *Leptogium puberulum* (expressed as FPSII) and *Peltigera rufescens* and the cyanobacterium *Nostoc commune* (expressed as FPSII) (Lakatos et al. 2012; Lange et al. 1989; Miloš et al. 2018). This might be because the high water content in the gelatinous sheath shaded the PSII of the photobiont cells. The Fv/Fm ratio varies across seasons, collection times, and hydration states (Baruffo and Tretiach 2007; Boonpeng et al. 2014; Węgrzyn et al. 2021). According to the results of the present study, the Fv/Fm of most lichens was greater in the rainy season than in the dry season. The maximal Fv/Fm value obtained from healthy leaves was 0.83 (Murchie and Lawson 2013), while the normal range for chlorolichens was 0.60 to 0.76 (Jensen and Kricke 2002). The Fv/Fm_{max} values found in the rainy season in this study ranged from 0.52 to 0.68 for the chlorolichens and from 0.43 to 0.48 for the cyanolichens. Among the chlorolichens, fruticose had a greater average Fv/Fm than did foliose. According to a study in temperate and alpine lichens in India, the Fv/Fm of lichens ranged from 0.02 to 0.66, of which the values of the cyanolichens were lower than those of the chlorolichens, and the Fv/Fm of the fruticose lichens was greater than that of the foliose (Nayaka et al. 2009). In addition, a study of foliose chlorolichens in Italy reported that the Fv/Fm of lichens ranged from 0.67 to 0.74 (Piccotto and Tretiach 2010). The WC_{opt} for Fv/Fm of all lichens was 9 to 273% DW lower than was the WC_{opt} for Pn, implying that the maximal performance of PSII occurred before the maximal Pn.

Field measurements of CO_2 gas exchange, chlorophyll fluorescence and thallus water content in the lichens were performed from approximately 6.00 a.m. to 12.30 p.m. because this period is the typical time for photosynthesis in lichens and could reveal the response curves of Pn in lichens during a day (Lange 2003b; Lange et al. 2000, 2004, 2006; Zotz et al. 1998). Chlorophyll fluorescence is an efficient tool for determining whether lichens are active or inactive (Lange et al. 1999; Leisner et al. 1996). Under field conditions and in the dry season, only the foliose chlorolichen *P. tinctorum* was metabolically active (indicated by FPSII and ETR) and had a positive Pn during the measuring time. This indicates that this lichen is well adapted to the use of water under limited water conditions. This characteristic might be advantageous for the growth, survival, and distribution of this species. In Thailand, this lichen has a relatively high growth rate of 15 to 30 mm yr^{-1} (Fuangkeaw 2018; Wannalux 2014) and is distributed in almost all forest types across the country at the elevation of approximately 50 to 1,500 m asl (most lichens were found between 700−1,500 m asl.). For the rainy season, the Pn and ETR of all lichens gradually increased when received PPFD intensity in the early morning, reached maximal values, decreased with decreasing WC, and ceased when the thalli desiccated (Figs. 4f, l and r and 5e, k and q). These response curves of the Pn were the typical types of diurnal Pn in lichens on clear sky days (Green et al. 2008; Lange 2003a; Lange and Green 2008; Lange et al. 2007; Reiter et al. 2008; Zotz et al. 2003). The photosynthetic period of the lichens in this study was approximately 2–3 h in the morning. The photosynthetic activity period of the cyanolichen was approximately 30 min longer than that of the chlorolichens due to the greater WC and WHC. In addition, the Pn of the cyanolichen was 1.8 to 2.2 times greater than that of the chlorolichens. This probably also compensates for the inability to use humid air to activate photosynthesis.

Conclusions

The ecophysiological parameters of the studied macrolichens in the tropical lower montane rainforest were influenced by water availability between the seasons. The STM, Pn, Fv/Fm, FPSII, ETR, chlorophyll and carotenoid contents of almost all the species were lower in the dry season than in the rainy season. The laboratory experiment reconfirmed that WC was the key factor controlling metabolism and carbon assimilation in the lichens. Despite providing the optimal WC, the Pn and PSII performance of the lichens were also lower in the dry season. This indicates that the lichens adapted to acclimate to limiting water availability during the drought period. Field measurements also confirmed the influence of drought on the lichens. The metabolism of most species was inactive in the dry season, and only the foliose chlorolichen *P. tinctorum* was active and showed slight carbon fixation in this season. Most parameters, including STM, WC_{max}, WHC, Pn_{max}, WC_{opt}, and all photosynthetic pigments from the cyanolichens, at least from one member of this group, showed higher values than did the chlorolichens, except for Fv/Fm_{max}. The cyanolichens required more WC from rain and dew to activate or reactivate their photosynthesis, and they were compensated by having higher photosynthetic rates and longer photosynthetically active periods. The results of this study provide additional insights into the ecophysiology of macrolichens in tropical forests and can be used as fundamental information for lichen conservation in these areas. This study is among the priorities of ecophysiological studies in tropical Asia, especially in Thailand. Additional studies on other species, ecosystems, areas, and parameters should be conducted to increase our knowledge of the ecophysiology of lichens.

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Declarations

Competing interests The authors declare they have no financial interests.

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