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

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មូលន័យសង្ខេប

ឧទាហរណ៍ជាគំរូមួយនៃព្រៃតឿនៅតាមភ្នំនៃព្រៃត្រូពិច អាចត្រូវបានឃើញនៅតំបន់ខ្ពង់រាបនៃជួរភ្នំដំរីក្នុងឧទ្យានជាតិបូកគោ។ ជម្រាលចោទនៅទិសខាងត្បូងនៃជួរភ្នំ និង ជិតសមុទ្របង្កើតជាតំបន់មានលក្ខខ័ណ្ឌសើមខុសប្រក្រតី ដែលមានកម្ពស់ទឹកភ្លៀងលើសពី ៥០០០ ម.ម នៃកម្ពស់ទឹកភ្លៀងប្រចាំឆ្នាំ មានសណ្តានដាច់ៗ និងមានអាស៊ីតខ្ពស់។ លក្ខខ័ណ្ឌទាំងនេះបង្កើតឲ្យមានព្រៃតឿ និង ទីចុលព្រឹក្សដែលភាគច្រើនជាប្រភេទ *Dacrydium elatum* (Podocarpaceae)។ បម្រែបម្រួលទំហំដើមឈើត្រូវបានប្រទះឃើញកម្ពស់ចាប់ពី ៥-៧ ម. នៅតាមជម្រាលជិតកំពូលនិងបន្តរហូតតាមតំបន់បម្រែបម្រួល និង កម្ពស់ដល់ ១៥ ម. ក្នុងតំបន់ក្បែរទឹកធ្លាក់ពពកវិល។ ស្លឹកដែលមានសណ្តានដូចស្រកានៃដើមឈើពេញវ័យ និង សណ្តានទ្រវែងស្រួចចុងនៃកូនរុក្ខជាតិប្រភេទ *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

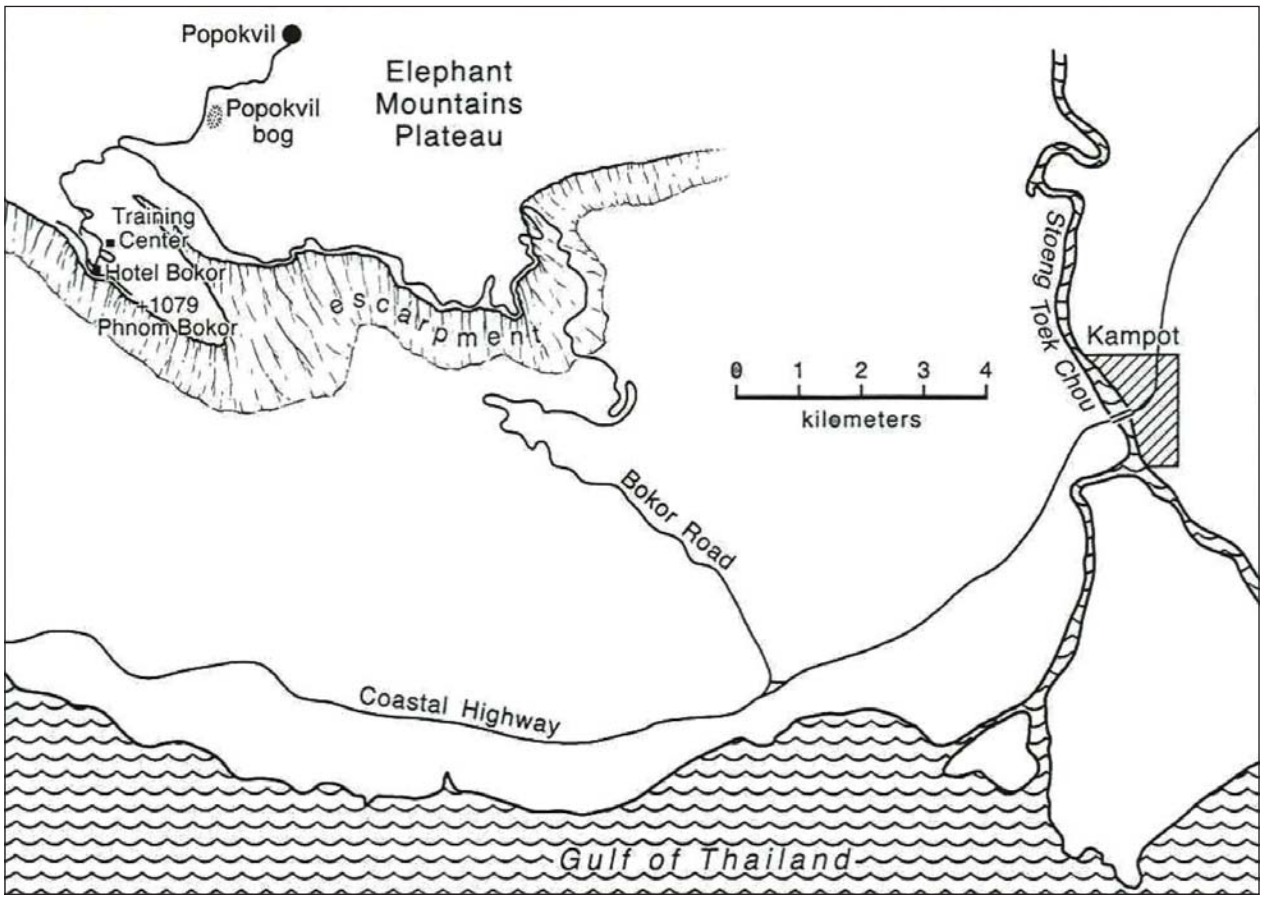

Fig. 1 Location of the study site in the Elephant Mountains Plateau of Bokor National Park. Phnom Bokor (Bokor Mountain) at 1,079 m, is the high point on the plateau. From Rundel *et al.* (2003).

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