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STRUCTURE AND ECOLOGICAL FUNCTION IN A TROPICAL MONTANE SPHAGNUM BOG OF THE ELEPHANT MOUNTAINS, BOKOR NATIONAL PARK, CAMBODIA

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ABSTRACT

The sandstone plateau of the southern tip of the Elephant Mountains in Bokor National Park, southeastern Cambodia, receives more than 5,000 mm of annual rainfall. These conditions produce shallow acid soils and a well-developed sphagnum bog called the Popkvil bog. The matrix of plant cover in the bog is dominated by four graminoid species: *Eremochloa eriopoda* (Poaceae), *Eriocaulon* cf. *henryanum* (Eriocaulaceae), *Leptocarpus disjunctus* (Restionaceae), and *Centrolepis cambodiana* (Centrolepidaceae). Sphagnum is abundant, growing in rings around graminoid clumps and low shrub islands of *Hedyotis rosmarinifolia* (Rubiaceae), *Ploiarium alternifolium* (Bonnetiaceae), *Calophyllum calaba* (Clusiaceae), *Syzygium zeylanicum* (Myrtaceae), and *Hygrophila angustifolia* (Acanthaceae). Maximum photosynthetic rates ranged from 4.4-8.1 μmol m^{-2} s^{-1} in four herbaceous perennials and from 5.8-14.7 μmol m^{-2} s^{-1} in the five shrub species measured, while the one C_4 species present, *Fimbristylis dichotoma* (Cyperaceae), had a higher value of 18.6 μmol m^{-2} s^{-1}. Carbon isotope ratios (δ) ranged from –26.1 to –28.8 o/oo in nine C_3 species measured, indicating relatively high water use efficiencies for such a wet environment. Increasing ecotourism in Bokor National Park will require special attention in managing the fragile habitat of the Popokvil bog.

INTRODUCTION

The sandstone massif of the Elephant Mountains rises abruptly from a narrow coastal plain along the Gulf of Thailand in southern Cambodia to an elevation of 1079 m. The combination of the steep south-facing slopes of the range and close proximity of the sea produces unusually wet conditions on the southwestern slopes and upper plateau of this range where more than 5000 mm of rain falls annually. This heavy rainfall acting on the quartz sandstone of the plateau bedrock of the Elephant Range has produced skeletal and highly leached acid soils. As a result of these conditions, the plateau supports unusual communities of dwarf forest and sclerophyllous shrubland despite the high rainfall (DY PHON, 1970). Within this matrix of dwarf forest and shrubland are small areas of permanent bog habitat where soils remain saturated throughout the year because of indurated soil

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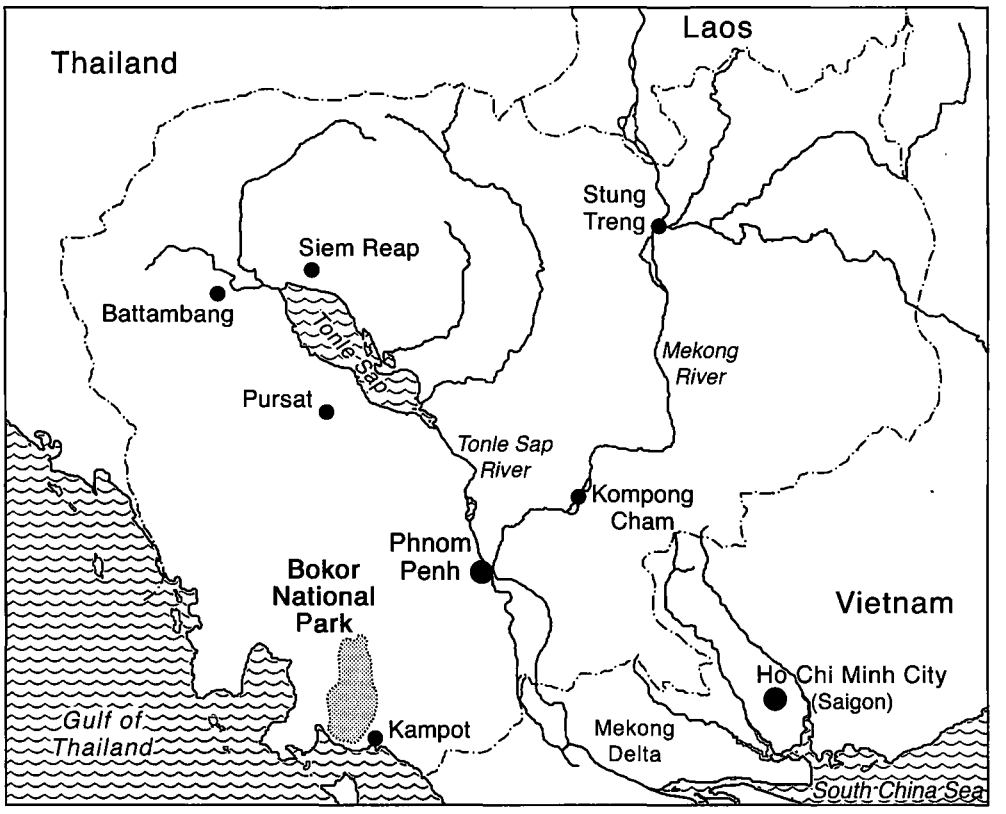

Figure 1. Location of Bokor National Park in southeastern Cambodia.

layers. Bogs of this type are relatively rare in mainland Southeast Asia and remain poorly studied. In this paper we report on the community structure of the Popokvil bog located in Bokor National Park near the southern margin of the Elephant Mountains (Fig. 1). We further characterize ecophysiological traits of ten of the important bog species to provide comparative data on photosynthetic capacity and water use efficiency for both herbaceous perennials and low shrub species.

MATERIALS AND METHODS

Site Description

Field studies were carried out over the period March 6–13, 2001, on the plateau area of the Elephant Mountains in Bokor National Park, Kampot Province, Cambodia (Fig. 1). Bokor National Park was established in 1997 and covers an area of 140,000 ha of largely undisturbed habitat. While small areas of rocky soils and vernal pools occur throughout the sclerophyll shrublands on the plateau area, we focused our attention on a unique sphagnum bog near the former village site of Popokvil. Sphagnum and many of the other bog species

described here are present in scattered patches on other rocky basins with poor drainage on the upper portions of the Bokor plateau, but only at the Popokvil site is there a well-developed bog community.

The Popokvil sphagnum bog is located approximately 4 km NNE of the old Hotel Bokor on the road to the former site of Popokvil (Fig. 2). Although an open area of grassy cover extends about 0.5 km in a north-south and east-west direction around the bog itself, most of this area is well enough drained to support tall grasses and low shrub cover. The sphagnum bog itself extends over a smaller area of approximately 200 x 80 m to the east of the road. The bog soils are saturated or have standing water over much of the year, drying out at their surface only in February and March.

We classified plant species into growth form categories of perennial graminoids, herbaceous perennials (non-graminoid, including petaloid monocots), subshrubs (perennials with a woody base), and low shrubs. Both of these latter groups would be considered to be chamaephytes as they do not reach 0.5 m in height. Plant collections made during our fieldwork were identified by DJM and other appropriate taxonomic experts for special groups. Voucher collections are filed as accessions to the Arnold Arboretum Herbarium (A) in the Harvard University Herbaria.

Rainfall is extremely high on the Bokor Plateau, averaging more than 5000 mm annually. Records for Bokor (950 m elevation) at the southern end of the plateau show a mean annual rainfall of 5309 mm (TIXIER, 1979, Fig. 3), while the Val d'Emeraude at a slightly lower elevation on the southeast margin of the plateau receives a mean of 5384 mm (DY PHON, 1970). The distribution of this rain, however, is strongly seasonal, peaking

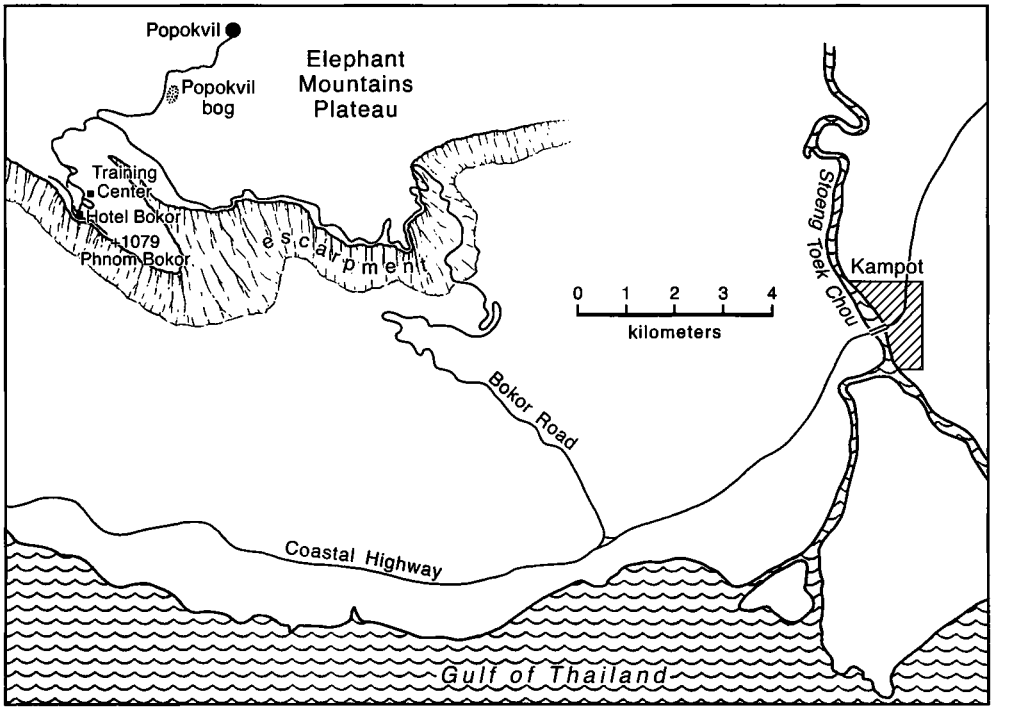

Figure 2. Map of field study site of Popokvil bog at the southern portion of Bokor National Park.

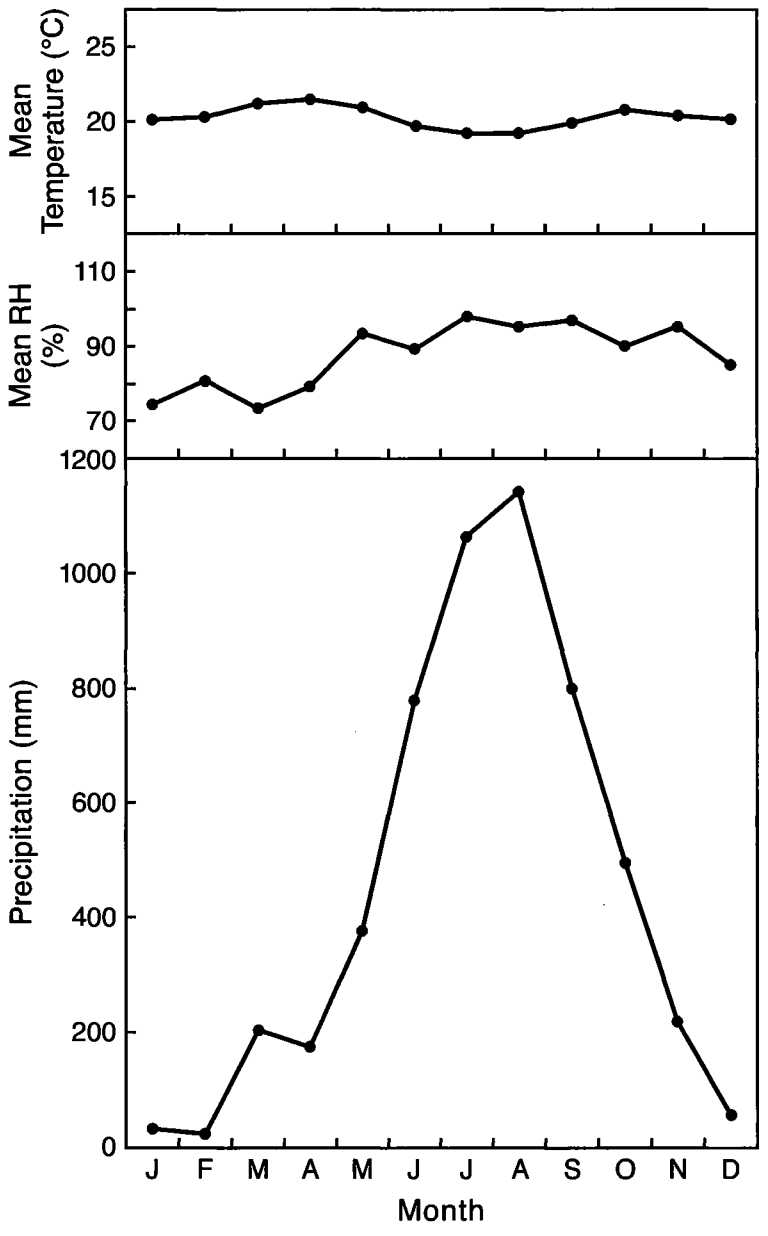

Figure 3. Seasonal course of mean daily temperature, mean daily relative humidity (RH), and rainfall at Bokor, Bokor National Park, Elephant Mountains, Cambodia. Data from Dy Phon (1972) and Tixier (1979).

July and August and dropping to 50 mm or less in January and February at both stations. The Val d'Emeraude experiences rain virtually every day from May through October, but on only 12 days on average in March, the month of our sampling (DY PHON, 1970). Mornings during our field studies were typically partially sunny with scattered clouds moving overhead, while heavier overcast and brief periods of intense rain were present almost every afternoon. Mean monthly temperatures are relatively constant throughout the year at Bokor (Fig. 3), 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).

The sandstone substrate of the plateau of the Elephant Mountains weathers into an acidic coarse white sand. Soil profiles of the sphagnum bog as described by Dy Phon (1970) consist of upper sandy *A* horizons no more than 90 cm in thickness with declining organic matter and increasing saturation with depth. The *B* horizon is a thin indurated layer of white sand, with yellowish sandstone parent material below this level. We measured the pH of the soil solution along the margin of the bog and in bog soils as 4.6 during our study.

Experimental Methods

The community structure of the *Sphagnum* bog was sampled using line transects. Semi-quantitative cover estimates were made by sampling a series 0.05-m^2 plots (20 x 25 cm) arrayed every 2 m along 100 m of line transects running across the central bog area. From these data, the relative frequency of occurrence within the 50 plots was calculated. For each of the plot plots sampled, every species present was categorized into one of six levels of coverage: + = present with <1% cover, 1 = 1–5% cover, 2 = 6–10% cover, 3 = 11–25% cover, 4 = 26–50% cover, and 5 = >50% cover. A mean coverage indicator value for all plots was calculated for each species by summing the numerical category values and dividing by 50, the number of plots sampled. Also calculated was a mean coverage indicator value for those plots where that particular species was present. Thus, an infrequent but locally abundant species would have a low value for all plots but a relatively high value for plots where it was present. Neither of these two indicator values is truly quantitative as they represent a semi-quantitative indication of the relative amount of cover for each species.

Ecophysiological measurements were carried out to characterize the photosynthetic rates, water use efficiencies as measured by carbon isotope ratios, and metabolic systems for five common herbaceous perennials and five common low subshrub and shrub species in the Popokvil bog. Gas exchange measurements were made under natural light conditions in the morning using a LICOR-6200 gas exchange system (LICOR, Lincoln, Nebraska). Individual measurements were made on leaf tissue from each of three individuals of each study species.

Samples of photosynthetic tissues were collected from each of three individual plants of all study species at the field site and air-dried. Natural $\delta^{13}C$ ratios were measured on these samples at the Duke University Phytotron (Durham, North Carolina) on a SIRA Series II isotope ratio mass spectrometer (VG Isotech, Middlewich, U.K.) operated in automatic trapping mode after combustion of samples in an elemental analyzer (NA1500, Carlo Erba Instrumentazion, Milan, Italy). The reference CO_2, calibrated against standard Pee Dee belemnite (PDB), was obtained from Oztech (Dallas, Texas).

RESULTS AND DISCUSSION

Community Structure and Diversity

There are relatively sharp forest/grassland boundaries around the margin of the open area that supports the Popokvil bog. A west-east gradient across this habitat begins with dense bracken and low shrub cover on disturbed areas with less saturated soils along the Popokvil road. Dominant species indicative of disturbance included *Pteridium aquilinum* (L.) Kuhn (Dennstaediaceae), *Melastoma malabathricum* L. ssp. *normale* (D.Don) K. Meyer (Melastomataceae), *Rhodomyrtus tomentosa* Wight (Myrtaceae), *Dicranopteris linearis* (Burm.) Underwood (Gleicheniaceae), and *Elephantopus scaber* L. (Asteraceae). This community graded into the waterlogged central bog habitat where sphagnum and typical bog graminoids are present. At the other margin of the bog there was a rapid transition to a low forest community 5–15 m in height dominated by *Dacrydium elatum* (Roxb.) Wallich ex Hook. (Podocarpaceae), with *Podocarpus pilgeri* Foxw. (Podocarpaceae), *Vaccinium viscifolium* King & Gamble (Ericaceae), and *Lithocarpus leiophyllus* A. Camus (Fagaceae) as common associates.

A diverse community of graminoids dominated the general structure of the bog, forming a low matrix 20–30 cm in height. Scattered through this matrix with a very low total cover were small islands of shrub establishment where soils had built up to allow better drainage. Four graminoid species, each representing a different family, provided the major part of the matrix cover. These were *Eremochloa eriopoda* C.E. Hubb (Poaceae), *Eriocaulon* cf. *henryanum* Ruhl. (Eriocaulaceae), *Leptocarpus disjunctus* Mast. (Restionaceae), and *Centrolepis cambodiana* Hance (Centrolepidaceae). These were the only four vascular plant species that occurred with a coverage of 25% or more in any single 0.05 m^2 plot. *Eremochloa* and *Eriocaulon* were almost ubiquitous in their distribution in the bog. The highest coverage occurred with *Eremochloa eriopoda* which had a mean cover value of 2.6 (Table 1), indicating that the average plot had close to 10% cover. This species was present in 92% of the plots sampled. Second in importance was *Eriocaulon* cf. *henryanum* with a mean cover value of 1.5 (2.3 in plots where it was present) and a relative frequency of 86%. *Leptocarpus disjunctus* and *Centrolepis cambodiana* were each present in 50% of the plots sampled, and had mean cover values of 1.2 and 1.1, respectively. Both had mean cover values above 2 in plots where they were present.

Two other monocot species had relatively high frequency values in the sample plots but low cover values (Table 1). *Xyris complanata* R.Br. (Xyridaceae) was present in 44% of the sampled plots and had a mean cover value of 0.7. An unidentified species of *Panicum* had a relative frequency of 38% and a mean cover value of 0.6. Next in importance among species forming elements of the matrix of graminoid cover in the bog was the sedge *Fimbristylis dichotoma* (L.) Vahl subsp. *dichotoma* with a relative frequency of 16% and a mean cover value of 0.3. This low mean cover value masks the local abundance of this species which occurred with up to 25% cover in some plots where it was present.

Sphagnum was found in 86% of the plots sampled, usually as rings around graminoid clumps or small shrub islands, and had a mean cover value of 2.0. Tixier (1979) identified these as *S. beccarii* Hpe. and *S. cuspidatum* Her. Microbial crusts of cyanobacteria cementing areas of open soil were present in 24% of the plots sampled and had a mean cover value of 1.3 (Table 1).

An additional eight vascular plant species were encountered in low frequencies in less than 10% of the sample plots (Table 1). Eight species were observed in the area of the sample plots but not sampled, giving a total of 23 species present. The flora included four species of small carnivorous plants. These were *Drosera burmannii* Vahl. (Droseraceae), *Nepenthes kampotiana* Lecomte (Nepenthaceae), and *Utricularia bifida* L. and *U. caerulea* L. (Lentibulariaceae). *Nepenthes kampotiana*, a tiny plant with pitchers only a few cm in length, has been considered to be a local endemic at Bokor. However, there is a distinct gradation in morphological form between this taxon and the larger *N. thorelii*, which is common at the forest edge around the bog, suggesting that the two forms may not warrant species separation.

Other small herb species present in the bog included the tiny *Gentiana ting-nung-hoae* Halda (Gentianaceae), *Xyris capensis* Thunb. (Xyridaceae), *Burmannia disticha* L. (Burmanniaceae), *Salomonia longiciliata* Kurz. (Polygalaceae), and *Lycopodium cernuum* L. (Lycopodiaceae). Other species reported from this bog (Dy Phnon 1970) that were not collected in our study included *Drosera peltata* Smith (Droseraceae), *Carex indica* L. (Cyperaceae), and an unidentified terrestrial species of *Dendrobium* (Orchidaceae).

Small shrub islands scattered across the bog were dominated by single or multiple species reaching to no more than 30–50 cm in height and low mounds 0.5–2 m across.

Table 1. Relative frequency and coverage values for dominant plant species in the Popokvil bog of Bokor National Park. See text for discussion of the mean cover values and how they were calculated. A value of 1 = a cover of 1–5%, 2 = a cover of 6–10%, and 3 = a cover of 11–25%.

Species	Family	Growth form	Relative frequency (%)	Mean cover value	Mean cover value where present
Eremochloa eriopoda	Poaceae	perennial graminoid	92	2.6	2.8
Eriocaulon cf. *henryanum*	Eriocaulaceae	perennial graminoid	86	1.5	2.3
Leptocarpus disjunctus	Restionaceae	perennial graminoid	50	1.2	2.4
Centrolepis cambodiana	Centrolepidaceae	perennial graminoid	50	1.1	2.2
Xyris complanata	Xyridaceae	herbaceous perennial	44	0.7	1.5
Panicum sp.	Poaceae	perennial graminoid	38	0.6	1.5
Fimbristylis dichotoma	Cyperaceae	perennial graminoid	16	0.3	2.0
Hedyotis rosmarinifolia	Rubiaceae	subshrub	10	0.1	1.4
Nepenthes kampotiana	Nepenthaceae	herbaceous perennial	10	0.1	1.0
Utricularia bifida	Lentibulariaceae	herbaceous perennial	10	0.1	1.0
Drosera burmannii	Droseraceae	herbaceous perennial	10	0.1	1.0
Ploiarium alternifolium	Bonnetiaceae	shrub	8	0.1	1.2
Gentiana ting-nung-hoae	Gentianaceae	herbaceous perennial	6	0.1	1.0
Syzygium zeylanicum	Myrtaceae	shrub	2	+	1.0
Lycopodium cernuum	Lycopodiaceae	herbaceous perennial	2	+	1.0
Sphagnum spp.	Sphagnaceae	moss	86	2.2	2.0
Microbial crust		cyanobacteria	70	1.9	1.3

These islands were small mounds rising a few centimeters above the general soil level of the bog. Rings of *Sphagnum* were commonly present around the edges of these shrub islands at the edge of the canopies. Low subshrubs and shrubs forming these islands were *Hedyotis rosmarinifolia* (Pitard) Craib (Rubiaceae), *Ploiarium alternifolium* (Vahl) Melchior (Bonnetiaceae), *Calophyllum calaba* L. (Clusiaceae), *Syzygium zeylanicum* (L.) DC. (Myrtaceae), and *Hygrophila angustifolia* R.Br. (Acanthaceae). Although not present within the Popokvil bog itself, other nearby wetlands have small populations of the tree *Melaleuca cajuputi* Roxb. (Myrtaceae), a species more characteristic of brackish wetlands near the coast or along the Mekong delta area.

Vascular plant species richness in the sample plots was moderately high despite their small size of 0.05 m^2. Only one of the 50 plots sampled had less than three species present, with a modal number of 5 species and a high of 8 species present.

Physiological Ecology

Comparisons of photosynthetic rates between herbaceous perennial and subshrub/shrub species did not find clear differences. The highest mean rate measured was 18.6 μmol m^{-2} s^{-1} in *Fimbristylis dichotoma*, a species that uses C_4 metabolism as shown by carbon isotope ratios (Table 2). Photosynthetic rates ranged from 4.4–8.1 μmol m^{-2} s^{-1} in the other four herbaceous perennials measured (*Eriocaulon* cf. *henryanum, Leptocarpus disjunctus, Xyris complanata,* and *Nepenthes kampotiana*). These values are generally lower than those of the five subshrub and shrub species, but without a statistically significant difference. *Hygrophila angustifolia* had a moderately high mean photosynthetic rate of 14.7 μmol m^{-2} s^{-1}, while the other four shrub and subshrub species (*Syzygium zeylanicum, Ploiarium alternifolium, Calophyllum calaba,* and *Hedyotis rosmarinifolia*) varied from 5.8–10.2 μmol m^{-2} s^{-1}.

These photosynthetic rates are those present under conditions when light is not limiting. It is almost certainly true, however, that light is limiting over much of the year at this site. Light saturation occurs at about 400 μmol m^{-2} s^{-1} in the Bokor shrub species that we have studied. Even under the relatively dry conditions in March when we carried out or measurements, light was frequently below this level for much of the day, particularly in the afternoon. We would expect that light is limiting on most days of the year from April through November when rains are heavy.

The mean carbon isotope ratio ($\delta^{13}C$) measured in *Fimbristylis dichotoma* was –11.5 o/oo (Table 2), clearly indicating the presence of C_4 metabolism in this species. The five subshrub and shrub species showed a moderately small range of $\delta^{13}C$ values from –27.5 o/oo in *Ploiarium alternifolium* to –28.7 o/oo in both *Syzygium zeylanicum* and *Hediotys rosmarinifolia. Nepenthes kampotiana* had a similar value of –28.8 o/oo. The three other herbaceous perennials, however, all showed lower δ values of –26.0 to –26.9 o/oo, suggesting a higher water use efficiency than that present in the five subshrub and shrub species. These are high values for a site with such high annual rainfall, but consistent with hypotheses about the physiological consequences of xeromorphy in response to low nutrient availability in bog habitats (SMALL, 1972). Limited rooting distribution on raised mounds in saturated bog soils may produce periods of physiological drought for sub-shrub and shrub species during the brief periods of sunny weather.

Table 2. Photosynthetic maximum (mean and standard deviation), relative water use efficiency as measured by carbon isotope ratios ($\delta^{13}C$; mean and standard deviation), and metabolic systems for five important herbaceous perennials and five low subshrub and shrub species in the Popokvil bog, Bokor National Park.

Species	Growth form	Photosynthetic maximum ($\mu mol\ m^{-2}\ s^{-1}$)		$\delta^{13}C$ (o/oo)		Metabolic system
		mean	sd	mean	sd	
Eriocaulon cf. *henryanum*	perennial graminoid	5.1	1.0	-26.1	1.6	C_3
Leptocarpus disjunctus	perennial graminoid	8.1	2.6	-26.0	0.5	C_3
Xyris complanata	herbaceous perennial	4.4	2.7	-26.9	0.2	C_3
Nepenthes kampotiana	herbaceous perennial	5.7	1.7	-28.8	0.8	C_3
Fimbristylis dichotoma	perennial graminoid	18.6	7.2	-11.5	0.1	C_4
Ploiarium alternifolium	subshrub	6.7	2.9	-27.5	0.8	C_3
Hedyotis rosmarinifolia	subshrub	11.4	1.6	-28.7	0.4	C_3
Syzygium zeylanicum	low shrub	5.8	1.3	-28.7	1.1	C_3
Calophyllum calaba	low shrub	9.6	0.1	-28.0	0.9	C_3
Hygrophila angustifolia	subshrub	14.7	1.2	-28.2	1.0	C_3

CONCLUSIONS

Peat bog forests are widespread in Southeast Asia and have been described in some detail (PAGE, 1997), including Cambodia where they are widespread around Tonle Sap and in the Mekong Delta area. The Popokvil sphagnum bog in the Elephant Mountains is very different, however, in that large peat deposits have not formed. Only scattered descriptions of bog habitats in Southeast Asia have been previously published. One such account is that of sphagnum bogs near Dalat in Vietnam (BARRY *ET AL.*, 1956). Perhaps the most relevant ecological literature for understanding the Popokvil bog and its isolation comes from studies of tropical inselbergs in South America and Africa (POREMBSKI *ET AL.*, 1994; POREMBSKI & BARTHLOTT, 2002).

The carnivorous genus *Nepenthes* ranges through Southeast Asia in open peat bog forests and acid swamps (PHILLIPS, 1996; DE FOUCAULT, 2000), indicating an ecological linkage with the Popokvil bog. However, the genus has a relatively limited distribution in mainland Southeast Asia where seasonal rainfall regimes are typical. Similarly, *Drosera* species are present in scattered montane location across Southeast Asia where skeletal acid and nutrient poor soils are present, as in pine forests at Phu Kradung in Thailand.

The flora of the Popokvil bog, like those of Indomalesian bogs, shows interesting affinities with the Southern Hemisphere (Table 3). The importance of such families as the Restionaceae and Centrolepidaceae among the bog herbs and the added presence of sclerophyll shrublands with Proteaceae and Myrtaceae and the conifer genus *Dacrydium* in the surrounding dwarf forests all are reminiscent of a Gondwanaland element in the flora.

The Elephant Mountains are home to a number of endemic vascular plant species (DY PHON, 1970), and at least two of these are present in the bog flora at Popokvil. These are *Gentiana ting-nung-hoae* and *Nepenthes kampotiana*, if it the latter is indeed distinct from *N. thorelii*.

Table 3. Biogeographic distributions of Popokvil bog species. These distributions reflect the current literature but these species may well occur in other places that are poorly collected.

Burmannia disticha.—Widely distributed in the Asian and Australasian tropics and inhabits a wide range of ecological conditions including permanently waterlogged soil to fissures in rock up to 3500 m altitude.

Centrolepis cambodiana.—Known from Cambodia, Laos and northern and eastern Thailand. It is described as only tolerating seasonally waterlogged soil rather than permanently waterlogged soil (see Larsen, Flora of Thailand 2: 161; 1972)

Drosera burmannii.—Known from India to Japan and through Indochina and Malaysia to northeastern Australia.

Eremochloa eriopoda.—Known from Thailand and Indochina.

Eriocaulon cf. *henryanum.*—This species is known from China and Vietnam but has not previously been recorded for Cambodia; fertile material should be collected to verify this identification.

Gentiana ting-nung-hoae—Known only from Bokor.

Fimbristylis dichotoma—Pantropical

Hedyotis rosmarinifolia—Cambodia and Thailand.

Leptocarpus disjunctus—An outlier in a genus otherwise found in Chile and Australasia. In its Southeast Asian and Malesian distribution it is considered typically as a plant of sandy areas near the sea or inland saline sandy soil. It is known from Hainan, Vietnam, Laos, Cambodia, Thailand and the Malay Peninsula.

Ploiarium alternifolium—This species is part of a western Malesian distribution that extends into Peninsular Thailand and then makes the jump over to Cambodia. It is otherwise known in Malaysia, Borneo and Sumatra. It is clearly very rainfall dependent and will not tolerate prolonged dry periods.

Salomonia longiciliata—Burma, Cambodia, Vietnam, Borneo and the Philippines; in bogs, grassy areas and forest.

Syzygium zeylanicum—From India and Sri Lanka through Malaysia; in peat swamp, mixed deciduous and evergreen forests.

Utricularia bifida—From India to Japan and through Indochina and Malaysia to northeastern Australia.

Utricularia caerulea—From India to Japan and through Indochina and Malaysia to northeastern Australia.

Xyris capensis—Pantropical in South America, South Africa, India, China, Indochina and Malaysia in wet open places.

Xyris complanata—A widespread species found from India and China to Australia in wet open places.

As Bokor National Park becomes increasingly visible for ecotourism and visitor usage increases, there will be increasing pressures on preserving the natural features and biodiversity of the park (ANONYMOUS, 2002). The fragile habitat of the Popokvil bog will require special attention in managing this area.

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