Leaf traits in the dwarf montane heathland of the Bokor Plateau, Cambodia

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Paper submitted 1 August 2019, revised manuscript accepted 7 November 2019.

មូលន័យសង្ខេប

ភាពគ្របដណ្តប់ដោយពពកជាញឹកញាប់ រួមជាមួយនឹងរបបទឹកភ្លៀងកម្រិតខ្ពស់ និងខ្យល់ខ្លាំង ផ្សំជាមួយកត្តាប្រភេទដីថ្មភក់ (sandstone soils) ដែលមានកម្រិតអាស៊ីតទាបនៅលើតំបន់ខ្ពង់រាបបូកគោនៃជួរភ្នំដំរី វាបង្កើតឱ្យមានលក្ខខណ្ឌកំណត់មួយដែលធ្វើមាននូវប្រភេទព្រៃក្រិននៃតំបន់ភ្នំត្រូពិក។ វាមានកម្ពស់ដើមឈើខុសគ្នាខ្លាំង គឺពី២០-៣០ម៉ែត្រ សម្រាប់ព្រៃរងទឹកភ្លៀងនៅតាមទីជម្រាលភ្នំ និងបន្ទាប់មកជាប្រភេទព្រៃឈើដែលមានកម្ពស់ទាបៗ និងចុងក្រោយគឺមានពពួករុក្ខជាតិក្រិនស្លឹករឹង កម្ពស់ពី ៣-៤ម៉ែត្រ (sclerophyll heathland) មានវត្តមាននៅលាយឡំជាមួយពពួកដើមឈើទាបៗ (shrub canopy matrix)។ លក្ខណៈរូបសាស្ត្រនៃទំហំនិងទម្ងន់ស្លឹក លក្ខណៈរស្មីសំយោគនៃមធ្យមអតិបរមានៃអត្រាសម្រូប(assimilation rate) រួមជាមួយនឹងប្រសិទ្ធភាពនៃការប្រើប្រាស់ទឹក ($\delta^{13}C$) គឺមានភាពខុសគ្នារវាងពពួករុក្ខជាតិក្រិន និងពពួកដើមឈើទាបៗ (ទាំង woody shrubs និងlow-stature colonizing shrubs) នូវលក្ខណៈតែមួយគឺភាពមានទំហំស្លឹកធំជាប់លាប់។ ខ្សែរកោងឆ្លើយតបទៅនឹងលក្ខខណ្ឌពន្លឺបានបង្ហាញឱ្យឃើញថា ជម្រាបឆ្អែតនៃថាមពលពន្លឺ (saturating irradiance) កើតមាននៅចន្លោះពី៤០០-៥០០μmol m^{-2} s^{-1} គឺតិចជាង១/៤នៃពន្លឺព្រះអាទិត្យ(full sun)។ ទោះបីជាពេលរសៀលហាក់ដូចជាលក្ខខណ្ឌប្រសើរសម្រាប់ធ្វើរស្មីសំយោគ ប្រភេទរុក្ខជាតិដែលបានសិក្សានោះតែងបង្ហាញលក្ខណៈបិទស្តូម៉ាតជាញឹកញាប់ និងបន្ទាបកម្រិតអត្រាស្រូបពន្លឺរបស់វារហូតដល់តម្លៃជាអវិជ្ជមាន។

Abstract

The frequent cloud cover and associated high levels of rainfall and strong winds combined with shallow acidic sandstone soils on the Bokor Plateau of the Elephant Mountains produce classic limiting conditions that lead to the formation of a dwarf tropical montane forest. Tree stature grades quickly from rainforest canopies 20–30 m in height on sheltered slopes, to lower stunted forest, and finally to a low sclerophyll heathland with scattered dwarfed treelets 3–4 m in height in a low shrub canopy matrix. Leaf morphological traits of size and specific leaf weight, photosynthetic traits of mean maximum assimilation rate and integrated water use efficiency ($\delta^{13}C$) differed between dwarfed treelets and both woody shrubs and low-stature colonizing shrubs in only the single trait of having consistently larger leaves. Light response curves showed that saturating irradiance occurred at 400–500 μmol m^{-2} s^{-1}, less than one quarter of full sun. Despite seemingly favourable conditions for photosynthesis in the afternoon, study species frequently exhibited stomatal closure and low to even negative rates of net assimilation.

Keywords Bokor National Park, dwarf forest, heathland, leaf traits, tropical mountain cloud forest.

CITATION: Rundel, P.W., Sharifi, M.R., King-Rundel, J. & Middleton, D.J. (2019) Leaf traits in the dwarf montane heathland of the Bokor Plateau, Cambodia. *Cambodian Journal of Natural History*, **2019**, 77–84.

Introduction

Tropical montane cloud forests, characterized by the persistent presence of mist or low clouds that result in deposition of water on the vegetation, are widespread throughout tropical regions of the world (Hamilton *et al.*, 1995; Aldrich *et al.*, 1997). These forests are typically low in stature with slow growth and are commonly described as dwarf forests. Their low stature and associated slow rates of growth have been attributed to a complex interaction of diverse potential limiting factors. These include cloud cover that reduces solar radiation levels for photosynthesis, relatively low ambient air temperatures, strong winds, high rainfall that leaches soils and slows rates of mineralization and decomposition, and limited nutrient availability (Bruijnzeel & Proctor, 1995; Tanner *et al.*, 1998; Bruijnzeel & Veneklaas, 1998; Bruijnzeel *et al.*, 2011).

Examples of tropical montane cloud forests can be seen in southern Cambodia in the Cardamom and Elephant Mountains where proximity to the Gulf of Thailand brings unusually high levels of rainfall (Daltry & Momberg, 2000; Rundel *et al.*, 2016). These mountain ranges are largely Mesozoic sandstone, with localized areas of limestone and volcanic rock. Acid lithosols develop over the sandstone parent material that characterizes much of the Elephant Mountains. These thin acidic soils are heavily leached by the high rainfall and easily eroded in disturbed conditions.

The weathered Bokor Plateau exhibits a classic example of a tropical montane cloud forest with dwarf trees. As the plateau slopes gently over a linear distance of about 4 km from near Popokvil Waterfall (920 m) southwards towards the coastal escarpment at the old Bokor Hotel (1,062 m), rainforest canopies 20–30 m in height first give way to a stunted forest 10–15 m in height, and finally to a low sclerophyllous heathland with scattered dwarfed treelets 3–4 m in height in a low shrub canopy matrix of only 1–2 m. Dy Phon (1970) termed this *la lande de myrtacées et vacciniacées* because of the dominance of these two families.

While the flora of the plateau has distinct elements (Rundel *et al.*, 2017), many forest tree species occur on both the upper mountain slopes and the plateau itself, providing an opportunity for comparative studies. The gradient in growing conditions has been described for the canopy dominant *Dacrydium elatum* (Roxb.) Wall. ex Hook.f across the plateau. Trees near the Popokvil Waterfall are 14–16 m in height, drop to 8–10 m across the plateau, and finally reach only 4–6 m to the south near the coastal escarpment (Rundel *et al.*, 2016).

Our objective in this study was to investigate comparative patterns of leaf morphological and ecophysiological traits in a group of 19 woody species growing near the coastal escarpment of the Bokor Plateau where high rainfall and shallow heavily weathered soils produce dwarfing conditions for forest trees. Our study species included monopodial treelets dwarfed from their normal canopy height, shrubby taxa of intermediate height, and low-growing shrubs that colonize open sites (Table 1). We looked for traits that might be associated with the dwarfed tree species and help explain their slow growth. An additional objective was to use measurements of net photosynthetic assimilation to establish the maximum rates present and potential role of heavy cloud cover and reduced irradiance in limiting photosynthesis.

Field Site and Methods

Study site and species

Field studies were carried out from 3–13 March 2001 on the Bokor Plateau of the Elephant Mountains in Bokor National Park, Kampot Province, Cambodia. Bokor National Park was established in 1997 and covers an area of 140,000 ha (Rundel *et al.*, 2003; Tagane *et al.*, 2017). Our measurements took place about 0.8–1.0 km north of the old hotel in sclerophyllous heathland habitat. The sandstone substrate of this area of the plateau was heavily weathered with shallow rocky soil and fracture lines forming soil pockets of coarse acidic white sand. Soil pH was 4.7.

Rainfall is extremely high on the Bokor Plateau, averaging more than 5,000 mm annually. Records for Bokor (950 m elevation) at the southern end of the plateau show a mean annual rainfall of 5,309 mm (Tixier, 1979), while the Val d'Emeraude on the southeast margin of the plateau receives a mean rainfall of 5,384 mm (Dy Phon, 1970). The distribution of this rain, however, is strongly seasonal, peaking in July and August. These stations have been reported to receive an average of 170 and 223 days a year of rainfall, respectively (Anonymous, 1979). The dry season at these stations is restricted to 2–3 months from December through February and rainfall drops to 50 mm or less in January and February at both stations. The Val d'Emeraude experiences rain almost every day from May through October, but on only 12 days on average in March (Dy Phon, 1970), the month of our sampling. Mornings during our field studies were typically semi-sunny with scattered clouds moving overhead, while heavier overcast conditions and brief periods of intense rain occurred almost every afternoon. Mean monthly temperatures are relatively constant throughout the year at Bokor, varying only from a low of 19.2°C in July and August to a high of 21.5°C in April (Dy Phon, 1970).

Leaf trait analyses

Our study species were characterized as treelets with a single main stem, shrubs with a branched form of canopy architecture, or low shrubs with a low to prostrate growth form. Mean height was measured and compared to maximum heights at favourable forest sites as indicated in the literature. Examples of leaf morphology for four of our study species are shown in Fig. 1. Samples of three leaves from each of three individual plants for each study species were collected for measurement of leaf morphological traits and these represented the youngest fully mature leaf on an actively growing branch. Foliar areas were measured on fresh leaves using a LI-COR portable leaf area meter (LI-COR Inc., Lincoln, Nebraska, USA), then archived for dry weight measurements in a laboratory. Specific leaf weight was calculated as the leaf dry weight per unit area.

Stable carbon isotope ratios of ^{13}C and ^{12}C ($\delta^{13}C$) provide a measure of integrated water use efficient over the period in which carbon was used in leaf construction. Values are negative with lower (more negative) values indicating low water use efficiency while less negative numbers indicate higher water use efficiency (Ehleringer *et al*., 1986). Ground leaf samples from each species were analyzed for $\delta^{13}C$ by the Stable Isotope Analysis Facility at the University of California, Davis. Samples were analyzed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The final delta values are expressed relative to international standards V-PDB (Vienna PeeDee Belemnite).

Gas exchange measurements were carried out using both a LI-COR 6200 and 6400 gas exchange instruments (LI-COR Inc., Lincoln, Nebraska, USA). Three individuals of each study species were selected for measurements and replicated measurements of photosynthetic assimilation and stomatal conductance were made in mid-morning and early afternoon over several days to calculate mean maximum rates. Light response curves were measured under constant leaf-to-air vapour pressure deficit (VPD) and temperature conditions. The ambient temperature inside the leaf chamber was kept at 22°C, a level close to the maximum ambient daytime temperature when the measurements were made. The VPD was maintained

Fig. 1 A) *Lithocarpus leiophyllus*, B) *Machilus bokorensis*, C) *Syzygium antisepticum*, D) *Ardisia smaragdina*. (© M.R. Sharifi)

Table 1 Growth form, habitat, mean leaf area and ecophysiological traits of 19 common species in the heathland community of the Bokor Plateau.

Key: Growth form—Ls=Low shrub, Tr=Treelet, Sh=shrub; Habitat—Rs=Rocky soil, Ri=Riparian, Sp=Soil pockets, Co=Colonizer.

Family / species	Growth form	Habitat	Heathland height (m)	Forest height (m)	Leaf area (cm^2)	SLW ($mg\ cm^{-2}$)	SLA ($m^2\ kg^{-1}$)	$d^{13}C$ (o/oo)	Assimilation ($\mu mol\ m^{-2}\ s^{-1}$)	Conductance ($mmol\ m^{-2}\ s^{-1}$)	ci/ca
Calophyllaceae											
Calophyllum calaba var. *cuneatum*	Ls	Rs	0.8-1.5	30	25.3	14.8	67.4	-28.1	9.7	129	0.57
Clusiaceae											
Garcinia merguensis	Tr	Sp	2.0-4.0	20	13.8	14.0	71.5	-26.7	4.9	72	0.61
Ericaceae											
Rhododendron klossii	Sh	Rs	1.5-2.5	5	16.5	15.6	64.2	-30.4	6.0	74	0.55
Vaccinium bracteatum	Sh	Rs	1-1.5	6	7.0	12.1	82.3	-29.0	9.6	186	0.69
Vaccinium viscifolium	Tr	Sp	4.0	6	23.1	20.8	48.0	-29.4	6.7	105	0.63
Fagaceae											
Lithocarpus elephantum	Tr	Rs	2.0-3.0	18	115.1	17.8	56.0	-28.0	8.8	122	0.53
Lithocarpus leiophyllus	Tr	Co	1.0-4.0	5	29.2	17.7	56.6	-28.5	10.9	137	0.49
Lauraceae											
Machilus bokorensis	Tr	Rs	1.0-4.0	10	37.3	17.7	75.3	-28.9	9.7	168	0.63
Melastomataceae											
Melastoma malabarica subsp. *normale*	Ls	Co	0.5-1	3	7.3	14.2	70.1	-27.4	12.3	250	0.68
Myrtaceae											
Rhodamnia dumetorum	Ls	Co	0.5-1.5	5	6.1	19.3	51.7	ND	7.4	114	0.60
Rhodomyrtus tomentosa	Ls	Co	1.0-2.0	4	12.6	13.5	74.1	-29.4	12.1	235	0.65
Syzygium antisepticum	Ls	Rs	0.3-0.5	15	1.9	ND	ND	-27.8	11.4	222	0.65
Syzygium claviflorum	Sh	Rs	1.0-2.5	2	15.2	17.0	58.7	-27.2	8.5	167	0.66
Syzygium formosum	Tr	Ri	4.0-5.0	20	90.9	16.4	61.1	-29.5	13.4	270	0.75
Pandanaceae											
Pandanus capusi	Sh	Sp	1.5-3.5	4	ND	18.1	55.2	-26.6	3.9	53	0.58
Pentaphyllaceae											
Eurya nitida var. *nitida*	Sh	Rs	2.0-3.0	10	5.1	ND	ND	-28.1	6.4	85	0.53
Primulaceae											
Ardisia crenata subsp. *crassinervosa*	Ls	Co	1.0-1.5	3	7.7	10.0	100	-28.5	7.8	144	0.66
Ardisia smaragdina	Ls	Co	1.0-1.5	1.5	9.6	14.3	70.1	-27.9	6.4	116	0.67
Rutaceae											
Achronychia pedunculata	Tr	Rs	2.0-3.0	35	23.0	14.1	70.8	-28.0	9.6	182	0.72
Mean					**24.8**	**15.7**	**66.7**	**-28.3**	**8.7**	**149.0**	**0.62**

at 0.5–0.9 kPa. The CO_2 concentration inside the leaf chamber was kept constant at 375 mmol mol^{-1} for the light response curves with CO_2 supplied from a pressurized 12-gram gas cylinder. For the CO_2 response curves, light was provided by an internal red/blue LED light source (LI6400-02B) and kept constant at a saturating intensity of 900 µmol m^{-2} s^{-1}. Gas exchange measurements allowed a calculation of the ratio of internal CO_2 concentration within the leaf tissue to that of the ambient air. This ci/ca ratio provides a second indication of water use efficiency, with a higher ratio indicating less draw down of internal CO_2 concentration with better stomatal control and thus more efficient use of water. Although March is usually a relatively dry month at Bokor, our measurements were frequently interrupted by short but intense showers during the afternoon.

Results

Nineteen common woody species present 1.0–1.5 km north of the old hotel on the Bokor Plateau were selected for comparative study (Table 1). Seven of these were treelets with a single main stem: *Garcinia merguensis* Wight, *Vaccinium viscifolium* King & Gamble, *Lithocarpus leiophyllus* A. Camus (Fig. 1A), *Lithocarpus elephantum* (Hance) A. Camus, *Machilus bokorensis* Yahara & Tagane (Fig. 1B), and *Syzygium formosum* (Wall.) Masam. and (L.) Miq. The small stature of these treelets at the study site, typically 3–4 m in height, masks their potential to grow as tall forest trees up to 20 m or more in height in favourable sites (Table 1). This dwarfing is notable in *Achronychia pedunculata* for instance, which was only 2–3 m in height at the study site but can reach 35 m in moist forests.

Five study species had an upright shrubby form of growth: *Rhododendron klossii* Ridl., *Vaccinium bracteatum* Thunb., *Syzygium claviflorum* (Blume) Merr. & L.M> Perry, *Pandanus capusi* Mart. and *Eurya nitida* Korth. var. *nitida*. These species were typically 2–4 m in height, similar to the stature of the treelets, but had the potential to reach intermediate heights of 5–10 m in favourable sites. In addition, we sampled two low shrubs that never reached above 1.5 m in height and were often much lower. These were *Calophyllum calaba* L. var. *cuneatum* Symington ex M.R.Henderson & Wyatt-Smith which was 0.8–1.5 m in height and *Syzygium antisepticum* (Blume) Merr. & L.M.Perry (Fig. 1C), which never exceeded 0.5 m. The dwarf *Calophyllum* is especially interesting as there are varieties of this species that can reach 30 m in height.

As a comparison group to the dwarfed shrub and tree species, we included five species of low-stature colonizing shrubs 1–1.5 m in height that were common in open and disturbed areas of our study site. These were *Melastoma malabarica* subsp. *normale* (D.Don) K.Meyer, *Rhodamnia dumetorum* (DC.) Merr. & L. M. Perry, *Rhodomyrtus tomentosa* Wight, *Ardisia crenata* Sims subsp. *crassinervosa* (Walker) C.M.Hu & Vidal, and *Ardisia smaragdina* Pitard (Fig. 1D).

The study species exhibited a broad range of leaf sizes with a mean area of 24.2 cm^2, but this mean was heavily influenced by two species with large leaves. *Lithocarpus elephantum* had the largest leaves at 115 cm^2 followed by *Syzygium formosum* with leaves of 90.7 cm^2. With just one exception, treelets had leaf areas of over 20 cm^2, larger than the upright and low-growing shrub species (Table 1). All five of the low colonizing shrubs had small leaves which were less than 13 cm^2 in area, but similarly small leaf sizes were also present in several of the upright shrub species. *Syzygium antisepticum* had the smallest leaf size of 1.9 cm^2. Specific leaf weights showed a relatively small range of variation from a low of 10.0 mg cm^{-2} in *Ardisia crenata* to a high of 20.8 cm^{-2} in *Vaccinium viscifolium,* with a mean value of 15.7 cm^2 for all species (Table 1). There was no significant relationship between leaf size and specific leaf weight, or between growth form and specific leaf weight.

Mean maximum rates of leaf net assimilation ranged from a low of 3.9 µmol m^{-2} s^{-1} in *Pandanus capusi* and 4.9 µmol m^{-2} s^{-1} in *Garcinia merguensis* to a high of 13.4 µmol m^{-2} s^{-1} in *Syzygium formosum* and 12.3 µmol m^{-2} s^{-1} in *Melastoma malabarica*. The mean rate for all species was 8.7 µmol m^{-2} s^{-1} (Table 1). Values of ci/ca ratio ranged from 0.49 to 0.52, but most were close to the mean value of 0.60. There was a significant positive linear relationship between ci/ca ratio and stomatal conductance. No significant difference in photosynthetic rates or ci/ca ratio between dwarfed treelets and other growth forms was found.

Rates of stomatal conductance showed a highly significant linear relationship to rates of photosynthetic assimilation, with a mean value of 149 mmol m^{-2} s^{-1} (Fig. 2A). This relationship suggests strong stomatal control over rates of photosynthesis. Although an inverse relationship might be expected between leaf specific weight and photosynthesis, this was not present (Fig. 2B).

Values of stable carbon isotope ratio ($\delta^{13}C$) were indictive of a mesic habitat with relatively low water stress, these ranging from -30.4 o/oo in *Rhododendron klossii* to -26.7 o/oo in *Garcinia merguensis*. The mean value of $\delta^{13}C$ for all species was -28.3 o/oo. The range and mean for

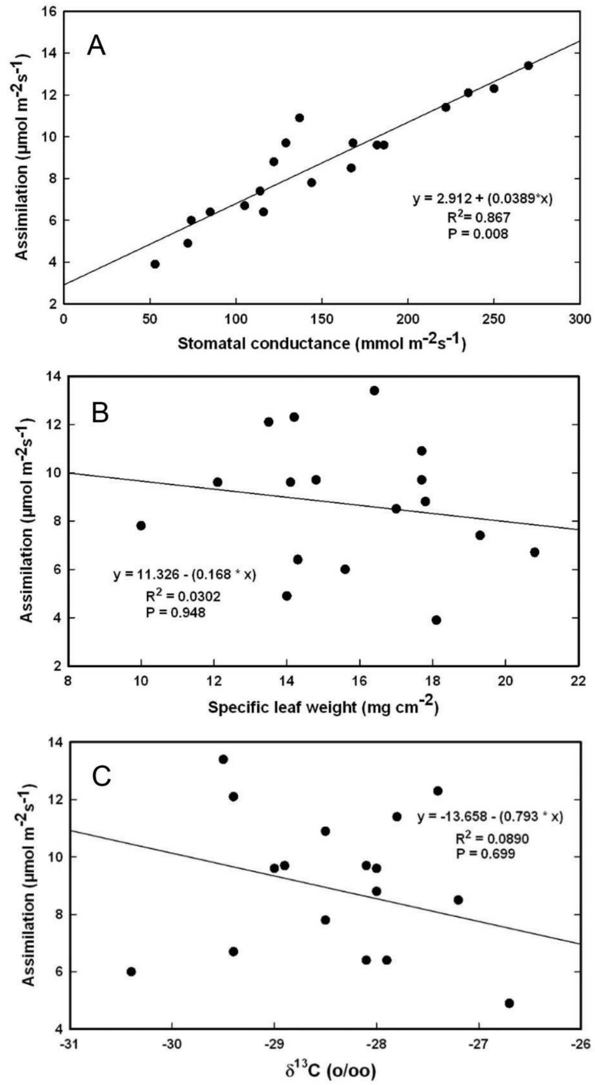

Fig. 2 Relationship of net photosynthetic assimilation to A) Stomatal conductance, B) Leaf specific weight), and C) Leaf $\delta^{13}C$.

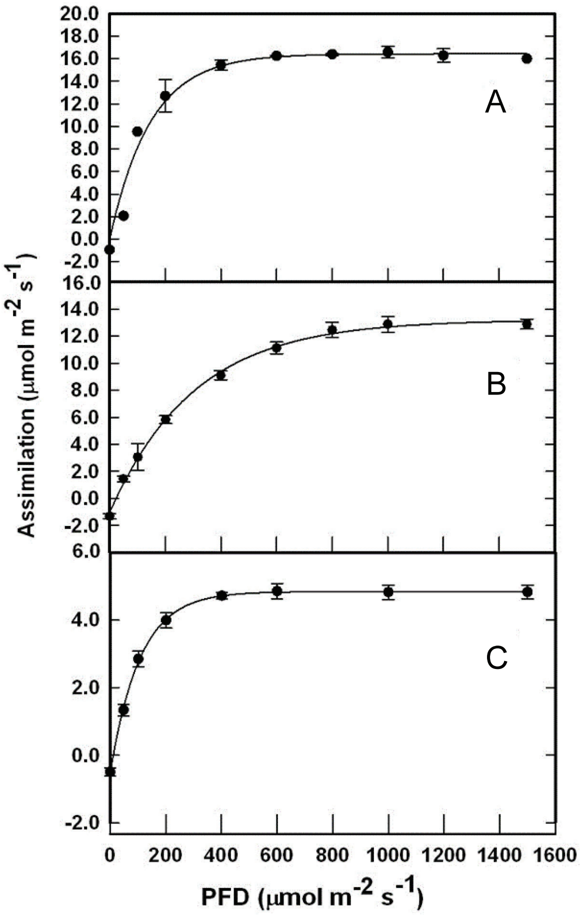

Fig. 3 Photosynthetic light respose curves: A) *Machilus bokorensis*, B) *Syzygium formosum*, and C) *Lithocarpus elephantum*.

our study species are similar to published values for wet tropical forests (Bonal *et al*., 2000). No significant relationship was present between $\delta^{13}C$ and photosynthetic rate (Fig. 2C), indicating that water use efficiency was not a strong control on photosynthesis. No significant difference in $\delta^{13}C$ between dwarfed treelets and other growth forms was found.

Light response curves measuring net photosynthetic assimilation against solar irradiance showed an adaptation to growth at relatively low light intensities which is a result of the day time cloud cover that characterizes Bokor for much of the year. *Machilus bokorensis* and *Lithocarpus elephantum* showed peak rates of photosynthesis at a light intensity of only 450-550 µmol m^{-2} s^{-1}, a level less than one quarter that of full sun, whereas *Syzygium formosum* showed higher light saturation at about 800 µmol m^{-2} s^{-1} (Fig. 3).

An unexpected result of our gas exchange studies was the observation that afternoon values of net photosynthetic assimilation were often low to very low compared to morning measurements from the same plants. In some cases, we observed complete stomatal closure during the afternoon. An example of this phenomenon is depicted with CO_2 response curves for *Lithocarpus elephantum* (Fig. 4). Despite constant temperature, VPD regulation and saturating light intensity throughout the measurements, the assimilation rate at saturating CO_2 concentrations was about 15 µmol m^{-2} s^{-1} in the morning, three times the rates observed in afternoons under identical conditions.

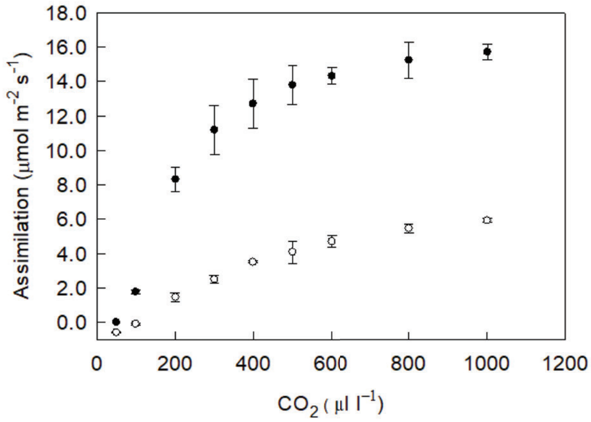

Fig. 4 CO_2 response curves for *Lithocarpus elephantum* under saturating light intensity of 900 µmol m^{-2} s^{-1} in mid-morning (closed circles) and mid-afternoon (open circles).

Discussion

The dwarfing of what are, at lower elevations, commonly tall trees involves a complex gradient in interactions between soil depth, water relations, soil nutrient availability, and wind exposure. The leaf morphological and ecophysiological traits measured in our study revealed only one trait where dwarfed treelets differed significantly from woody shrubs and low-stature colonizing shrubs. This trait was leaf size with dwarfed treelets having consistently larger leaves.

Dwarfing and restrictions on rates of tree growth could be hypothetically related to the presence of thick leaves with a high leaf specific weight in response to high winds. If this were the case, we would have expected to find the widespread presence of leaves with a high leaf specific weight. However, the ranges and means for leaf specific weight did not differ significantly between dwarfed treelets, shrubs, and low-stature colonizing shrubs in our study. Moreover, the ranges of values for our study species are consistent with published ranges for wet tropical forests (Reich *et al*., 1991; Reich, 1993; Kenzo *et al*., 2004; Long *et al*., 2015).

A variety of additional hypotheses have been proposed to explain the low stature and slow growth of tropical montane cloud forests (Weaver *et al*., 1986; Bruijnzeel & Veneklaas, 1998; Tanner *et al*., 1998; Bruijnzeel *et al*. 2011). Two of these hypotheses relate to low fertility and extreme soil acidity coupled with reduced decomposition and mineralization rates and waterlogged soils that reduce root respiration. While not tested in our research, these contributing factors are clearly present given the skeletal acidic sandstone substrate and high rainfall present on the Bokor Plateau. Strong winds are likewise responsible for impacting the architecture and stature of trees in coastal sites and are certainly a secondary factor in Bokor and many other dwarf cloud forests.

More relevant to our work is the hypothesis that cloudy conditions with low levels of solar radiation and cool growing season temperatures limit rates and total amounts of net photosynthetic assimilation (Graham *et al*., 2003). As described above, our measured rates of net photosynthetic assimilation are consistent with those reported in many other studies of wet tropical forest trees where dwarfing does not occur (Reich *et al*., 1991; Reich, 1993; Kenzo *et al*., 2004). This strongly suggests that limits on maximum rates of photosynthesis are not the cause of dwarfing and slow growth rates in heathland scrub on the Bokor Plateau. Rather than being limited by low levels of solar irradiance under frequent heavy cloud cover, our measurements demonstrate a widespread adaptation to low light conditions at Bokor with light saturation for photosynthesis at irradiance levels of only about one quarter those of full sun. This is a significantly lower light saturation level than that reported for canopy leaves of tropical Dipterocarpaceae (Kenzo *et al*., 2006). Similar photosynthetic adaptation to low light levels has previously been reported in *Dacrydium elatum* (Roxb.) Wall. ex Hook. (Podocarpaceae) in Bokor (Rundel *et al*., 2016).

Our observations of afternoon stomatal closure and low rates of assimilation are difficult to explain given what would appear to be favourable conditions in the afternoon. It has been suggested that periodic water shortages may occur in montane tropical forests where shallow rocky soils are present despite high rainfall. Although we cannot fully test this hypothesis without more controlled greenhouse and field studies (Harley *et al*., 1987), our observation of common stomatal closure in the afternoon suggests that this may be possible since stomatal closure has been observed in tropical montane cloud forests in response to high evaporative demands (Körner *et al*., 1983) and has been reported in tropical tree saplings in wet forests in Costa Rica (Oberbauer, 1985). Extreme sensitivity of stomata to soil drought has also been shown in tropical rainforest trees in French Guiana (Bonal *et al*., 2000). As such, it may be that the skeletal soils on the Bokor Plateau limit water availability on a diurnal basis due to limits on effective root volume. An alternative hypothesis was suggested by Zhang *et al*. (2009), who noted that afternoon stomatal closure in both the wet and dry season was related to high levels of photorespiration acting as a photo-protectant.

Acknowledgements

We thank Meng Monyrak, Sok Sothea, and Hong Lork for field assistance, and the Department of Nature Conservation and Protection in the Cambodian Ministry of the Environment for arranging permission to work in Bokor National Park. Our field work was greatly assisted by Kansri Boonpragob and the late Mark Patterson. We gratefully acknowledge the logistic support of the national park staff in providing housing. This project was funded in part by the UCLA Asian Studies Center and Arnold Arboretum of Harvard University.

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