



Phenology of 13 fern species in a tropical monsoon forest of southern Taiwan

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ABSTRACT

In the present study, phenological events of 13 fern species were monitored in the Kenting Uplifted Coral Reef Nature Reserve (N 21°58', E 120°48'; alt: 250–300m), a tropical monsoon forest located in southern Taiwan, during 1997 and 2000. This region has a distinct alternation of dry and wet seasons, in November–March and April–October, respectively. The phenological events of leaf emergence/expansion and spore maturation/release mainly occurred in the wet season and significantly positively correlated with average monthly temperature and monthly precipitation. However, the leaf senescence of these ferns is generally aseasonal. All species produced both sterile and fertile leaves except *Arthropteris palisotii* and *Microsorium punctatum*, which only produced sterile leaves. Despite monomorphic, except *Ctenitopsis dissecta*, the other 10 species develop their sterile and fertile leaves in significantly different sizes, and some species showed different phenological patterns and life span between their sterile and fertile leaves. Fertile leaves remained green for 5–16 months after releasing spores, and no more sorus was produced during this time. This is the first insight of fern phenological study in the paleotropical monsoon forests, and the information herein provides basic references for further studies to facilitate the understanding of the fern biology and ecology.

Keywords : dry-wet season, fertile leaf, life span, seasonality, sterile leaf.

INTRODUCTION

Plant phenology deals with seasonal change in plant growth events, such as development, reproduction, etc., and is important in understanding responses of plants to the environmental conditions (Farrar *et al.* 2008, Mehltreter 2008). In the region with apparent alternation of wet and dry season, plant phenological traits are much

affected by seasonal change (Jeanneret & Rutishauser 2009). In the tropical deciduous forests in India, leaves of most trees emerge during wet season and flowering/fruitletting soon occurs subsequently (Singh & Kushwaha 2006). However, in the tropical forests of Costa Rica, Mexico, and Brazil, most trees blossom and fruit during dry season (Borchert *et al.* 2004, Vasconcelos *et al.* 2010). Two fern species in the

Neotropical, *Thelypteris angustifolia* (Willd.) Proctor (Sharpe 1997) and *Acrostichum daneaefolium* Langsd. & Fisch. (Mehlreter & Palacios-Rios 2003) produce leaves mostly before the coming of rainy season.

Phenological events could be affected by some environmental factors, such as precipitation, temperature, and day-length. In the monsoon forests of Thailand and India, the reason of most trees emerging their leaves in the dry season is attributed to the increase of day-length (Elliot *et al.* 2006). The phenology of some ferns, in the tropical regions, is correlated with seasonal rainfall (Mehlreter & Garcia-Franco 2008). For example, *Lygodium microphyllum* (Cav.) R. Br., found in a semi-deciduous forest of Mexico, shows a significant correlation between its growth/senescence and precipitation (Mehlreter 2006). Temperature is also demonstrated to be significantly correlated with the leaf emergence of many ferns in the subtropical forests of Taiwan (Chiou *et al.* 2001, Lee *et al.* 2009).

Hengchun is located at southern Taiwan with a distinct alternation of dry and wet seasons (Wu *et al.* 2007). Phenological studies of flowering plants show that most of them sprout leaves in the late dry season (February to April), bloom in the early rainy season (April to June), and fruit during June and December (Ho 1968, 1971). We suspect that fern phenology in this region is affected by seasonal change as shown in other regions with apparent alternation of wet and dry season (Jeanneret & Rutishauser 2009). In the present study, 13 fern species were monitored to reveal their phenological traits and the correlation of these traits with climatic factors were also analyzed.

MATERIALS & METHODS

This investigation was conducted at the Kenting Uplifted Coral Reef Nature Reserve, located at Hengchun, southern Taiwan (N 21°58', E 120°48'; alt: 250–300m) during September 1997 and August 2000. It is an evergreen forest mixed with deciduous trees. The dominant trees include *Diospyros maritima* Blume, *Ficus benjamina* L., *Aglaia formosana* (Hayata) Hayata, *Bischofia javanica* Blume, and *Diospyros blancoi* A. DC. According to the Hengchun weather station, the annual mean temperature is 25.4°C (max. 28.0°C at July–August; min. 21.6°C at January) and precipitation

is 2500 mm/year. Precipitation was mostly at June–October (>200 mm/month) and rare at November–May (<100 mm/month). Because the precipitation during November and March is less than the potential evaporation (i.e., temperature × 2; Walter 1985), this period is defined as the dry season and April–October is called wet season as the precipitation is higher than the potential evaporation (Fig. 1).

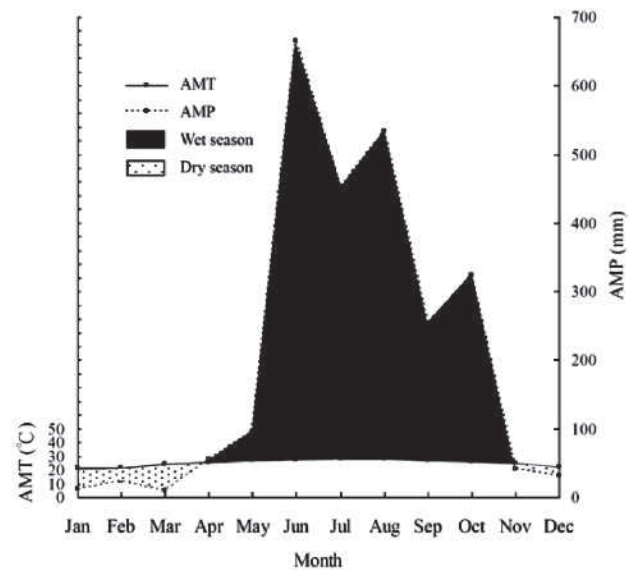


Fig. 1—Average monthly temperature (AMT) and precipitation (AMP) from September 1997 to August 2000. The precipitation is less than the potential evaporation (i.e., temperature × 2; Walter 1985) during November and March, indicating the dry season.

The phenology of 13 fern species was monitored which include *Arthropteris palisotii* (Desv.) Alston, *Asplenium excisum* C. Presl, *Colysis pothifolia* (Buch.-Ham. ex D. Don) C. Presl, *Colysis wrightii* (Hook. & Baker) Ching, *Ctenitis subglandulosa* (Hance) Ching, *Ctenitopsis dissecta* (G. Forst.) Ching, *Cyclosorus truncatus* (Poir.) Farw., *Diplazium chinense* (Baker) C. Chr., *Diplazium dilatatum* Blume, *Microlepia strigosa* (Thunb.) C. Presl, *Microsorium punctatum* (L.) Copel., *Tectaria devexa* (Kunze) Copel., and *Tectaria subtriphyllo* (Hook. & Arn.) Copel. var. *subtriphyllo*. Five individual plants of each species were sampled, except *C. dissecta*, in which only four individuals were sampled because of non-availability of more plants, and in *C. wrightii*, six individuals were included (Table 1). Each individual plant of a species was at least 5 m from conspecifics to reduce genetic homogeneity.

The leaves were labeled with a plastic tag when they emerged and grew to sufficient size. Every month the width and length of tagged leaves were measured until their no more expansion. Leaf senescence (totally brown) and spore maturation (ca. 50% of sporangia turned to dark color) and release (all sporangia almost empty as observed with hand lens) were also recorded. The life span of a leaf was counted from its emergence to senescence. Some leaves damaged by falling tree branches, animals, or other unknown factors were not included in the final analysis. At the end of the survey, some leaves monitored were still in coiled status, and many leaves were still alive. Therefore, the leaf numbers recorded for expansion were smaller than (or the same as) emergence numbers, and the numbers for senescence were smaller than expansion numbers (Table 1).

Student's *t* test was used to determine the significant difference for the comparison of various phenological parameters. The correlation between the phenological event and average monthly temperature (AMT) and precipitation (AMP) were determined by Pearson product-moment correlation coefficient. The variables were square rooted for reducing the deviation in correlation analysis.

RESULTS

Leaf emergence—Among the 65 plants of 13 species, totally 1,250 leaves, including 929 sterile and 321 fertile ones, emerged during the monitoring period. Ratios of sterile to fertile leaves among species were different, and no fertile ones were produced in *A. palisotii* and *M. punctatum* (Table 1).

Table 1— Phenology of the 13 fern species studied at the Kenting Uplifted Coral Reef Nature Reserve, southern Taiwan, from September 1997 to August 2000.

species	Plants (n)	Number of leaves			
		Emergence ¹⁾		Expansion	Senescence
		Sterile	Fertile		
<i>Arthropteris palisotii</i>	5	177(A)	- ²⁾	149	20
<i>Asplenium excisum</i>	5	11(B)	43(B)	54	22
<i>Colysis pothifolia</i>	5	42(B)	14(B)	56	46
<i>Colysis wrightii</i>	6	125(A)	34(B)	146	39
<i>Ctenitis subglandulosa</i>	5	43(A)	31(A)	74	38
<i>Ctenitopsis dissecta</i>	4	7(B)	27(A)	34	23
<i>Cyclosorus truncatus</i>	5	64(A)	11(C)	75	51
<i>Diplazium chinense</i>	5	71(A)	37(A)	100	71
<i>Diplazium dilatatum</i>	5	65(A)	59(A)	120	78
<i>Microlepia strigosa</i>	5	115(A)	9(C)	87	69
<i>Microsorium punctatum</i>	5	81(A)	-	79	27
<i>Tectaria devexa</i>	5	37(A)	39(A)	73	43
<i>Tectaria subtriphyllo</i> var. <i>subtriphyllo</i>	5	91(B)	17(B)	106	38
Total (Average)	65	929	321	1153	565

¹⁾ (A): the event occurred throughout the year (at least 10 month); (B): the event occurred mainly in the wet season (April–October); (C): the event occurred mainly in the dry season (November–next March).

²⁾ Fertile leaf was not found.

Most sterile leaves emerged during May and August (50.7%) whereas most fertile ones emerged during May and June (44.0%). In the winter (December to February), which was a less precipitation period, less number of leaves emerged (ca. 17.0%) (Fig. 2). However, the number of emerged leaves in each month varied by species. In addition, sori were observed as soon as leaves unfurled, whereas those leaves did not produce sori when they first unfurled remained sterile throughout their life. Thus sterile and fertile leaves are determined in the early beginning of development although they are monomorphic ferns.

Table 2—Correlations (*r* value) between phenological events of the 13 species at Kenting area and monthly climate (temperature and precipitation) factors.

Phenological events	Temperature	Precipitation
sterile emergence	0.47**	0.58**
sterile expansion	0.29 ^{ns}	0.48**
sterile senescence	0.09 ^{ns}	0.08 ^{ns}
fertile emergence	0.33*	0.35*
fertile expansion	0.47**	0.54**
fertile senescence	-0.10 ^{ns}	-0.15 ^{ns}
spore maturation	0.48**	0.59**
spore release	0.46**	0.60**

ns : not significant; *: 0.01 < *p* < 0.05; **: *p* < 0.01

The leaf emerging pattern could roughly be classified into (A) whole-year (at least 10 months) emergence, (B) wet-season (April–October) emergence, and (C) dry-season emergence. There were 9 and 4 species with their sterile leaves attributing to whole-year emergence and wet-season emergence, respectively. But no species emerged their sterile leaves mainly during the dry season. The fertile leaves could emerge as one of the three patterns depending on species (Table 1). However, even emerged as the same pattern, some differences might occur among species. For example, although sterile leaves of both *C. wrightii* and *C. subglandulosa* emerged every month (A type), in the case of former it was more concentrated in the wet season whereas the latter was not showing any apparent difference among months. Therefore the former was significantly positively correlated with AMT and AMP, whereas the latter was not.

The emergence pattern between sterile and fertile leaves of the species with monomorphic leaves might be different (Table 1). Even as the same emerged pattern, they might show some differences. For example, sterile leaves emerged more evenly than fertile leaves for *D. chinense* (both were A type), and therefore the latter was significantly positively correlated with AMT, whereas the former was not.

Frequencies of both sterile and fertile leaves emergence were significantly correlated with AMT and AMP (Table 2).

Regarding the emergence of sterile leaves, *A. excisum*, *C. pothifolia*, *C. wrightii*, *D. dilatatum*, and *T. subtriphylla* var. *subtriphylla*, were significantly positively correlated to AMT and AMP; *C. dissecta* was only significantly positively correlated to AMP; the other species did not present significant correlation with these two factors. For fertile leaf emergence, *A. excisum* and *C. pothifolia* were significantly positively correlated to AMT and AMP; *D. dilatatum* was significantly positively correlated to AMT only; *C. truncatus* and *M. strigosa* were mainly emerged in dry season and significantly negatively correlated to AMT and AMP; the other species were not significantly correlated with these two factors.

Leaf expansion—It took 0.4 months (*M. punctatum* and *T. subtriphylla* var. *subtriphylla*) to 1.5 months (*C. pothifolia*) for leaf expansion since their emergence (Table 1). Most sterile leaves achieved their full sizes during June and September, and fertile ones in June and July (Fig. 2). Leaf expansion of both kinds of leaves, in total, was significantly correlated with AMT and AMP (Table 2). However, some species did not present these significant correlations.

Leaf senescence—Leaf senescence occurred every month but varied among species and was somewhat different between the sterile and fertile leaves of each species (Fig. 2). The correlations of both sterile and fertile leaves with AMT and AMP were not significant for every species.

Spore maturation and release—It took 1.0 month (*C. subglandulosa*) to 3.8 months (*M. strigosa*) from fertile leaf emergence to spore maturation (Table 3). Spores of most species matured from July to August and were released from July to September. Both spore

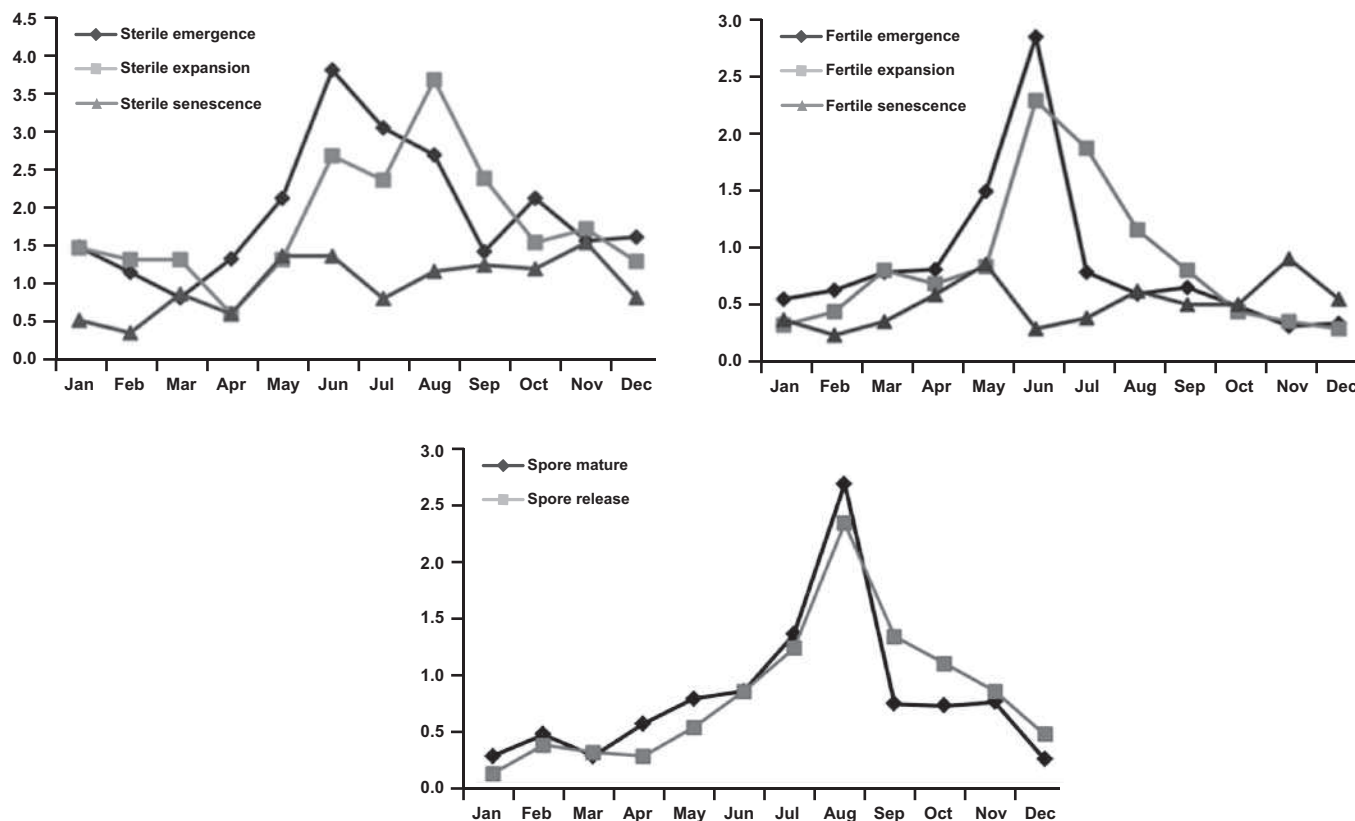


Fig. 2— The phenological patterns for these 13 species at Kenting area during September 1997 and August 2000. (Y axis: total leaf numbers/year).

maturation and release were significantly correlated with AMT and AMP (Table 2). However, the correlations varied among species. Spore maturation of *C. pothifolia*, *D. chinense*, *T. devexa*, and *T. subtriphylla* var. *subtriphylla* were significantly correlated with both of AMT and AMP; significant correlation of spore release with both of AMT and AMP were found in *M. strigosa* and *T. devexa*. Other species might have significant correlation with AMT or AMP, or without such correlation.

Leaf life spans—The average life span of leaves ranged from 6.3 months and 7.3 months (sterile and fertile leaves of *D. chinense*, respectively) to 23.6 months (sterile leaves of *A. palisotii*). The sterile leaves of *C. pothifolia* lived significantly longer than its fertile leaves (15.5 vs. 11.8 months); the fertile leaves of *C. subglandulosa* and *M. strigosa* lived significantly longer than their sterile leaves (17.5 vs. 9.6 and 17.1 vs. 11.9 months, respectively). There were no significantly different life spans between the sterile and fertile leaves

of other species (Table 4). The time interval from spore release to leaf senescence ranged from 5.1 months (*D. chinense*) to 16.1 months (*C. subglandulosa*) (Table 3). No sorus was produced on the fertile leaves after their first cohort of sori detached.

Leaf sizes—Except for *A. palisotii* and *M. punctatum*, which did not produce fertile leaves in this study, fertile leaves of most species were significantly longer and wider than sterile ones. The width of sterile leaves of *C. wrightii* was not significantly different from its fertile leaves, but the length of its fertile leaves was significantly longer. Difference of *C. dissecta* was not significantly, but only two sterile leaves were measured (Table 5).

DISCUSSION

Leaf emergence—Phenological studies in tropical regions have demonstrated that phenology of many trees are correlated with the change of the dry-wet season (Singh & Kushwaha 2006, Vasconcelos *et al.* 2010).

Table 3— Time interval (months±SD) of fertile leaves from emergence to senescence of the 13 fern species studied at the Kenting Uplifted Coral Reef Nature Reserve, southern Taiwan, from September 1997 to August 2000.

species	Emergence to spore maturation (#)	Spore maturation to release (#)	Spore release to senescence (#)
<i>Arthropteris palisotii</i> ¹⁾	--	--	--
<i>Asplenium excisum</i>	3.1±0.8 (43)	1.3±0.6 (43)	10.3±5.2 (15)
<i>Colysis pothifolia</i>	1.9±0.7 (14)	1.6±1.3 (14)	8.4±3.7 (8)
<i>Colysis wrightii</i>	1.8±0.7 (34)	0.9±0.8 (33)	13.0±4.9 (7)
<i>Ctenitis subglandulosa</i>	1.0±0.7 (31)	0.4±0.3 (31)	16.1±2.9 (12)
<i>Ctenitopsis dissecta</i>	1.7±0.4 (22)	1.0±0.7 (22)	6.6±3.2 (22)
<i>Cyclosorus truncatus</i>	2.1±0.5 (10)	1.3±0.8 (9)	6.8±1.6 (8)
<i>Diplazium chinense</i>	1.8±0.6 (37)	1.2±0.8 (36)	5.1±2.0 (21)
<i>Diplazium dilatatum</i>	2.9±1.7 (59)	0.3±0.4 (59)	12.3±4.8 (34)
<i>Microlepia strigosa</i>	3.8±0.8 (9)	2.2±1.3 (9)	11.7±2.4 (4)
<i>Microsorium punctatum</i> ¹⁾	--	--	--
<i>Tectaria devexa</i>	1.8±1.0 (39)	0.6±0.7 (39)	7.3±4.3 (25)
<i>Tectaria subtriphylla</i> var. <i>subtriphylla</i>	1.5±0.9 (17)	0.5±0.5 (15)	15.2±4.8 (5)
Average	2.2±1.1 (315)	1.0±1.1 (310)	9.7±5.1 (161)

¹⁾ Fertile leaf was not found.

Table 4—Average life span (months±SD) of fertile and sterile leaves of 13 fern species at Kenting area.

species	Sterile leaves		Fertile leaves		Differences ¹⁾
	#	Lifespan	#	lifespan	
<i>Arthropteris palisotii</i> ²⁾	20	23.6±6.3			
<i>Asplenium excisum</i>	7	15.5±1.4	15	14.8±4.7	-0.7ns
<i>Colysis pothifolia</i>	38	15.5±5.7	8	11.8±3.6	-3.7*
<i>Colysis wrightii</i>	32	19.5±5.4	7	15.8±5.0	-3.7ns
<i>Ctenitis subglandulosa</i>	26	9.6±3.4	12	17.5±2.7	+7.9**
<i>Ctenitopsis dissecta</i>	1	10.9	22	9.6±3.2	
<i>Cyclosorus truncatus</i>	43	10.1±2.6	8	10.7±2.2	+0.7ns
<i>Diplazium chinense</i>	50	6.3±2.2	21	7.3±1.8	+1.0ns
<i>Diplazium dilatatum</i>	44	15.4±4.6	34	15.6±4.9	+0.2ns
<i>Microlepia strigosa</i>	65	11.9±3.8	4	17.1±1.6	+5.2**
<i>Microsorium punctatum</i> ²⁾	27	11.6±4.2			
<i>Tectaria devexa</i>	18	11.7±2.7	25	10.1±4.3	-1.7ns
<i>Tectaria subtriphylla</i> var. <i>subtriphylla</i>	33	16.3±6.8	5	18.0±5.6	+1.7ns

¹⁾ + indicates that fertile leaves had longer life span; - indicates that sterile leaves had long life span. ns: not significant; *: 0.01<p<0.05, t-test; **: p<0.01, t-test.

Table 5— The average size (cm±SD), indicated by length (L) and width (W), of the sterile and fertile leaves at Kenting area.

Species	L/W	#	Sterile leaves	#	Fertile leaves	D ¹⁾
<i>Arthropteris palisotii</i> ²⁾	L	98	23.8±8.3			
	W		6.0±1.5			
<i>Asplenium excisum</i>	L	10	17.4±4.8	25	30.6±8.9	13.2**
	W		6.3±1.3		9.5±2.1	3.2**
<i>Colysis pothifolia</i>	L	43	56.4±26.6	10	83.3±13.3	26.9**
	W		24.0±8.8		30.0±2.9	6.0**
<i>Colysis wrightii</i>	L	98	18.9±5.1	17	26.9±6.5	8.0**
	W		2.9±1.0		3.0±0.7	0.1ns
<i>Ctenitis subglandulosa</i>	L	30	35.5±12.8	19	65.3±17.1	29.8**
	W		20.9±8.2		41.3±10.8	20.4**
<i>Ctenitopsis dissecta</i>	L	2	31.0±18.3	18	40.5±16.4	9.5ns
	W		9.0±4.2		14.6±6.1	5.6ns
<i>Cyclosorus truncatus</i>	L	47	54.8±23.1	8	83±15.2	28.2**
	W		17.2±6.7		23.1±3.8	5.9**
<i>Diplazium chinense</i>	L	49	19.3±5.3	19	34.4±4.2	15.1**
	W		10.9±4.6		20.7±3.8	9.8**
<i>Diplazium dilatatum</i>	L	50	77.9±23.5	42	96.9±22.1	19.0**
	W		33.2±12.8		48.9±20.2	15.7**
<i>Microlepia strigosa</i>	L	68	44.7±20.2	4	35.3	
	W		16.7±7.9		32.0±2.2	15.3**
<i>Microsorium punctatum</i> ²⁾	L	42	19.8±7.5			
	W		2.8±0.8			
<i>Tectaria devexa</i>	L	24	17.5±4.3	26	23.4±6.8	5.9**
	W		8.1±2.0		10.7±3.6	2.6**
<i>Tectaria subtriphylla</i> var. <i>subtriphylla</i>	L	60	42.4±12.4	11	58.5±12.4	16.1**
	W		25.7±8.7		36.2±8.9	10.5**

¹⁾ Differences between fertile length (/width) and sterile length (/width). ns: not significant; **: $p < 0.01$, t-test.

²⁾ Fertile leaf was not found.

This phenomenon has also been found for some ferns in tropical deciduous forests (Mehlreter 2006, Mehlreter & Garcia-Franco 2008). Present study site is a tropical monsoon forest (Peel *et al.* 2007, Su 1984) with apparent alternation of dry and wet season. Results show that emergences of both sterile and fertile leaves in general were positively significantly correlated with AMT and AMP (Table 2). More leaves emerged during the wet season (April–October), when temperature was higher

(Fig. 1) though some species did not fit this generality. In fact, all species were in A or B type, except that *C. truncatus* and *M. strigosa* emerged their fertile leaves in the dry season (C type).

The fact that leaves emerged before the rainy season is also discovered in some ferns (Sharpe 1997, Mehlreter & Palacios-Rios 2003), but these species grow in wet habitat. In the tropical region, some woody plants, such as *Tristaniaopsis*, *Eugenia*, and *Anneslea* in

north Thailand, also emerge their leaves during the dry season (Elliot *et al.* 2006). The trees in this studied region also mainly sprout their leaves in the late dry season (Ho 1968, 1971). It is probably because sturdy roots of these woody plants are able to grow into the deep soil and use water therein (Borchert 1994). Shallow roots of ferns cannot absorb water from deep soil so do not emerge most leaves during the dry season. However, in some cases leaves emerged during the dry season probably because the understory condition where sufficient water remains at some microhabitats and provide the requirement for their leaf emergences.

The leaf emergence of some trees in the tropical region is also affected by the day length (Morellato *et al.* 2000, Rivera *et al.* 2002, and Elliot *et al.* 2006). Many leaf emergence in this study occurred during May and June (–August). Not only more precipitation and higher temperature, this period was also with longer day length.

Leaf expansion—Most woody plants in the tropical region sprout and develop their leaves in the wet season (Machado *et al.* 1997, Elliot *et al.* 2006, Vasconcelos *et al.* 2010). The leaf development is attributed to the higher air humidity (Do *et al.* 2005). In the present study, leaves of these ferns achieved their full sizes at ca. one month after their emergence, no matter they emerged in the wet or dry season. Because most leaves emerged during the wet season (and with higher temperature), the leaf expansion is also significantly correlated with the AMT and AMP (Table 2).

Leaf senescence—In tropical regions with a wet-dry season alternation, the leaf senescence may be different depending on the amount of precipitation. In the tropical forest of northeastern Brazil, the annual precipitation is < 1,000 mm with 6–7 month dryness; leaves mainly fall in the dry season that is attributed to insufficient water (Vasconcelos *et al.* 2010). On the other hand, in a tropical forest in Puerto Rico with > 3,000 mm annual precipitation and 3–4 months dryness, most leaves fall in the rainy season (Zalamea & Gonzalez 2008). The leaves of *Alsophila firma* (Baker) D.S. Conat, a tree fern found in Mexico deciduous forest with 1,950 mm of annual precipitation, drop more frequently in rainy season than in dry season (Mehltreter & Garcia-Franco 2008). The leaf, either sterile or fertile, senescence in this study is not significantly correlated to AMT and AMP. It seems that the less water in the dry

season of this habitat is not the key factor triggering the leaf senescence, as the phenomenon of *Alsophila firma* in the Mexico and the hypothesis (Borchert 1980) that the dry degree is not sufficiently to cause a large number of leaf senescence.

The senescence of fertile leaves of *C. truncatus*, the only exception of this study, mainly occurs in dry season. Interestingly, the fertile leaves of this species are mainly produced in the dry season (C-type). However, the fertile leaves of *M. strigosa* also emerged in the same pattern (C-type) but withered in the wet season. The monitored fertile leaves of these two species (11 and 9, respectively) were relatively fewer.

Spore maturation and release—Flowering is correlated with precipitation. Borchert *et al.* (2004) found that more than 50% of plants bloom in the wet season if 6–7 months/year are wet season, such as in Guanacaste (Costa Rica) and in Yucatan (Mexico), whereas < 1/3 of plants bloom in the dry season if 3–4 months/year belong to wet season, such as in Sonora (Mexico). Similarly, spore maturation and release are also highly correlated with the climate factors (Arosa *et al.* 2009). In this study, the correlations between spore maturation/release and AMT/AMP are positively significant. This study site is with 7 months/year of wet season, as the blooming in Guanacaste and Yucatan, fern spore maturation/release herein also mainly occur in the wet season. Previously studies of flowering phenology in this region also found most plants bloom in the early rainy season (Ho 1968, 1971).

Spore release is related to temperature and dryness. Arosa *et al.* (2009) found that some ferns postpone their spore release as they grow at higher elevation, where the temperature is lower but the humidity is higher than the lower elevation. Comparing to the phenology in Fushan, a subtropical forest of northeastern Taiwan (Lee *et al.* 2009), the time interval between spore maturation and release was significantly shorter in present study site than in Fushan (1.0 vs. 1.6 month, $p < 0.01$, t-test). In Fushan the annual precipitation (5,000 mm) is much higher, and the average monthly temperature (18.2°C) is lower than this site in southern Taiwan. The time interval between spore maturation and release is longer in the temperate region than in the subtropical and tropical regions (Johnson-Groh & Lee 2002) is also likely attributed to the lower temperature.

Leaf life span—All leaves of these 11 species (two species only presented sterile leaves) are monomorphic in terms of their outlines, although some species are with significantly different sizes between fertile and sterile leaves. Most species' sterile leaves had longer life span than their fertile leaves, but some species were with shorter life span for their sterile leaves. After releasing spores those fertile leaves did not produce second cohort of sori but still lived for several months to ca. 16 months and functioned as the sterile leaves for photosynthesis. Similar phenomenon was found in another phenological study in northeastern Taiwan (Lee *et al.* 2009).

Sterile leaves vs. fertile leaves—Most studies emphasize the difference of sterile and fertile leaves of dimorphic ferns, including the morphology and phenology (e.g., Wagner & Wagner 1977, Sharpe & Jernstedt 1990, Lee *et al.* 2008, 2009, Chiu *et al.* 2013). However, the sterile and fertile leaves of monomorphic ferns may also present different phenologies and/or develop different sizes (Lee *et al.* 2009). In this study, all species are monomorphic, but their sterile and fertile leaves develop to significantly different sizes except for *C. dissecta*. Some species also expressed different emergence/expansion seasonality and/or life spans.

The emergence seasons of sterile and fertile leaves of ferns are variable with geographical areas. In northern and northeastern Taiwan, fertile leaves generally emerge in late winter to early spring, whereas sterile leaves mainly in summer (Chiou *et al.* 2001, Lee *et al.* 2009). In southern Taiwan, this study reveals no such difference: the emergence seasons of fertile and sterile leaves are similar in general. Sterile and fertile leaves mostly emerged during April and October, the wet season (71.4% and 75.5%, respectively). In the south Taiwan, insufficient water is probably a limited factor for leaf emerging in the dry season. In the north and northeastern Taiwan, no distinct dry season, the different emerged seasons of sterile and fertile leaves should be attributed to the other factor(s), which needs to be further clarified. Similarly, the correlations between senescence of fertile/sterile leaves with AMT/AMP were not significant (Table 2). This indicates the senescence seasons of fertile and sterile leaves in this study were no significantly different. However, no such data in other regions is available for comparison.

Sterile leaves may have higher (*Pyrossia lingua* L.; Chiou *et al.* 2005) or lower (*Dryopteris filix-mas* (L.) Schott.; Bauer *et al.* 1991) photosynthesis rate than that of fertile leaves. It is likely due partly to the degree of sorus coverage on the fertile leaves that affect the CO₂ uptake and thus photosynthesis capacity (Chiou *et al.* 2005).

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