Dacrydium elatum (Podocarpaceae) in the montane cloud forest of Bokor Mountain, Cambodia

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ឧទាហរណ៍ជាគំរូមួយនៃព្រៃតឿនៅតាមភ្នំនៃព្រៃត្រូពិច អាចត្រូវបានឃើញនៅតំបន់ខ្ពង់រាបនៃជួរភ្នំដំរីក្នុងឧទ្យានជាតិបូកគោ។ ជម្រាលចោទនៅទិសខាងត្បូងនៃជួរភ្នំ និង ជិតសមុទ្របង្កើតជាតំបន់មានលក្ខខ័ណ្ឌសើមខុសប្រក្រតី ដែលមានកម្ពស់ទឹកភ្លៀងលើសពី ៥០០០ ម.ម នៃកម្ពស់ទឹកភ្លៀងប្រចាំឆ្នាំ មានសណ្ឋានដាច់ៗ និងមានអាស៊ីតខ្ពស់។ លក្ខខ័ណ្ឌទាំងនេះបង្កើតឲ្យមានព្រៃតឿ និង ទីចុលព្រឹក្សដែលភាគច្រើនជាប្រភេទ *Dacrydium elatum* (Podocarpaceae)។ បម្រែបម្រួលទំហំដើមឈើត្រូវបានប្រទះឃើញកម្ពស់ចាប់ពី ៥-៧ ម. នៅតាមជម្រាលជិតកំពូលនិងបន្តរហូតតាមតំបន់បម្រែបម្រួល និង កម្ពស់ដល់ ១៥ ម. ក្នុងតំបន់ក្បែរទឹកធ្លាក់ពពកវិល។ ស្លឹកដែលមានសណ្ឋានដូចស្រកានៃដើមឈើពេញវ័យ និង សណ្ឋានទ្រវែងស្រួចចុងនៃកូនរុក្ខជាតិប្រភេទ *D. elatum* បង្ហាញពីទំនោរកទិសពន្លឺធ្វើរស្មីសំយោគ ហើយលក្ខណៈនេះក៏បង្ហាញពីការបន្សាំទៅនឹងលក្ខខ័ណ្ឌពពកច្រើននៃជម្រកនៅភ្នំបូកគោ។ ទម្រង់ទាំងពីរបានឈានដល់ ៥០% នៃអត្រាអតិបរមានៃការជ្រាបថាមពលពន្លឺកម្រិតទាបគឺត្រឹមតែ ២០០មីក្រូម៉ូល/ម៉ែត្រ/ វិនាទី។ អត្រាអតិបរមានៃការជ្រាបថាមពលពន្លឺឡើងខ្ពស់រហូតដល់ប្រហែល ៨០០ មីក្រូម៉ូល/ម៉ែត្រ/ វិនាទី នៅក្នុងទម្រង់ស្លឹកទាំងពីរ ប៉ុន្តែវាខ្ពស់ជាងនេះសម្រាប់ស្លឹកកូនរុក្ខជាតិតូចៗ។ អត្រាធ្វើរស្មីសំយោគខ្ពស់កើតមាននៅពេលប្រសិទ្ធភាពនៃការប្រើប្រាស់ទឹកថយចុះ។

Abstract

A classic example of a dwarf montane tropical forest can be seen in the plateau area of the Elephant Mountains in Bokor National Park. The steep south-facing slopes of the range and close proximity of the ocean produces unusually wet conditions with more than 5,000 mm of rainfall annually, and skeletal and highly leached acid soils. These conditions produce a dwarf forest and sclerophyllous shrubland dominated by *Dacrydium elatum* (Podocarpaceae). A distinct gradient in tree size is present, ranging from heights of only 5–7 m near the escarpment through a transition zone to heights of 15 m about 4 km inland near the Popokvil Falls. The scale-like foliage of mature trees and linear-lanceolate foliage of saplings of *D. elatum* display distinctive light response curves for photosynthesis, with both showing adaptations to the cloudy conditions of their habitat on Bokor Mountain. Both forms reached 50% of maximum rates of net assimilation at a low irradiance of only 200 μmol m^{-2} sec^{-1}. Maximum assimilation rates peaked at about 800 μmol m^{-2} sec^{-1} in both forms, but were higher in the sapling foliage. Higher rates of photosynthesis come at the expense of declining water use efficiency.

Key Words Bokor National Park, *Dacrydium*, Podocarpaceae, tropical cloud forest, photosynthetic rate.

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Introduction

Although tropical montane cloud forests throughout the world exhibit a characteristic structure of dwarfed stature and low productivity, there is no single environmental factor, with the exception of physically low cloud cover, that is shared by all of these forests (Bruijnzeel & Veneklaas, 1998). High winds, saturated soils, impeded root respiration, physiological drought, high soil leaching with low nutrient availability, limited rooting volume of shallow soils, reduced solar insolation, and high humidity with reduced transpiration rates have individually or in combination been suggested as causal agents in stunting (Grubb, 1971, 1977; Weaver *et al.*, 1973). It has also been suggested that the collective influence of these limiting factors may be seen in low rates of canopy photosynthesis (Bruijnzeel & Veneklaas, 1998).

The plateau areas of the Cardamom and Elephant Mountains in southern Cambodia provide classic examples of dwarf tropical montane forests. While lower elevations support a rich wet evergreen forest community of angiosperm trees, the shallow soils and waterlogged depressions on the summits of these mountains are dominated by local mosaics of low sclerophyllous evergreen forest no more than 12–16 m in height. These dwarf forests can occur at any elevation, but are most typical of depressions on the summits or windward ridges of hills at 900–1,400 m elevation on poorly drained sites in a matrix of taller wet evergreen forest (Dy Phon, 1970; Rollet, 1972; Ayervanov *et al.*, 2003). The dominant species in these waterlogged sites are commonly *Dacrydium elatum* (Roxb.) Wall. ex Hook. (Podocarpaceae) and *Tristaniopsis merguensis* (Griff.) P.G.Wilson & J.T.Waterh. (Myrtaceae). A mixture of other tree species may be present, commonly including the conifers *Podocarpus pilgeri* Foxw. and *Dacrycarpus imbricatus* (Blume) de Laub. (Podocarpaceae). Although differing in floristic composition, these dwarf evergreen forests share many ecological features with the better-known *kerangas* heath forests of Borneo, as well as in the presence of *Dacrydium elatum* as a dominant or co-dominant tree (Brünig, 1974).

Our research has been focused on the massif of the Elephant Mountains in Bokor (Preah Monivong) National Park which rises abruptly from a narrow coastal plain along the Gulf of Thailand in southern Cambodia to an elevation of more than 1,000 m asl (above sea level), forming a vertical escarpment at its southern face (Fig. 1). The combination of the steep south-facing slopes of the range and close proximity of the ocean produces unusually wet conditions on the upper plateau of this range where more than 5,000 mm of rain falls annually and the dry season is relatively short (Averyanov *et al.*, 2003). This heavy rainfall has acted on the quartz sandstone substrate of the plateau of the Elephant Mountains to produce skeletal and highly leached acid soils. As a result of these conditions, the plateau supports unusual communities of dwarf forest and sclerophyllous shrubland (Fig. 2) 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 layers (Rundel *et al.*, 2003).

There were two objectives to our study. The first was to assess patterns of canopy architecture in *Dacrydium elatum*, the dominant canopy tree on the Bokor Plateau, in a gradient of sites from near Popokvil Falls to the southern escarpment of Bokor Mountain 4 km to the southwest. This gradient followed declining forest height, shallower soil profiles, and inferred increases in rainfall, cloud cover, and strength of wind. Our second objective was to collect ecophysiological data on the relationship of photosynthesis to solar irradiance in the foliage of *D. elatum* to assess its adaptation to the reduced irradiance caused by frequent cloud cover on Bokor Mountain, and to compare its responses to that of other conifers, both within tropical cloud forests and outside these habitats.

Methods

Study species

Dacrydium elatum is a relatively widespread species of Podocarpaceae with a range of distribution that includes southern China, Myanmar, Cambodia, Thailand, Laos, Vietnam, Malaysia (Peninsular, Sabah, and Sarawak), western Sumatra, and the Philippines where it is commonly found in montane or hill evergreen forests at elevations of 700–2,000 m (Ridley, 1911; Smitinand, 1968; Nguyen & Vidal, 1996; Rundel, 2001; Farjon 2010). It is one of only seven conifer species known from Cambodia (Thomas *et al.*, 2007). Despite its characteristic montane habitat, *D. elatum* is tolerant of saturated soil and oligotrophic conditions and occurs in lowland kerangas forests in Malaysia and Indonesia (Mead, 1925; Kartawinata, 1980; Maloney & McCormac, 1996; Farjon, 2010). In the Cardamom and Elephant Mountains of southern Cambodia it occurs in low evergreen forest, frequently with *Dacrycarpus imbricatus* (Blume) de Laub. (Nguyen & Vidal, 1996).

Under favourable growing conditions, *Dacrydium elatum* forms a tree of moderate size with heights up to 35 m or more and diameters up to 120 cm. The trunk is typically straight with ascending branches that form a

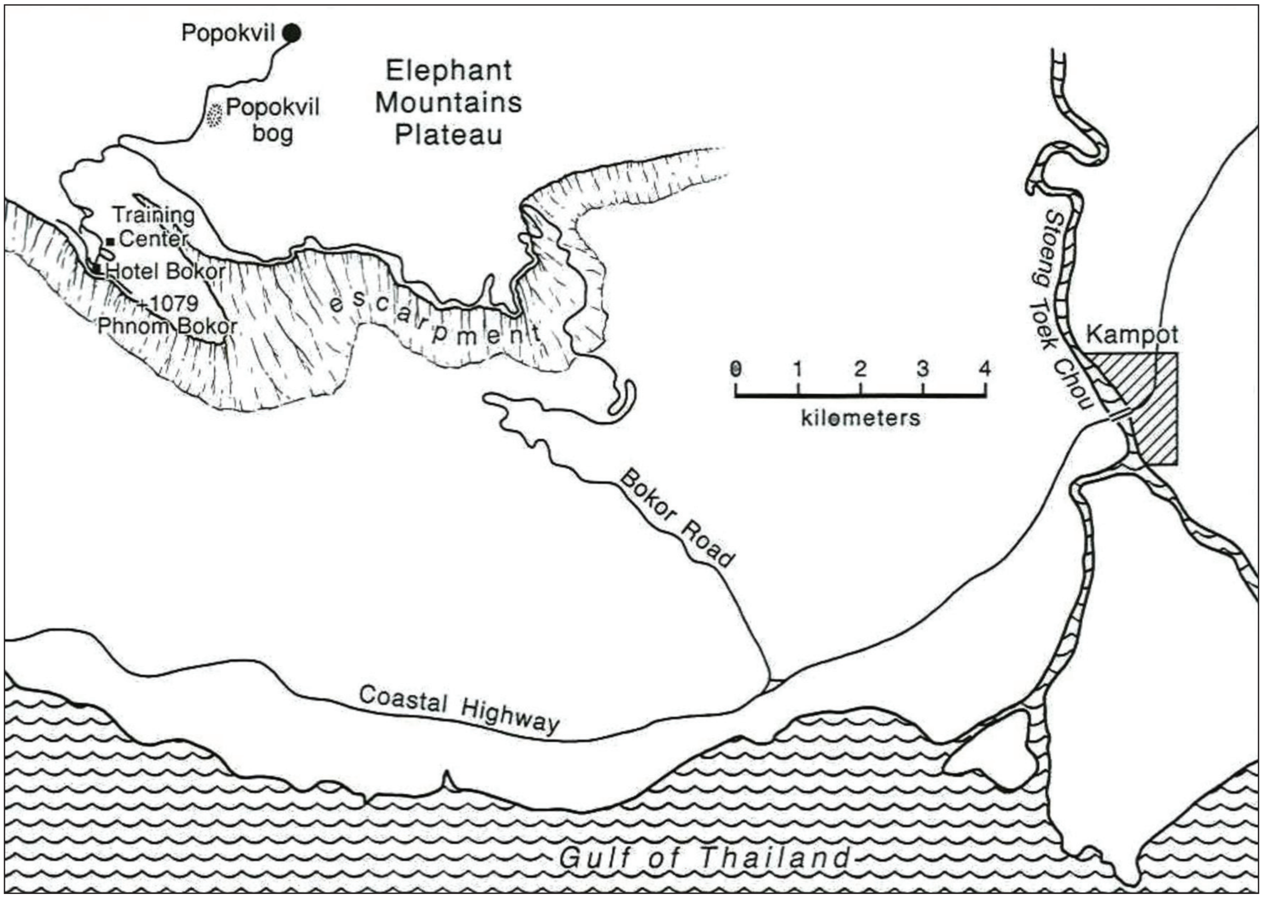

Fig. 1 Location of the study site in the Elephant Mountains Plateau of Bokor National Park. Phnom Bokor (Bokor Mountain) at 1,079 m, is the high point on the plateau. From Rundel *et al.* (2003).

domed canopy. The rough red bark of the trunk splits along vertical fissures and develops peeling strips. One of the unusual features of the species is the dimorphic form of foliage between saplings and mature trees. Juvenile foliage characteristic of young trees is comprised of spreading linear-lanceolate leaves up to 15–20 mm in length and keeled on four sides. In contrast, the foliage on mature trees consists of small and scale-like triangular leaves pressed to the branch shoots (Fig. 3).

Site description

Field studies were carried out from 3–13 March, 2001, on the plateau area 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, much of it relatively undisturbed because of the steep topography (Rundel *et al.*, 2003).

The relatively high plateau of the southern Elephant Mountains slopes gently northward from its peak elevation of 1,062 m at the Bokor Palace Hotel at the edge of the escarpment (10°39′21.82″N, 104°01′35.20″E). Elevation drops 140 m over a 4 km distance from this high point to the site of Popokvil Falls (10°39′29.34″N, 104°03′04.38″E). This distance formed our study gradient and there is a significant change in the height of the dominant vegetation cover. Although environmental microclimates along our gradient were not quantified, the uplift of winds off the Gulf of Thailand produce the strongest wind speeds and highest amounts of rainfall near the south-facing escarpment, and these factors decrease in significance moving inland.

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), consisted of upper sandy A horizons 90 cm thick with declining organic matter and increasing saturation with depth. The B horizon at 90–105 cm was an indurated layer of white sand, with yellowish sandstone parent material below this level. We measured the pH of the soil solution as 4.6 in spot measurements made along the margin of the bog and in bog soils.

The impacted area around the sites of the old hotel and casino complex of Bokor were heavily disturbed and at the time of study (2001) were slowly undergoing a succession from weedy grasses and *Pteridium aquilinum* (L.) Kuhn to a scattered cover of low colonizing shrubs such as *Rhodamnia dumetorum* (DC.) Merr. & L.M. Perry (Myrtaceae), *Melastoma malabathricum* L. (Melastomataceae), *Ardisia crenata* Sims subsp. *crassinervosa* (E. Walker) C.M. Hu & J.E. Vidal, and *A. smaragdina* Pit. (Primulaceae). Most of this area has since been transformed with the development of new infrastructure and a hotel.

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 of 5,384 mm (Dy Phon, 1970). The distribution of this rain is strongly seasonal, however, peaking in July and August and dropping to 50 mm or less per month 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 on Bokor Mountain, 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).

Sampling design

We sampled stem diameters at breast height and heights of 12–20 individual *D. elatum* at three positions along our study gradient: near Popokvil Falls, about 700–800 m north of the old Bokor Hotel, and roughly midway between these locations. Replicated gas exchange measurements were carried out over the course of the study at the intermediate site to evaluate the photosynthetic responses of mature foliage of both sapling and mature tree leaf morphologies. Net photosynthetic rate (A), stomatal conductance (g), transpiration (E), instantaneous (A/E) water-use efficiency (WUE), intrinsic WUE (A/g) and internal CO_2 concentration (C_i) were determined using a LI-6400 portable gas exchange system (LI-COR Inc., Lincoln, Nebraska, USA). The LI-6400 maintains steady-state conditions with respect to temperature, CO_2 and water vapour concentration within the assimila-

Fig. 2 Dwarf shrubland landscape of the Bokor Plateau, about 0.5 km north of the old Bokor Palace Hotel (© Leon Meerson).

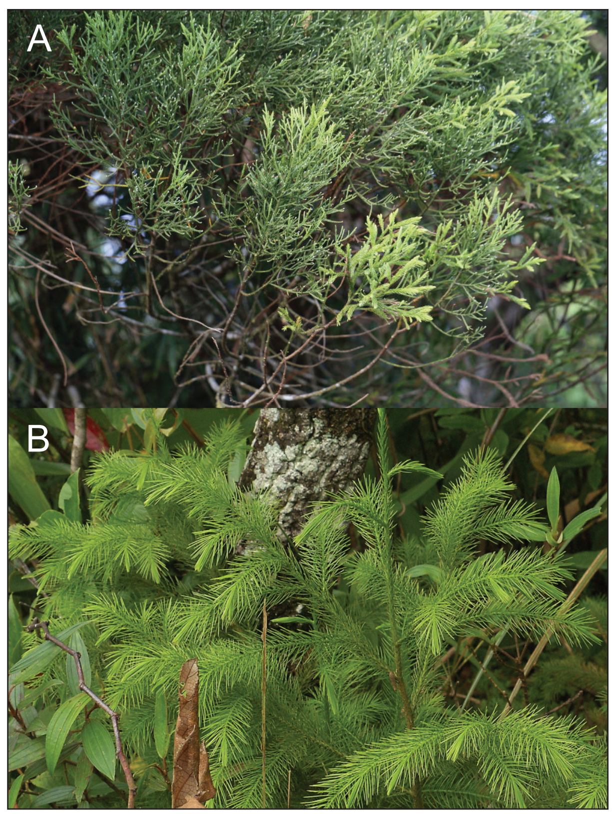

Fig. 3 Dimorphic foliage of *Dacrydium elatum*: A) Mature tree (© biodivinf); B) Sapling (© Tony Rodd).

tion chamber. For the data curves we present, each data point represents the mean of 3–5 replicated measurements. Light response curves were also developed with replicated measurements for foliage of both saplings and mature individuals of *D. elatum*.

Light response curves were measured under constant leaf-to-air vapour pressure deficit (VPD) and temperature conditions. Field measurements were made by slowly increasing irradiance (PFD) from 0 to 1,400 μmol m^{-2} sec^{-1}. The ambient temperature inside the leaf chamber was kept at 20°C. This temperature was close to the maximum ambient daytime temperature when the measurements were made. The leaf-to-air vapour pressure deficit (VPD) was maintained at 0.5–0.9 kPa. The CO_2 concentration inside the leaf chamber was kept constant at 375 mmol mol^{-1} during the light response curves with CO_2 supplied from a pressurized 12 gram gas cylinder. Light was provided by an internal red/blue LED light source (LI6400-02B). The projected leaf area of foliage used in each measurement was determined after gas exchange measurement using millimetre graph paper.

Results

Small pockets of dwarf forest trees first appeared about 500 m north of the escarpment and more commonly about 1 km distant where we sampled dwarf populations of *D. elatum*. In these mosaic pockets, woody species with a clear tree-like growth form were found in fissures in the sandstone substrate where organic material had collected and soils had developed. In addition to *D. elatum*, common species of trees 3–5 m in height were *Neolitsea zeylanica* (Nees & T. Nees) Merr. (Lauraceae), *Vaccinium viscifolium* King & Gamble (Ericaceae), *Garcinia merguensis* Wight. (Clusiaceae), *Lithocarpus leiophyllus* A. Camus (Fagaceae), *P. pilgeri* (Podocarpaceae), *Dacrycarpus imbricatus* (Podocarpaceae), and *Syzygium formosum* (Wall.) Masam. (Myrtaceae). *Pandanus* cf. *capusii* Mart. (Pandancaceae) was also present as a common subcanopy species. Two semi-woody climbers occured among the shrubs and treelets: *Jasminum nobile* C.B. Clark (Oleaceae) and *Smilax davidiana* A.DC. (Smilacaceae). Open areas of rocky outcrop with shallow and seasonally inundated soils occurred as openings in the sclerophyll scrub, supporting stands of herbaceous species dominated by *Leptocarpus disjunctus* Mast. (Restionaceae) and the clump-forming sedge *Carex indica* L.

Mature individuals of *Dacrydium elatum* in these pockets of dwarf forest had diameters of up to 20–23 cm but reached only 5–7 m in height (Fig. 4). Moving inland along the gradient to a position roughly midway from the old Bokor Hotel to Popokvil Falls, there was a clear transition zone where soils were less shallow, with a more diverse set of associated species, and here mature individuals of *D. elatum* were 30–35 cm in diameter and 8–10 m in height. Finally, moving along the gradient approximately four km inland onto deeper soils in the area round Popokvil Falls, diameters of *D. elatum* reached 45–50 cm or more and heights up to 15 m. This area had a closed forest canopy with associated canopy trees that included taller individuals of those listed above as well as *Machilus odoratissimus* Nees (Lauraceae), *Syzygium lineatum* (DC.) Merr. & L.M. Perry (Myrtaceae), *Acronychia pedunculata* (L.) Miq. (Rutaceae), and *Calophyllum calababa* L. var. *cuneatum* (Symington ex M.R. Henderson & Wyatt-Smith) P.F. Stevens (Calophyllaceae). These are all trees that can reach 30–40 m in height under favorable growing conditions, although their height was comparable to *D. elatum* at the site.

Both mature and juvenile leaf morphologies of *D. elatum* have a light response curve for photosynthesis that shows adaptations to the cloudy conditions of their habitat on Bokor Mountain. Both forms reached 50% of maximum rates of net assimilation at an irradiance of only 200 μmol m^{-2} sec^{-1} (Fig. 5). Maximum assimilation rates peaked at about 800 μmol m^{-2} sec^{-1} in both forms but with very divergent maximum rates of net assimilation. Mature foliage reached light saturation at about 800 μmol m^{-2} sec^{-1} with a maximum assimilation rate of about 6 μmol m^{-2} sec^{-1}. While juvenile foliage morphology peaked at the same level of irradiance, it peaked at a much higher assimilation rate of about 10.5 μmol m^{-2} sec^{-1}.

Because transpiration rates increased faster than assimilation rates in both leaf morphologies as irradiance increased beyond about 400 μmol m^{-2} sec^{-1}, water use efficiency measured as the ratio of assimilation to transpiration peaked at this relatively low light level (Fig. 6). Higher rates of photosynthesis thus come at the expense of declining water use efficiency (Fig. 7).

Discussion

Only rarely are Podocarpaceae able to establish stand dominance in competition with angiosperm trees. Such a pattern is most common in azonal tropical montane sites with stressful conditions for plant growth, as in heath and swamp forests and in areas with skeletal oligotrophic soils. The dominance of *D. elatum*, with the associated *Dacrycarpus imbricatus* and *Podocarpus pilgeri*, on the Bokor Plateau fits a pattern seen widely in such habitats in Malesia and New Guinea (Enright & Jaffré, 2011). The causal factors for this dominance can be understood

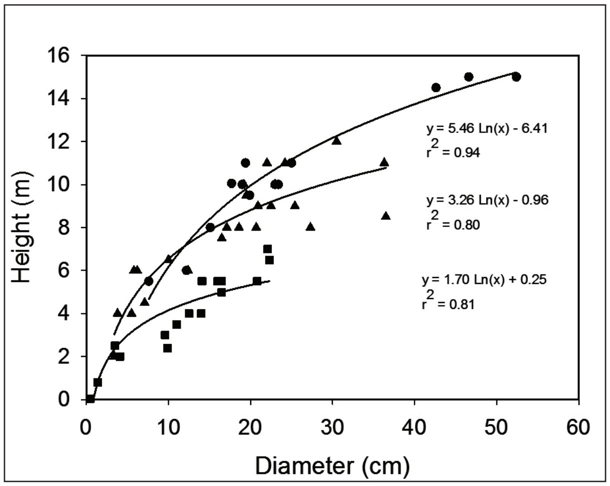

Fig. 4 Relationships of tree height to basal diameter in forest (circles), transition zone (triangles), and dwarf (squares) populations of *Dacrydium elatum* along a stress gradient across the Bokor Mountain Plateau of Bokor National Park, Cambodia. See text for details. Each symbol represents a measured individual.

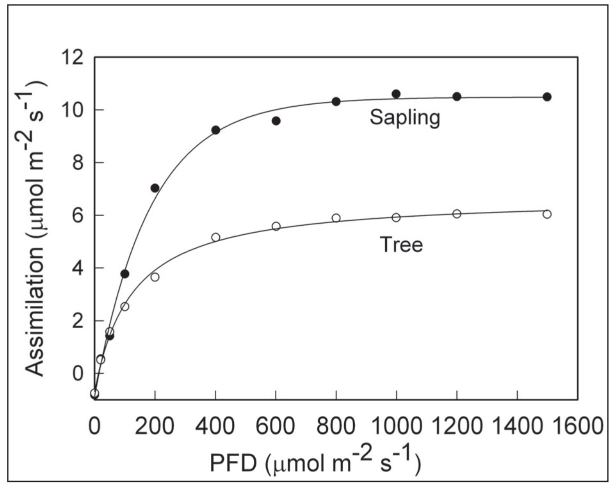

Fig. 5 Light response curve of mature tree and sapling foliage of *Dacrydium elatum* in Bokor National Park, Cambodia. These curves show replicated measurements on single co-occurring individuals located in the middle of the study gradient.

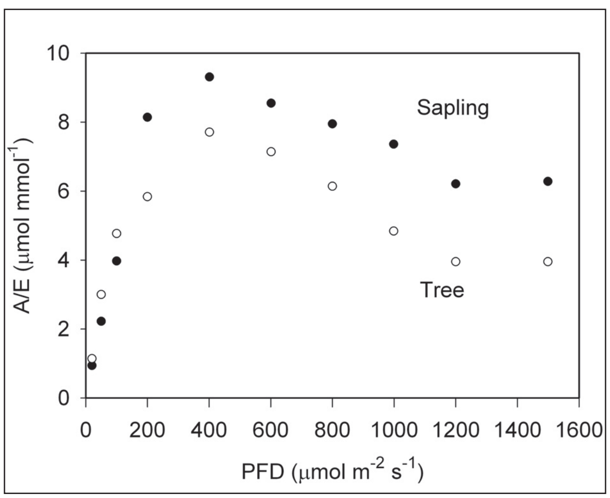

Fig. 6 Water use efficiency, measured as the ratio of assimilation (A) to transpiration (E), in relation to irradiance (PFD) in sapling and mature tree foliage of *Dacrydium elatum* in Bokor National Park, Cambodia. These curves show replicated measurements on single co-occurring individuals located in the middle of the study gradient.

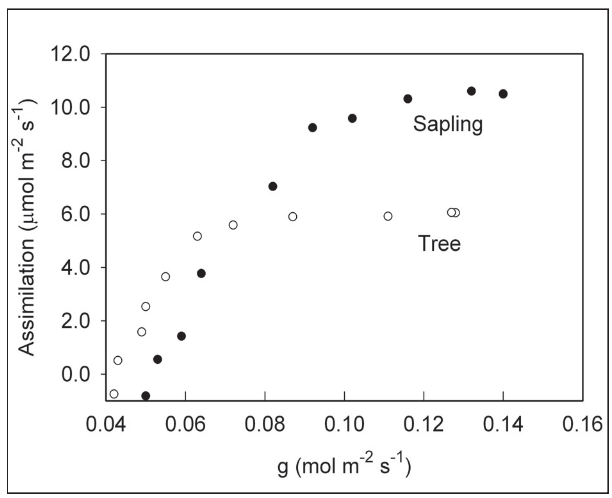

Fig. 7 Assimilation (A) to stomatal conductance (g) in sapling and mature tree foliage of *Dacrydium elatum* in Bokor National Park, Cambodia. These curves show replicated measurements on single co-occurring individuals located in the middle of the study gradient.

in traits broadly present in the Podocarpaceae. Although outcompeted on more productive sites, these conifers are able to persist in tropical forests using anatomical and morphological adaptations that increase the efficiency of light harvesting (Brodribb, 2011). Like many conifers, their slow growth also provides them a competitive advantage on oligotrophic soils. However, the Achilles heel of Podocarpaceae lies in the structure of their xylem systems and wood anatomy which makes them vulnerable to cavitation and thus drought stress (Brodribb, 2011), giving them poor hydraulic efficiency (Pitterman *et al.*, 2006). This morphology limits these taxa to areas of high water availability. The very high rainfall and shallow oligotrophic soils of the Bokor Plateau provide the conditions where these Podocarpaceae are able to maintain canopy dominance despite decreased stature.

The specific causal factors in the observed gradient in stature of *D. elatum* on Bokor Mountain are clearly complex, a pattern observed in other dwarf montane cloud forests (Bruijnzeel & Veneklaas, 1998). Increased dwarfing in growth form is associated with greater wind speeds, higher rainfall, shallower oligotrophic soils, and increased water logging. Photosynthetic measurements indicate that physiological limitations for carbon fixation may be less important than the abiotic stressors. The light response curve in foliage of *D. elatum* demonstrates clear adaptation to the low light levels present under the frequent cloud cover on Bokor Mountain. Moreover, the maximum rates of photosynthesis are high in comparison to published values for other Podocarpaceae (Meinzer *et al.*, 1984; Rundel *et al.*, 2001; Lusk *et al.*, 2003; Brodribb *et al.*, 2007). It is difficult to speculate about the possible significance of the higher rate of assimilation measured in juvenile foliage. The morphological differences in adult and juvenile foliage may have selective significance in promoting early growth and establishment of saplings in these oligotrophic conditions.

Globally, dwarf stands of conifers on oligotrophic soils are not restricted to the Podocarpaceae and tropical montane cloud forests. A classic example of these can be seen in the cool Mediterranean-climate of Mendocino County in northern California where highly leached and acidic beach terraces are locally present in an area known as the Pygmy Forest. Here, the endemic *Hesperocyparis pygmaea* (Lemmon) Bartel. (pygmy cypress), and *Pinus contorta* Loudon. subsp. *bolanderi* (Parl.) Critchf. (Bolander pine) often reach no more than 1–2 m in height after a century of growth (Westman, 1975).

The montane cloud forest of Bokor National Park is an important conservation resource deserving of additional study and protection. Much of this area, however, has been subject to recent development and clearing, putting many of the rare species and habitat at risk.

Acknowledgements

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