Research paper

Ecophysiological Characteristics of Three *Cyathea* Species in Northeastern Taiwan

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【Summary】

Tree ferns are conspicuous in subtropical and tropical rainforests. Some closely related species of tree ferns often coexist in the forest; however, the mechanisms are poorly understood. The ecophysiological characteristics of 3 tree ferns, *Cyathea lepifera*, *C. spinulosa*, and *C. podophylla*, growing in forests of northeastern Taiwan were investigated. Results showed that *C. lepifera* preferred an open habitat (mean canopy openness (MCO) of 29.2%), while *C. spinulosa* and *C. podophylla* preferred a shaded habitat (MCOs of 7.0 and 5.0%, respectively). The light-saturated photosynthetic rate of *C. lepifera* was significantly higher than that of *C. podophylla*, and *C. spinulosa* had a medium one (11.46, 8.27, and 6.34 μmol CO_2 m^{-2} s^{-1} for *C. lepifera*, *C. spinulosa*, and *C. podophylla*, respectively). The light saturation point of *C. podophylla* was significantly lower than those of the other 2 species (1220, 1100, and 808 μmol photon m^{-2} s^{-1} for *C. lepifera*, *C. spinulosa*, and *C. podophylla*, respectively). The light compensation point (LCP) and dark respiration rate (R_d) of *C. lepifera* were significantly higher than those of *C. spinulosa* and *C. podophylla*. *Cyathea lepifera* had the shortest frond life spans (6.6 mo for fertile fronds and 7.2 mo for sterile fronds) among the 3 species, which was followed by those of *C. spinulosa* (7.2 mo for fertile fronds and 7.3 mo for sterile fronds), and the longest frond life spans were in *C. podophylla* (13.0 mo for fertile fronds and 12.0 months for sterile fronds). *Cyathea lepifera*, *C. spinulosa*, and *C. podophylla* respectively belonged to shade-intolerant species, mid-shade-tolerant species, and shade-tolerant species as inferred from their habitat preference and ecophysiological characteristics. Roads, trails, frequent typhoons, and occasional tree falls create habitats with different canopy openness levels which increase the opportunity of these 3 *Cyathea* species to coexist in this forest.

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研究報告

台灣東北部三種桫欏屬植物之生態生理特性

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摘 要

樹蕨為亞熱帶及熱帶雨林中顯著物種，一些近緣樹蕨常在森林中共存，然而，其共存機制鮮為瞭解。本研究調查生長在台灣東北部森林筆筒樹、台灣桫欏與鬼桫欏三種樹蕨生態生理特性。結果顯示筆筒樹偏好生長於開闊生育地(平均樹冠開闊度29.2%)，而台灣桫欏與鬼桫欏則偏好生長於鬱閉生育地(平均樹冠開闊度分別為7.0及5.0%)。筆筒樹光飽和光合作用速率顯著高於鬼桫欏，台灣桫欏居中(筆筒樹、台灣桫欏及鬼桫欏分別為11.46, 8.27及6.34 μmol CO_2 m^{-2} s^{-1})；鬼桫欏光飽和點顯著低於其它兩物種(筆筒樹、台灣桫欏及鬼桫欏分別為1220, 1100及808 μmol photon m^{-2} s^{-1})；筆筒樹的光補償點與暗呼吸率顯著高於台灣桫欏及鬼桫欏。另外，此三種物種以筆筒樹具最短之葉片壽命(孕性葉6.6月，營養葉7.2月)，台灣桫欏其次(孕性葉7.2月，營養葉7.3月)，鬼桫欏之葉片壽命則為最長(孕性葉13.0月，營養葉12.0月)。根據它們的棲地偏好及生態生理特性，筆筒樹、台灣桫欏及鬼桫欏分別屬於非耐陰性物種、中度耐陰性物種及耐陰性物種。道路及步道、頻繁颱風干擾和偶發性樹倒創造出不同樹冠開闊度棲地，提昇這三種桫欏屬植物共存在此一森林中的機會。

關鍵詞：樹冠開闊度、筆筒樹、鬼桫欏、台灣桫欏、葉片壽命。

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INTRODUCTION

Tree ferns are conspicuous components of subtropical and tropical mountain rainforests, sometimes making a large contribution to the total basal area and stem density (Bystriakova et al. 2011). They have been recognized as a ‘‘keystone species’’ because their dense crowns act as filters on tree regeneration processes (Coomes et al. 2005, Bystriakova et al. 2011). Although closely related species of tree ferns often coexist in the forest (Jones et al. 2006), the mechanisms that enable local coexistence are poorly understood.

In a heterogeneous environment, the availability of resources for plants to successfully survive and develop may change with time or microsites (Durand and Goldstein 2001a). Those environmental factors, including light, water, and nutrients, vary at different canopy openness levels even in a small forest area.

Heterogeneity of light environments can influence the photosynthesis of plants by means of a direct effect on the photosynthetic apparatus. However, plants can be damaged by photooxidative destruction under stress conditions (Valladares and Pearcy 1997, Saldaña et al. 2010). Plants growing at low light levels tend to have a lower photosynthetic capacity, light compensation point (LCP) and dark respiration rate (R_d) than those growing in sunny conditions (Björkman et al. 1972). Shade tolerance is a product of a combination of traits that enable plants to maintain a positive carbon balance in deep shade. Plants' growth is influenced by the rate of photosynthesis and by the costs of leaf R_d and leaf construction (Givnish 1988). Having a lower R_d is advantageous for plants growing in the shade, because it may help them maintain a positive carbon balance under low light conditions (Boardman 1977).

Different species of tree ferns under various light environments may have distinct ecophysiological characteristics, e.g., photosynthetic rate and R_d (Pattison et al. 1998, Durand and Goldstein 2001a, Bystriakova et al. 2011). Jones et al. (2007) discovered that habitat preferences of 4 common tree fern species (Cyatheaceae) in a lowland neotropical rainforest were strongly associated with different sheltered topographic positions such as terraces or valleys. Therefore, exploring the explicit ecophysiological characteristics of tree ferns under different light environments is essential to understanding physiological adaptations to their habitats.

Many studies have shown that the life span of leaves is negatively correlated with the photosynthetic rate in gymnosperms, angiosperms, and some ferns. Species with higher photosynthetic rates usually have shorter leaf life spans than those with lower photosynthetic rates (Durand and Goldstein 2001b, Matsuki and Koike 2006, Karst and Lechowicz 2007). However, correlations among the above ecophysiological characteristics of leaves have been widely reported in angiosperms but less so in ferns (Karst and Lechowicz 2007).

The Cyatheaceae is the main family among tree ferns. There are 7 species of this family native to Taiwan. Among these species, *Cyathea lepifera* (J. Sm. ex Hook.) Copel., *C. spinulosa* Wall. ex Hook., and *C. podophylla* (Hook.) Copel. are common and often sympatrically distributed in subtropical broadleaf forests of northeastern Taiwan. In this study, we first elucidated differences in their habitat preferences, and then documented relationships among habitat preferences, ecophysiological characteristics, and life spans of fronds in these tree ferns.

MATERIALS AND METHODS

Study area

Plants of *C. lepifera*, *C. spinulosa*, and *C. podophylla* which grew in a subtropical broadleaf forest at an elevation of about 600 m in the Fushan Botanical Garden in northeastern Taiwan (24°46'N, 121°34'E) were monitored monthly from March 2011 to March 2013.

Canopy openness

The canopy openness of sampled tree ferns was measured in July and August, 2012. A digital, hemispherical photograph was taken at about 0.5 m above each individual plant using a Cannon EOS 400 digital camera with a fisheye lens attachment. Images were then analyzed using Gap Light Analyzer software (Frazer et al. 1999, Watkins Jr. et al. 2007) to estimate the percentage of total light transmittance. There were 13, 21, and 21 samples of *C. lepifera*, *C. spinulosa*, and *C. podophylla*, respectively. (Table 1).

Measurement of photosynthetic light responses

In situ photosynthetic light responses of

Table 1. Forest canopy openness (%) above plants of *Cyathea lepifera*, *C. spinulosa*, and *C. podophylla*

Species	Number of plants	Canopy openness (s)
Cyathea lepifera	13	29.9±14.1[a]
Cyathea spinulosa	21	7.0±3.7[b]
Cyathea podophylla	21	5.0±2.2[b]

Different superscript letters indicate a significant difference (by Scheffe's test, $p < 0.05$) among species.

the 3 tree ferns were measured in February 2012. Three sampled fronds each from different individuals of the 3 species were chosen for measurements. The sampled fronds of *C. lepifera* and *C. spinulosa* were 4 m above the ground, and those of *C. podophylla* were 1 m above the ground. Portable construction platforms were used to access the sampled fronds for the photosynthetic measurements. Net photosynthetic rates were measured with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA) with an artificial red/blue LED light source. Measurements were made at light levels (photosynthetic photon flux density; PPFD) of 0, 5, 10, 25, 50, 100, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, and 2000 μmol photon m^{-2} s^{-1}. The leaf chamber environment was maintained as follows: CO_2 of 400 μl L^{-1}, a temperature of 22℃, and a relative humidity of 65~70%. Measurements were taken from 08:00~11:00 under clear to partly cloudy skies. The value of 95% of the highest net photosynthetic rate (A_{max}) of each light response was regarded as the light-saturated photosynthetic rate (A_{sat}). For each light response, the corresponding light intensity of the A_{sat} was regarded as the light saturation point (LSP). The LCP and R_d were calculated from a linear regression equation of the light intensity below 50 μmol photon m^{-2} s^{-1}. The corresponding light intensity at a zero net photosynthetic rate of each light response was the LCP. The net photosynthetic rate in the dark was the R_d.

Frond life span

Thirty plants of *C. lepifera*, and 40 plants each of *C. spinulosa* and *C. podophylla* were selected in this study. All fronds of selected plants were labeled with plastic tags. Their fertility and development stages from emergence and expansion to death were investigated monthly from March 2011 to March 2013. Therefore, the frond life span was calculated based on the timing of fronds from emergence to senescence (Lee et al. 2009b).

Statistical analysis

A two-way analysis of variance (two-way ANOVA) followed by Scheffe's method and Duncan's multiple-range test were carried on to determine differences among species and fronds for each variable measured. All statistical analyses were run using Microsoft Office Excel 2007 (Microsoft, Inc. 2007) and SPSS Statistics program 16.0 (SPSS, Inc. 2007).

RESULTS

Habitat and canopy openness

Cyathea lepifera, *C. spinulosa*, and *C. podophylla* are abundant and often sympatrically distributed in this study area. However, the mean canopy openness above *C. lepifera* was significantly greater than those of *C. spinulosa* and *C. podophylla* (29.9, 7.0, and 5.0%, respectively) (Table 1). According to our field observations, *C. lepifera* mainly appeared in open habitats. In contrast, *C. spinulosa* and *C. podophylla* were dominant in shaded habitats.

Photosynthesis

The net photosynthetic rate increased

with increasing PPFD from dark to the light saturation point. The LCP of *C. lepifera* (6.77±1.25 μmol photon m^{-2} s^{-1}) was significantly higher than those of *C. spinulosa* (2.21±0.44 μmol photon m^{-2} s^{-1}) and *C. podophylla* (1.88±0.37 μmol photon m^{-2} s^{-1}). The LSP was estimated to be about 1220, 1100, and 808 μmol photon m^{-2} s^{-1} for *C. lepifera*, *C. spinulosa*, and *C. podophylla*, respectively. The LSPs of the former 2 species were significantly higher than that of *C. podophylla.* A_{sat} values of *C. lepifera*, *C. spinulosa*, and *C. podophylla* were 11.46±1.34, 8.27±0.69, and 6.34±0.54 μmol CO_2 m^{-2} s^{-1}, respectively. R_d values of *C. lepifera*, *C. spinulosa*, and *C. podophylla* were 0.56±0.06, 0.17±0.02, and 0.30±0.08 μmol CO_2 m^{-2} s^{-1}, respectively. The R_d of *C. lepifera* was significant higher than those of the other 2 species, but there were no significant difference between *C. spinulosa* and *C. podophylla* (Table 2).

Frond life span

Totally 433 *C. lepifera*, 371 *C. spinulosa*, and 79 *C. podophylla* fronds were examined from emergence to senescence. The mean life spans of both fertile and sterile fronds of *C. podophylla* (13.0 and 12.5 mo, respectively) were significantly longer than those of *C. lepifera* (6.6 and 7.2 mo, respectively) and *C. spinulosa* (7.2 and 7.3 mo, respectively). In *C. lepifera*, the life span of fertile fronds was significantly shorter than that of sterile fronds although with only a half-month difference. Life spans of fertile and sterile fronds did not differ in *C. spinulosa* or *C. podophylla* (Table 3).

DISCUSSION

Habitat and photosynthetic characteristics

Cyathea lepifera has long been regarded as a shade-intolerant tree fern and often regenerates in disturbed sites (e.g., Tsai et al. 2001). In contrast, *C. podophylla* is attributed

Table 2. Light-saturated photosynthetic rate (A_{sat}), light saturation point (LSP), light compensation point (LCP), and dark respiration rate (R_d) of *Cyathea lepifera*, *C. spinulosa*, and *C. podophylla*

	C. lepifera	*C. spinulosa*	*C. podophylla*
A_{sat} (μmol CO_2 m^{-2} s^{-1})	11.46 ± 1.34^{a}	8.27 ± 0.69^{ab}	6.34 ± 0.54^{b}
LSP (μmol photon m^{-2} s^{-1})	1220 ± 68^{a}	1100 ± 33^{a}	808 ± 80^{b}
LCP (μmol photon m^{-2} s^{-1})	6.77 ± 1.25^{a}	2.21 ± 0.44^{b}	1.88 ± 0.37^{b}
R_d (μmol CO_2 m^{-2} s^{-1})	0.56 ± 0.06^{a}	0.17 ± 0.02^{b}	0.30 ± 0.08^{b}

Different superscript letters on the same line indicate a significant difference (by Duncan's multiple-range test, $p < 0.05$) among the 3 *Cyathea* species.

Table 3. Life spans (mo) of fertile and sterile fronds of *Cyathea lepifera*, *C. spinulosa*, and *C. podophylla*

Species	Life span (no. of fronds)	
	Fertile fronds	Sterile fronds
Cyathea lepifera	6.6 ± 1.3^{a} (277)	7.2 ± 1.4^{b} (156)
Cyathea spinulosa	7.2 ± 1.5^{b} (128)	7.3 ± 1.9^{b} (243)
Cyathea podophylla	13.0 ± 5.1^{c} (34)	12.5 ± 5.0^{c} (45)

Different superscript letters indicate a significant difference (by Scheffe's test, $p < 0.05$) among species and frond fertility.

to a shade-tolerant species (e.g., Wang et al. 2003). *Cyathea lepifera* and *C. podophylla* are often respectively found in open and shaded habitats in this study area. On the other hand, although *C. spinulosa* usually occurred at intermediate sites, its canopy openness significantly differed from that of *C. lepifera* and was slightly higher than that of *C. podophylla*.

The A_{sat}, LSP, LCP, and R_d of shade-intolerant and early-successional species are higher than those of shade-tolerant and late-successional species (Bazzaz 1979, Sumbele et al. 2012). This generality is widely accepted in flowering plants. This study documents that *C. lepifera* had a higher A_{sat}, LSP, LCP, and R_d than those of *C. podophylla*, whereas *C. spinulosa* possessed intermediate values of these photosynthetic characteristics except for R_d. Many studies concerning frond ecophysiology of ferns mostly coincided with this generality. For example, in Hawaii, the LSP and A_{max} of the invasive tree fern *Sphaeropteris cooperi* (W. J. Hooker *ex* F. von Mueller) Tryon, which grows at relatively high light levels, are significantly higher than those of the 3 native *Cibotium* tree ferns (*C. chamissoi* Kaulf., *C. menzeissi* Hook., and *C. glaucum* (Sm.) Hook. & Arn.), which live in shaded habitats. However, the light compensation points did not statistically differ between the 2 groups of ferns (Durand and Goldstein 2001a).

In general, tropical shade-intolerant and shade-tolerant trees have A_{sat} values within 10~20 and 4~7 μmol CO_2 m^{-2} s^{-1}, respectively (Larcher 1995, Strauss-Debenedetti and Bazzaz 1996, Zotz and Winter 1996). According to this criterion, *C. lepifera*, and *C. podophylla* belong to shade-intolerant species and shade-tolerant species, respectively; and *C. spinulosa* should be regarded as a mid-shade-tolerant species because of having an intermediate A_{sat} value between shade-intolerant and shade-tolerant species.

A plant with a greater photosynthetic capacity as presented by the A_{max}, indicates that it is more efficient at utilizing light energy and/or has more carboxylating enzymes, under a high light intensity (Durand and Goldstein 2001a). In Hawaii, the tree fern *Sphaeropteris cooperi*, which grows at relatively high light levels, has a significantly higher annual stem growth rate (15 cm) than 3 tree ferns in the genus *Cibotium* (2~3 cm) which live in shaded habitats (Durand and Goldstein 2001b). The mean annual stem height growth of *C. lepifera* is ca. 22 cm in a northeastern forest of Taiwan (Ying and Huang 1995), whereas that of *C. podophylla* is < 5 cm in a forest of central Taiwan (unpublished data). For those species in this study, *C. lepifera* is proposed to grow faster than the other 2 species due to its higher A_{sat} value.

It was suggested that the shade-tolerant species in low light environments still maintain growth because they have lower respiration rates and can use light resources more efficiently, whereas shade-intolerant species might not grow and have high mortality rates under low light levels (Givenish 1988, Walters and Reich 1996). A similar scenario may also occur for tree ferns of this study and explain their different habitat selections.

Forest roads and trails, frequent typhoons, and occasional tree falls create different gaps in the Fushan forest and provide various habitats for corresponding species to establish populations (Lin et al. 2006). These habitats with various canopy openness levels have a mosaic distribution and promote the coexistence of these 3 ferns with different ecophysiological characteristics in this forest.

Frond life span

In ferns, fertile fronds are expected to have a shorter life than sterile fronds because their reduced laminar surface makes them less photosynthetically efficient than sterile fronds (Mehltreter 2008). This was proven for dimorphic species in which fertile and sterile fronds distinctly differ in outline and size, but this generality does not always fit monomorphic fern species (Lee et al. 2009a, b). In this study, fronds of all 3 *Cyathea* species belonged to the monomorphic type. The life span of sterile fronds was significantly longer than fertile ones in *C. lepifera* (although only a half-month difference). However, life spans of both kinds of fronds were nearly the same in *C. spinulosa* and *C. podophylla*. The average life spans of fertile and sterile fronds were up to 26.1 and 25.8 mo in *C. podophylla* (Lee et al. 2009b), which were much longer than the life spans of *C. podophylla* fronds in this study. This may be attributed to the shorter observation period (2 yr), to only 28.5% (79/277) of total fronds being observed from emergence to senescence, and to serious damage by squirrels and fungal infections in this study.

Variations in leaf life span were found to be an important predictor of numerous plant responses (Mehltreter 2008). In general, leaves of angiosperms and ferns with a higher photosynthetic rate have a shorter leaf life span than those with a lower one (Reich et al. 1991, 1999, Durand and Goldstein 2001a, Craine et al. 2002, Matsuki and Koike 2006, Karst and Lechowicz 2007). The same tendency was observed among *C. lepifera*, *C. spinulosa*, and *C. podophylla*. Several studies demonstrated that species with long-lived leaves have higher costs (maintenance and defense) and fewer benefits (photosynthesis) than those with short-lived leaves (Chapin et al. 1980, Coley 1988, Reich et al. 1995). That is, in addition to the photosynthetic rate, the leaf life span is also associated with other leaf functional traits such as the leaf nitrogen content, leaf construction cost, and leaf mass per area (Matsuki and Koike 2006).

CONCLUSIONS

Cyathea lepifera, *C. spinulosa*, and *C. podophylla* are 3 common and often sympatric tree ferns in forests of northeastern Taiwan. They are classified as shade-intolerant, mid-shade-tolerant, and shade-tolerant species, respectively, as inferred from their habitat preferences and photosynthetic characteristics. Forest roads and trails, frequent typhoons, and occasional tree falls create habitats with different canopy openness levels. Hence, the 3 *Cyathea* species can coexist under various effective light resources of their habitats.

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