Research paper

Phenology of Three *Cyathea* (Cyatheaceae) Ferns in Northern Taiwan

Pei-Hsuan Lee,[1,3] Wen-Liang Chiou,[2,3] Yao-Moan Huang[2,4]

【Summary】

The phenology of 3 tree fern species, *Cyathea hancockii*, *C. metteniana*, and *C. podophylla* at Mt. Chihsing (25º9'N, 121º33'E) located in northern Taiwan was observed from June 2000 to May 2003. All observed plants produced both fertile and sterile leaves every year during this period. For every species, most fertile leaves emerged in cooler months, compared to the emergence months of sterile leaves. Phenological events, including leaf emergence, expansion, and senescence, and spore maturation and release were slightly correlated with the monthly precipitation but were relatively more highly correlated with the average monthly temperature although they were not significant. The sizes of fertile leaves were significantly larger than sterile ones in *C. hancockii* and *C. metteniana*, whereas they did not significantly differ in *C. podophylla*. The life spans of fertile and sterile leaves did not significantly differ for each of these 3 species. The mean life spans of fertile leaves were 15.9, 19.5, and 26.6 mo, whereas those of sterile leaves were 15.0, 21.2, and 28.3 mo in *C. hancockii*, *C. metteniana*, and *C. podophylla*, respectively. All fertile leaves remained alive for ca. 7~22 mo after releasing their spores. After releasing their spores, the sporangia detached, and no more sori were produced on the same leaf. All sterile leaves remained sterile throughout their lives.

Key words: *Cyathea hancockii*, *Cyathea metteniana*, *Cyathea podophylla*, life span, phenology.

Lee PH, Chiou WL, Huang YM. 2009. Phenology of three *Cyathea* (Cyatheaceae) ferns in northern Taiwan. Taiwan J For Sci 24(4):233-42.

[1] Taimali Research Center, Taiwan Forestry Research Institute, 6 Chiaotou, Dawang Village, Taimali, Taitung 96341, Taiwan. 林業試驗所太麻里研究中心，96341台東縣太麻里鄉大王村橋頭6號。

[2] Botanical Garden Division, Taiwan Forestry Research Institute, 53 Nanhai Rd., Taipei 10066, Taiwan. 林業試驗所植物園組，10066台北市南海路53號。

[3] These authors contributed equally to this work. 作者具相同貢獻。

[4] Corresponding author, e-mail:huangym@tfri.gov.tw 通訊作者。

Received June 2009, Accepted September 2009. 2009年6月送審 2009年9月通過。

研究報告

北台灣產三種桫欏屬植物(桫欏科)物候

李沛軒[1,3) 邱文良[2,3) 黃曜謀[2,4)

摘　要

本篇物候學研究對象為三種桫欏科樹蕨類植物，包括韓氏桫欏、台灣樹蕨與鬼桫欏；研究地區位於北台灣的七星山區(北緯25度9分，東經121度33分)。2000年6月至2003年5月調查期間內，所有調查植株每年均生產孕性葉與營養葉，相對於營養葉，大多數孕性葉發生於較冷的月份。有關葉片抽芽、展葉、枯萎、及孢子成熟與釋放等物候，與月降水量並沒有顯著相關；除少數例外，大部份與月均溫有顯著相關。韓氏桫欏與台灣樹蕨的孕性葉明顯大於營養葉，然鬼桫欏的兩者差異並不顯著。韓氏桫欏、台灣樹蕨與鬼桫欏的孕性葉壽命依序為15.9、19.5與26.6個月，營養葉依序為15.0、21.2與28.3個月，這三種植物的孕性葉與營養葉壽命都沒有明顯差異。所有孕性葉在孢子釋放後仍存活7至22個月。孕性葉片在孢子釋放後孢子囊掉落，沒有新的孢子囊產生；所有營養葉一生均維持不孕(沒有孢子)的狀態。

關鍵詞：韓氏桫欏、台灣樹蕨、鬼桫欏、壽命、物候。

李沛軒、邱文良、黃曜謀。2009。北台灣產三種桫欏屬植物(桫欏科)物候。台灣林業科學24(4):233-42。

INTRODUCTION

Plant phenology is affected by intrinsic and/or environmental factors (Mehltreter 2008) and is relevant to plant growth and reproduction (Sharpe and Jernstedt 1990). Studies of fern phenology are important in understanding fern biology and ecology (Farrar et al. 2008, Mehltreter 2008). However, most phenological studies focus on flowering plants rather than on ferns which are often the dominant vegetation of the forest understory.

Some previous studies demonstrated that fern phenology has a seasonality which may be related to rainfall or temperature (Farrar and Gooch 1975, Farrar 1976, Tanner 1983, Ash 1986, Sharpe and Jernstedt 1990, Page 1997, Sharpe 1997, Arens 2001, Johnson-Groh and Lee 2002, Lee et al. 2008), or may be non-seasonal (Tryon 1960). Most of those results were observed in either temperate regions where seasonal temperatures change significantly or tropical regions where dry and wet seasons are apparent. Thus, it was assumed that tropical rainforest ferns would have an aseasonal phenology (Tryon 1960). However, that viewpoint is being challenged by recent phenological studies of tropical ferns over the last 20 yr (Mehltreter 2008). In forests of northern and northeastern Taiwan which have greater seasonal temperature changes but smaller precipitation variations, fern phenologies are affected more by temperature rather than by rainfall (Chiou et al. 2001, Lee et al. 2009). More examples of this phenomenon are needed to confirm if it is a general rule for all ferns in this type of habitat.

In ferns, fertile and sterile leaves greatly differ in shape and size, so-called dimorphic species (e.g., Wagner and Wagner 1977). Fertile leaves of dimorphic ferns are reported to be slender and shorter-lived than sterile leaves of the same species (e.g., Sharpe and Jernstedt 1990, Sharpe 1997, Mehltreter and Palacios-Rios 2003). In contrast, fertile and sterile leaves of monomorphic species have similar profiles and sizes (Chiou et al. 2001, Lee et al. 2009). Unlikely dimorphic species, fertile leaves might have a longer life span than sterile leaves in monomorphic species (reviewed by Mehltreter 2008).

In this study, 3 Cyatheaceae (tree fern family) ferns, *Cyathea hancockii* Copel., *C. metteniana* (Hance) C. Chr., and *C. podophylla* (Hook.) Copel. growing in a forest of northern Taiwan were selected to determine their phenology, including leaf emergence, development, and senescence, and spore maturation and release. Among these 3 species, *C. hancockii* and *C. metteniana* are herbaceous, with short erect, and sometimes prostrate, rhizomes (caudexes) but without erect trunks; in contrast, *C. podophylla* is a tree fern with a trunk up to 2 m tall (Shieh 1994). Three main goals of this study were to (1) determine the phenological events of these 3 fern species; (2) determine differences in phenological events, sizes, and life spans between fertile and sterile leaves in each of the 3 species; and (3) analyze the correlation of their phenological events with environmental factors (i.e., precipitation and temperature).

MATERIALS AND METHODS

The phenology of *C. hancockii*, *C. metteniana*, and *C. podophylla*, growing in a subtropical rainforest, Mt. Chihsing (25º9'N, 121º33'E) at elevations of 560~820 m in northern Taiwan (Fig. 1), was monitored from June 2000 to May 2003. Ten plants each of *C. hancockii* and *C. podophylla* and 5 plants of *C. metteniana* were included in this study (Table 1). Each plant of the same species was at least 10 m apart to reduce genetic homogeneity.

Because ferns develop fertile leaves only after reaching a certain age or size (Prange and von Aderkas 1985, Huang et al. 2008), all plants chosen for this study had already produced spore-bearing leaves. Each leaf was labeled with a small plastic tag after it had grown big enough (> 5 cm long). Leaf emergence and senescence, and spore maturation and release were recorded at the end of each month. When mature, the length (from the base to the leaf tip) and width (at the widest part of the leaf) of each leaf were measured. At the end of the survey, some leaves still remained in a coiled status, and many leaves were still green. Thus, the numbers recorded for leaf expansion were smaller than

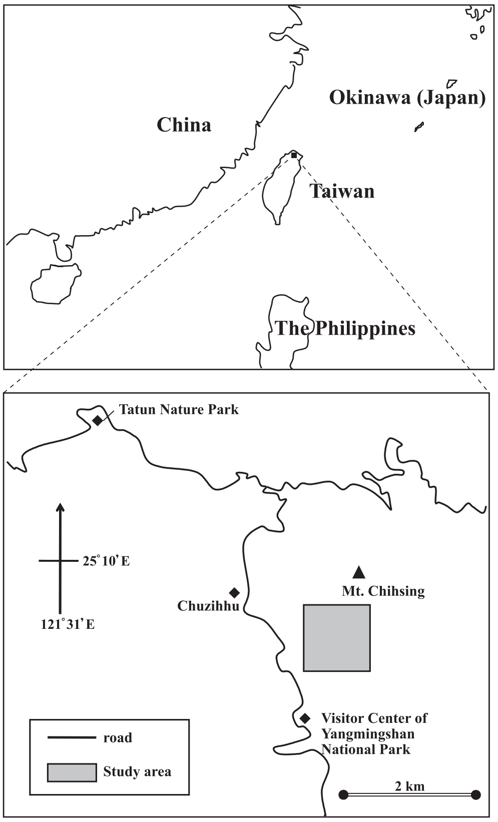

Fig. 1. Location of this study: Mt. Chihsing, Yangmingshan National Park (modified from http://maps.google.com).

emergence numbers, and the numbers for leaf senescence were smaller than expansion numbers (Table 1). Weather data (Fig. 2) were obtained from a nearby weather station at Chuzihhu (25º10'N, 121º32'E, at an elevation of 607 m; Fig. 1) (http://www.cwb.gov.tw).

RESULTS

Leaf emergence

Every species produced both fertile and sterile leaves every year in this study. In *C. hancockii*, most fertile leaves (23 of 30) emerged during February to April, whereas all 23 sterile leaves emerged in every month except January and November. In *C. metteniana*, all 18 fertile leaves emerged during January to August, whereas all 15 sterile leaves emerged during December to the following September. In *C. podophylla*, fertile leaves mainly emerged during November to the following May (63 of 68), whereas sterile

Table 1. Phenology of 3 *Cyathea* species studied at Mt. Chihsing from June 2000 to May 2003

Species	Plants (*n*)	Total number of leaves			Emergence to expansion (mo)*	Emergence to spore maturation (mo)*	Spore maturation to release (mo)*
		Emergence (no. of fertile leaves)	Expansion	Senescence			
C. hancockii	10	53 (30)	51	39	3.2±0.3	4.3±0.4	4.6±0.4
C. metteniana	5	33 (18)	33	19	3.4±0.4	3.9±0.6	4.3±1.0
C. podophylla	10	126 (68)	117	33	3.5±0.2	4.4±0.4	1.4±0.2

* Values are the mean±95% confidence interval.

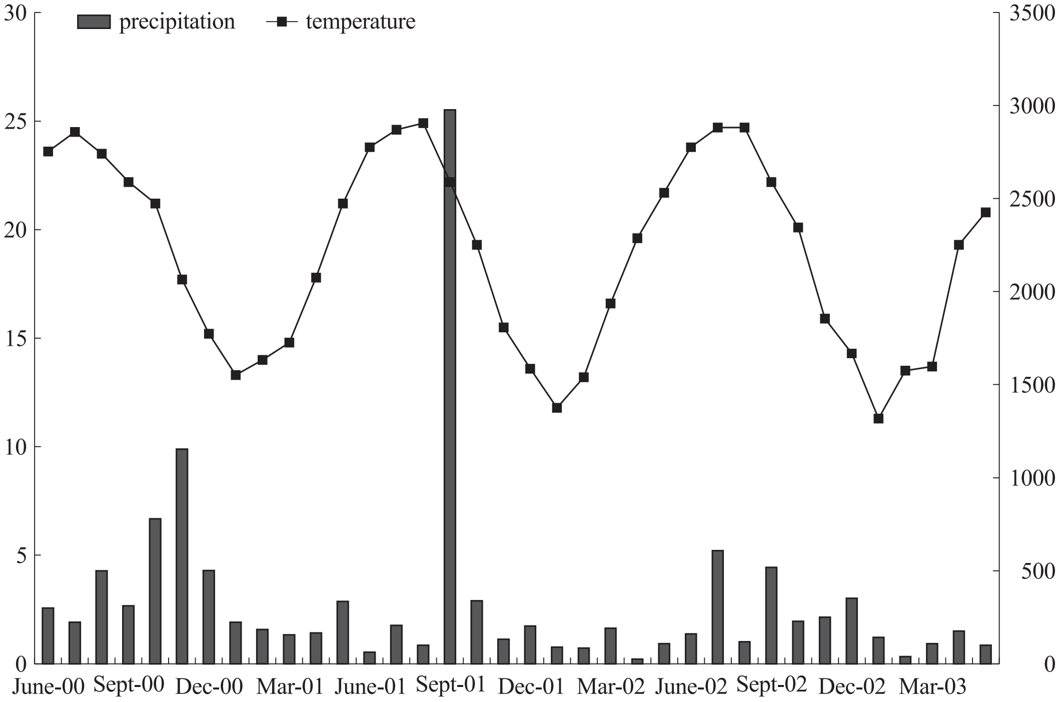

Fig. 2. Temperature (℃, left Y axis) and precipitation (mm, right Y axis) during June 2000 to May 2003 at the Chuzihhu weather station.

leaves (50 of 58) mainly emerged during April to August (Table 2). The emergences of fertile leaves of *C. hancockii* and *C. podophylla* were significantly negatively correlated with average monthly temperature (AMT), whereas the emergences of their sterile leaves were significantly positively correlated with the AMT. No significant correlation of AMT was noted with either fertile or sterile leaves of *C. metteniana*. No significant correlation of precipitation with fertile or sterile leaves of these 3 species was found (Table 3).

Leaf expansion and senescence

The average time from leaf emergence to full expansion ranged from 3.2 to 3.5 mo for both fertile and sterile leaves, and did not reach a significant difference among species (Table 1). Most leaves achieved full expansion from March to September, but this varied

Table 2. Total number of leaves of 3 fern species in each phenological stage by month from June 2000 to May 2003. 1: Emergence of fertile leaves, 2: expansion of fertile leaves, 3: senescence of fertile leaves, 4: emergence of sterile leaves, 5: expansion of sterile leaves, 6: senescence of sterile leaves, 7: spore maturation, 8: spore release

Stage	J	F	M	A	M	J	J	A	S	O	N	D	Total
Cyathea hancockii													
1	3	10	8	4	1	1	0	0	0	0	0	3	30
2	0	0	0	2	14	12	4	0	0	0	0	0	32
3	1	3	1	4	4	3	4	3	0	3	1	0	27
4	0	1	3	2	2	5	3	3	1	2	0	1	23
5	0	0	1	0	3	3	3	4	1	3	1	0	19
6	0	1	1	1	2	0	2	0	0	4	0	0	12
7	0	0	0	0	0	1	15	11	0	1	0	0	28
8	7	0	0	0	0	0	0	0	0	1	3	16	27
Cyathea metteniana													
1	4	4	2	2	2	2	1	1	0	0	0	0	18
2	0	0	1	1	5	5	3	2	0	1	0	0	18
3	2	5	0	0	1	0	2	0	0	0	0	1	11
4	1	2	2	2	1	2	1	1	1	0	0	2	15
5	0	0	1	2	5	2	1	2	1	0	1	0	15
6	0	0	1	1	1	0	0	1	0	2	2	0	8
7	0	0	0	0	0	2	9	4	1	1	0	1	18
8	1	0	1	2	2	0	1	0	3	5	1	2	18
Cyathea podophylla													
1	10	5	11	4	6	1	1	1	0	2	8	19	68
2	1	1	11	17	14	13	3	2	1	0	0	1	64
3	2	0	2	0	2	6	2	2	1	6	1	0	24
4	0	1	2	8	9	14	10	9	2	1	1	1	58
5	0	0	0	0	2	11	14	11	7	3	2	3	53
6	2	1	1	0	1	2	0	1	0	1	0	0	9
7	0	0	2	1	17	25	14	3	0	0	0	0	62
8	0	0	0	0	2	15	18	19	3	1	2	0	60

Table 3. Correlations (*r* value) between phenological events of 3 *Cyathea* species at Mt. Chihsing and monthly temperature and precipitation data, June 2000~May 2003

	Emergence		Expansion		Senescence		Spore	
	Fertile	Sterile	Fertile	Sterile	Fertile	Sterile	Maturation	Release
Temperature								
C. hancockii	-0.51**	0.39*	0.37*	0.59**	0.29	0.13	0.52**	-0.50**
C. metteniana	-0.33	-0.12	0.46**	0.31*	-0.24	0.00	0.55**	0.06
C. podophylla	-0.58**	0.63**	0.20	0.72**	0.23	-0.07	0.39*	0.59**
Precipitation								
C. hancockii	-0.20	0.02	-0.13	-0.10	-0.18	-0.10	0.03	-0.03
C. metteniana	-0.26	-0.20	-0.10	-0.10	-0.08	-0.03	0.11	0.24
C. podophylla	-0.15	-0.03	-0.19	0.02	-0.01	-0.20	-0.13	-0.02

* $0.01 < p < 0.05$; ** $p < 0.01$, *t*-test.

among different species. For example, fertile leaves of *C. hancockii* achieved full expansion during April and July, whereas sterile leaves of *C. podophylla* achieved full expansion during May to December and mostly during June to September (Table 2). Most leaf expansion was significantly positively correlated with the AMT, except fertile leaves of *C. podophylla*, but was less closely correlated (negatively) with precipitation (Table 3). Leaves which emerged during the warmer season took less time to achieve the stage of full expansion.

The leaf senescence of these 3 species varied. There were no significant correlations between the senescence of these leaves and AMT or precipitation (Table 3).

Spore maturation and release

It took 3.9~4.4 mo on average from the emergence of fertile leaves to spore maturation (Table 1). Spores mainly matured in July and August for *C. hancockii* (26 of 28) and *C. metteniana* (13 of 18), whereas maturation occurred mainly from May to July for *C. podophylla* (56 of 62; Table 2). The spore maturation times of these 3 species were significantly positively correlated with the AMT but less so with precipitation (Table 3).

From spore maturation to release, it took ca 1.4~4.6 mo (Table 1). The release time of *C. hancockii* was mainly in December and January (23 of 27) and was significantly negatively correlated with AMT (r = -0.50, $p < 0.01$) (Table 3). The spore release time of *C. metteniana* occurred in no specific season, whereas that of *C. podophylla* was mainly from June to August (52 of 60) and was significantly positively correlated with AMT (r = 0.59, $p < 0.01$). None of the spore release times of these 3 species was significantly correlated with precipitation (Table 3).

Life span of leaves

The average life span of leaves ranged 15.0~28.3 mo, depending on the species (Table 4). There was no significant difference between the life spans of fertile and sterile leaves for each species (Table 4). The sporangia detached sooner or later after the spores were released, and no 2nd cohort of sori or spores was produced on the same leaf. Fertile leaves lived 7.2~21.9 mo after spore release (Table 4).

Leaf size

All fertile leaves of *C. hancockii* and *C. metteniana* were significantly longer and

Table 4. Average life span (mo) of fertile and sterile leaves of 3 *Cyathea* species, and longevity (mo) of their fertile leaves from spore release to senescence (numbers in parentheses are the number of leaves observed)

Species	Life span (*n*)				Spore release
	Fertile	Sterile	Difference[1)]	$P^{2)}$	to senescence[3)]
C. hancockii	15.9±1.7 (22)	15.0±2.7 (11)	+0.9	0.2841	7.2±1.7
C. metteniana	19.5±2.8 (13)	21.2±3.7 (6)	-1.7	0.2517	11.3±3.3
C. podophylla	26.6±2.6 (31)	28.3±3.5 (12)	-1.7	0.2286	21.9±2.6

[1)] + Indicates that fertile leaves had a longer life span; - indicates that stertile leaves had a longer life span.
[2)] *p* values of the *t*-test showing significant differences of life span between fertile and sterile leaves.
[3)] Number of months fertile leaves survived after spore release.

Table 5. Average length and width of fertile and sterile leaves of 3 *Cyathea* species at Mt. Chihsing, northern Taiwan

Species	Frond length (cm)			Frond width (cm)		
	Fertile	Sterile	*p**	Fertile	Sterile	*p**
C. hancockii	54.9±8.4	37.8±8.3	0.0065	30.1±5.8	22.1±4.0	0.0235
C. metteniana	87.8±12.7	53.5±9.4	0.0002	62.2±9.6	28.8±7.9	0.0000
C. podophylla	160.9±12.1	150.4±12.3	0.1187	101.4±5.0	102.7±6.1	0.3694

* *p* value indicates a significant difference between the length (or width) of fertile and sterile leaves of each species conducted by *t*-test.

wider than sterile ones. However, the length and width of fertile and sterile leaves did not significant differ in *C. podophylla* (Table 5).

DISSCUSION

Seasonality

Fern phenology was reported in various different climate regimes. In strongly seasonal regions, leaf emergence might occur during the rainy season (Ash 1986, van Schaik et al. 1993), at the end of the dry season (Seiler 1981), or in the spring of a temperate region (Lee et al. 2008), or it might not be significantly correlated with temperature or precipitation (Mehltreter and Palacios-Rios 2003). The leaf emergence of *Cibotium taiwanense* Kuo, growing in northern Taiwan near this study area, was not correlated with precipitation because there is no distinct dry season but was closely correlated with temperature changes (Chiou et al. 2001). In northeastern Taiwan, the seasonal temperature and precipitation are similar to those of northern Taiwan, and the phenological events of many ferns are also generally correlated with the temperature but not with the precipitation (Lee et al. 2009).

In this study, none of the surveyed phenological parameters had a significant correlation with precipitation. On the other hand, greater or lesser correlations between those phenological events and temperature were found. In general, fertile leaves emerged in cooler months and sterile leaves emerged in relatively warmer months. Other phenological events such as leaf expansion and senescence and spore maturation and release mostly occurred in warmer months. The senescence of *C. metteniana* did not occur in a specific period probably due to the low sample number. Given a larger sample size, the statistical significance might have differed.

The phenological events of *C. podophylla* of northern Taiwan in this study were very similar with those in northeastern Taiwan as documented by Lee et al. (2009) probably due to the similar weather patterns and habitats. No other phenological data of *C. hancockii* and *C. metteniana* growing in other regions are available for comparison.

Longevity

In ferns, fertile leaves were previously predicted to have shorter lives than sterile leaves (Wagner and Wagner 1977, Sharpe and Jernstedt 1990, Sharpe 1997, Mehltreter and Palacios-Rios 2003). This was proven to be correct for 2 dimorphic *Plagiogyria* species (Lee et al. 2009) and a semi-dimorphic species *Osmuda claytoniana* L. in which spores only grow on the distal part of fertile leaves (Lee et al. 2008). However, this character of a longer life span of sterile leaves does not fit other monomorphic species (Chiou et al. 2001, Lee et al. 2009). In these 3 *Cyathea*, it was found that no significant differences existed in the life spans of fertile and sterile leaves in this study. No significant difference in the life spans of fertile and sterile leaves of *C. podophylla* was also reported in northeastern Taiwan (Lee et al. 2009).

Leaf size

Fertile leaves are generally longer and thinner than sterile leaves in dimorphic ferns (Wagner and Wagner 1977, Lee et al. 2009). *Cibotium taiwanense*, a monomorphic tree-like fern, was reported to have longer and wider fertile leaves than sterile leaves (Chiou et al. 2001). The longer and wider fertile leaves are also found in many other monomorphic ferns (Lee et al. 2009). In this study, *C. hancockii* and *C. metteniana* also had longer and wider fertile leaves. However in *C. podophylla*, fertile leaves were similar to sterile leaves in length and width. Still no definite patterns in leaf size of monomorphic ferns are recognized at present.

Development and function of fertile and sterile leaves

Ferns produce fertile leaves only when they achieve maturity (Wardlaw 1962, White 1971, Prange and von Aderkas 1985). Sorus production is affected by environmental conditions such as temperature and photoperiod (Wardlaw and Sharma 1963, Odland 1995). In these 3 species, sori were observed as soon as leaves had sufficiently unfurled. No leaves produced any sori after the 1st cohort of sori had detached. Leaves that did not have sori when they first unfurled remained sterile throughout their life. Apparently environmental factors affected the very early stage of leaf development and differentiation. Once a leaf begins to uncoil, its fate as a sterile or fertile leaf is determined. Fertile leaves had 2 functions, reproduction and photosynthesis, although these 3 ferns were monomorphic in shape. The same phenomena were documented in other ferns growing in northern Taiwan (Lee et al. 2009).

CONCLUSIONS

This study demonstrats that the phenological events of different congeneric species within a given area varied. Characteristics such as the life span and size of fertile and sterile leaves were also compared. The information herein provides a basis for future biological, ecological, and conservational research of these ferns. However, the causes of the variations and differences, either intrinsic (genetic) or extrinsic (environmental), were less clear. In order to be able to draw more-general phenological conclusions, it is necessary to monitor more species, carry out long-term and broad-scale studies at different latitudes and elevations, and investigate more microhabitat factors such as soil temperature and humidity.

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