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Factors affecting stipule sprouting of *Angiopteris somae* (Marattiaceae)

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ABSTRACT: *Angiopteris somae* (Hayata) Makino & Nemoto is an endemic and endangered fern in Taiwan, facing population decline due to inadequate habitat protection, plant competition, and illegal collection. *Ex situ* conservation is urgently needed, and stipule vegetative propagation is a practical method for this purpose. However, the low stipule production limits propagation efforts. This study investigated the correlations between phenotypic traits and sprouting parameters, finding no significant links between plant age or size and their sprouting ability. Juvenile stipules located near the apex of rhizomes produced more sprouts than those situated near the base. Additionally, deceased stipules were observed to be smaller and lighter. Sprout number did not correlate with stipule size, nor did the time for sprouting relate to age or size of the stipules. These findings can guide conservationists in selecting stipules with higher potential for sprout production, ultimately helping to minimize collection and protect mother plants during *ex situ* conservation.

KEY WORDS: *ex situ* conservation, sprout, sprouting percentage, sprouting time, vegetative propagation.

INTRODUCTION

Approximately 5–7% of fern species exhibit the potential to generate vegetative buds (sprouts) from various structures such as petioles, stolons, roots, and leaves (McVeigh, 1937; Troop and Mickel, 1968; Schmitt and Windisch, 2006; Sharpe and Mehlreter, 2010; Huang *et al.*, 2022). Among fern families, Marattiaceae is notably known for producing vegetative buds from stipules (Tryon and Tryon, 1982; Huang *et al.*, 2010). The stipules are situated on the rhizome at the base of each petiole and offer protection during the initial stages of leaf development. Notably, these stipules remain attached to the rhizome even after the rest of the leaf has senesced and abscised (Lehn and Lopes, 2017).

The gametophytes of some marattioid species exhibit slow growth rates, and/or their spores can be difficult to germinate (e.g., Chou *et al.*, 2007). Thus, stipules have become practical alternative propagules and are extensively utilized for conservation and horticultural purposes (Uffelen, 1994; Chiou *et al.*, 2006). Some rare marattioid species produce only a few leaves each year. Intensive collection of stipules can lead to plant damage or even death. Therefore, effectively utilizing stipules to propagate plantlets is crucial for conservation efforts.

Sprouting ability of vegetative propagules is linked to their inherent characteristics. In flowering plants, age of the plant is known to influence the sprouting (rooting) process of cuttings. A fundamental observation is that cuttings taken from juvenile plants exhibit significantly higher rooting success compared to those derived from

mature plants (Altoé *et al.*, 2011; Wendling *et al.*, 2014; Sahoo *et al.*, 2021). In addition, the position and age of the cuttings are recognized as crucial factors determining the outcome of rooting (Ott *et al.*, 2019). It has been observed that more juvenile branches, particularly those in good nutritional condition, tend to present better rooting ability (Wendling *et al.*, 2014). Additionally, cutting size may also affect rooting outcomes; cuttings with a larger diameter and longer length generally produce better rooting results (Leakey, 1983; 2004). However, our understanding of the factors affecting vegetative cultivation in ferns remains limited.

Almost 120 years ago, Gwynne-Vaughan (1905) noted the presence of meristematic tissues at the stipule margins in *Archangiopteris henryi* Christ & Giesenh. and *Kaulfussia aesculifolia* (Blume) Blume. (= *Christensenia aesculifolia* (Blume) Maxon). In recent decades, only a few studies have documented the factors affecting stipule sprouting (rooting) in marattioid species. The sprouting percentage of stipules and the number of sprouts per stipule varied somewhat among 5 marattioid ferns native to Taiwan. Subsequent researches revealed a positive correlation between stipule sizes and numbers of sprouts within each species (Chiou *et al.*, 2006; Huang *et al.*, 2010). However, the relationship between stipule size and sprouting time was weak in *Angiopteris somae* (Hayata) Makino & Nemoto (= *Ar. somai* Hayata) and virtually non-existent in *An. ×ittoi* (W.C.Shieh) J.M.Camus (= *Ar. ittoi* Shieh) (Chiou *et al.*, 2006).

Angiopteris somae is an endemic and famous eusporangiate fern to Taiwan (DeVol and Shieh, 1994).

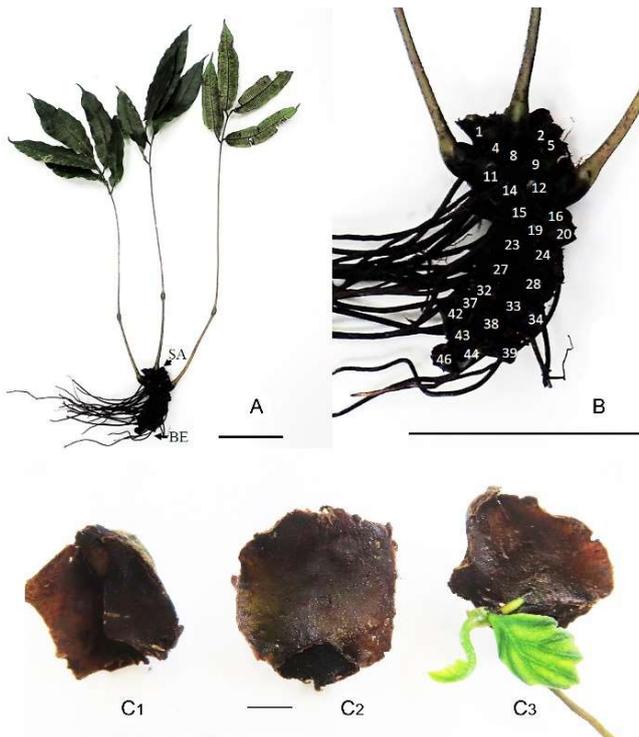


Fig. 1. *Angiopteris somae*. **A.** plant. SA: shoot apex; BE: basal end; **B.** stipules. Numbers: sequential numbers of stipules, starting from apical end progressing to the basal end of the rhizome. Bars = 10 cm. **C.** Statuses of stipules: **C1.** Deceased. **C2.** Arrested. **C3.** Sprouting. Bar = 1cm.

This species typically thrives in shady, moist soils in low-elevation forests (Huang *et al.*, 2019). Over the past century, two geographical populations of *A. somae* have been well-documented: one in Wulai, located in northern Taiwan, and another in Lienhuachih, situated in central Taiwan (Chou *et al.*, 2007; Huang *et al.*, 2016). Recently, a new population was discovered in Shouka, southern Taiwan, consisting of fewer than 10 individual plants (ZXC003186, TAIF). Due to its sparse distribution, with less than 1000 mature individuals, *A. somae* is categorized as an endangered species (Kuo, 1997; Editorial Committee of the Red List of Taiwan Plants, 2017).

The most effective strategy for the long-term conservation of this endangered species is to preserve its natural communities and populations in the wild, known as *in situ* preservation. Unfortunately, the original habitats of *A. somae* populations remain unprotected, and the existing populations continue to decline due to competition with coexisting plant species and ongoing illegal collection activities. Consequently, *ex situ* conservation plays an important supplement to maintain the endangered fern in its natural habitat. Initial studies on sexual propagation through spore culture for *ex situ* conservation were conducted by Chou *et al.* (2007), who discovered that propagating sporophytes through spores was a time-consuming, taking over 13 months, with a low success rate of only 3%. In contrast, stipule propagation

not only significantly reduced the sprouting time (ca. 3 months), but also increases the sprouting percentage (40–85%) (Chiou *et al.*, 2006; Huang *et al.*, 2016). It is important to note that production of stipules on intact plant was limited and occurred at a slow rate, averaging about 2 stipules per plant per year (Huang *et al.*, 2019). Therefore, the stipule collection for vegetative propagation warrants careful consideration (Huang *et al.* 2010).

This study aims to investigate the correlations between phenotypic traits of plants or stipules and sprouting parameters. Based on the results, we can infer how to choose stipules so as to obtain the most sprouts in the shortest time.

MATERIALS AND METHODS

Collecting site

Stipules on the rhizomes of 20 intact plants of *A. somae* were harvested in May 2020 from a subtropical broadleaf forest at the Lienhuachih Research Center of the Taiwan Forestry Research Institute in central Taiwan (23°55'43" N, 120°54'00" E, at an altitude of approximately 680 m).

Age

According to the field phenological investigation, the mean annual number of emergent leaves per plant at the study site was 1.97 (Huang *et al.*, 2019). Therefore, the number of stipules on each plant was divided by 1.97 to estimate the ages of plants (Equation 1). The ages of stipules were inferred using the following Equation 2.

$$\text{Age of plant (years)} = n/1.97 \quad \text{Equation 1}$$

$$\text{Age of stipule (years)} = i/1.97 \quad \text{Equation 2}$$

where n represents the total number of stipules on the rhizome, and i represents the sequential number of stipules on the rhizome (counted from the apex toward the base).

Modifying the methodologies established by Snow and Snow (1932) and Sharpe and Jernstedt (1991), stipules were designated based on their positional hierarchy, with stipule number 1 closest to the shoot (rhizome) apex. Subsequent stipules were then numbered sequentially towards the basal end (Fig. 1).

Position of stipule

The position of each stipule on the plant was then calculated following Equation 3.

$$\text{Position (\%)} = i/n \times 100\% \quad \text{Equation 3}$$

Stipule culture

Following the cultivation protocol established by Huang *et al.* (2010), stipules were carefully pulled out from the rhizome and subsequently rinsed for 3 minutes using tap water. Surface moisture was wiped off with paper towels, and their width and weight were measured.



Table 1. The correlations between sprouting parameters and phenotypic traits of *Angiopteris somae* plants based on multiple linear regression analysis. Phenotypic traits of plants: age (Ap), mean stipule width (MW), and mean stipule weight (MM).

	Coefficient	Std. Error	t	p
Sprouting percentage (%)				
Constant	92.634	33.226	2.788	0.013
Ap	-0.180	0.578	-0.312	0.759
MW	-1.032	3.137	0.329	0.746
MM	1.260	9.579	0.132	0.897
Mean sprouting number				
Constant	1.4700	0.611	2.406	0.029
Ap	-0.0039	0.0106	-0.367	0.718
MW	-0.0222	0.0577	-0.385	0.705
MM	0.0678	0.1760	0.385	0.705
Mean sprouting time (weeks)				
Constant	14.836	3.701	4.009	0.001
Ap	0.0414	0.0644	0.643	0.530
MW	0.0669	0.3490	0.191	0.851
MM	-0.609	1.0670	-0.570	0.576

Note: Number of stipules per plant was excluded from this analysis because it is collinear relationship with plant ages. All Ap, MW, MM had no ability to predict sprouting parameters, including mean sprouting number, and mean sprouting time of plants ($p > 0.05$).

Following this, stipules were partially buried in moist sphagnum moss and placed within plastic containers (11.4 cm × 8.6 cm × 10.2 cm, Phytatray™ II, SIGMA, USA). All cultures were maintained under white LED lighting (24 μ mol m⁻² s⁻¹ for 12 hours per day) at temperatures ranging from 20°C to 28°C.

Sprouting

During a 22-week culture period, the number of sprouts on each stipule was recorded at a 2-week interval. We modified the criteria of Sharpe and Jernstedt (1991), and categorized stipules into 4 statuses as following. (1) 2-sprout stipule: a stipule with 2 expanded sprouts (larger in size, featuring roots and/or leaves). (2) 1-sprout stipule: a stipule with a single expanded sprout. (3) deceased stipule: a non-sprouting stipule whose tissue has softened, browned, or became rotten; and (4) arrested stipule: a stipule that did not produce sprout but retained firm tissue (Fig. C). Both of 2-sprout stipule and 1-sprout stipule were recorded as sprouting stipules.

Three parameters of sprouting were defined. First, “sprouting percentage” indicated the number of sprouting stipules divided by the total number of stipules from an individual plant, ranging from 0 to 100%. Second, “number of sprouts” indicated the number of sprouts from an individual stipule, ranging from 0 to 2. Third, “sprouting time” indicated the duration in weeks from stipule culture initiation to sprouting. When stipules did not produce sprouts during the observation period, the sprouting time was labeled as “missing data” and not included in the calculation. When a stipule produced only one sprout, the sprouting time was calculated from this

unique sprout. If a stipule produced two sprouts, the sprouting time was derived from the mean value of both.

Analyses

The correlations between phenotypic traits (age, width and weight) of plants or stipules and sprouting parameters (sprouting percentage, number of sprouts, and sprouting time) were analyzed using multiple linear regression analysis. The phenotypic traits of various status stipules were analyzed using one-way ANOVA.

RESULTS

Plants

The numbers of stipules per plant ranged from 16 to 40. The corresponding ages of the plants, estimated from the numbers, ranged from 8.1 to 20.3 years. The mean stipule width and weight of the plants ranged from 12.2 to 20.9 mm and 1.5 to 4.0 g, respectively. Sprouting percentages of plant stipules ranged from 52.9% to 100.0%, and the mean sprouting numbers of sprouts ranged from 0.8 to 1.6, mean sprouting time ranged from 13.6±3.0 to 18.8±3.2 weeks among the 20 plants (Table S1)

Sprouting percentages, mean numbers of sprouts, or mean sprouting time did not have significant correlations with the phenotypic traits of plants (Table 1).

Stipules

A total of 512 stipules derived from 20 plants were cultured. Sprouts were observed at two distinct locations on the stipules, with no significant difference in the numbers of sprouts between the right (301) and left margins (296) of the proximal surface, as determined by a chi-square goodness of fit test ($\chi^2 = 0.0268$, $p = 0.870$). At the end of 22-week culture, 43.0% (220/512) of stipules produced 2 sprouts, 30.6% (157/512) produced 1 sprout, and 22.5% (115/512) remained at arrested status. The remaining 3.9% (20/512) were deceased (Table 2).

Comparing the four phenotypic traits of stipules across various statuses, two-sprout stipules were located closer to the apex of rhizome and were more juvenile than stipules of other statuses. One-sprout stipules were positioned next in proximity. However, the mean sprouting times did not differ significantly between these two statuses. Notably, the deceased stipules were found closest to the base of rhizome which were characterized as the oldest, smallest, and lightest in comparison to stipules of other statuses. Phenotypic traits of arrested stipules were intermediate between sprouting stipules and deceased ones (Table 2).

The presence of a collinear relationship is present between the positions and ages of stipules (coefficient of Pearson product moment correlation = 0.900, $p < 0.01$; VIF > 5, Table 3). It indicates those stipules located closer to the apex of the rhizome are also more juvenile in nature. The number of sprouts per stipule showed a significant

**Table 2.** Position of rhizome (%), age (year), width (mm), weight (g), and sprouting time (week) of stipules in various statuses.

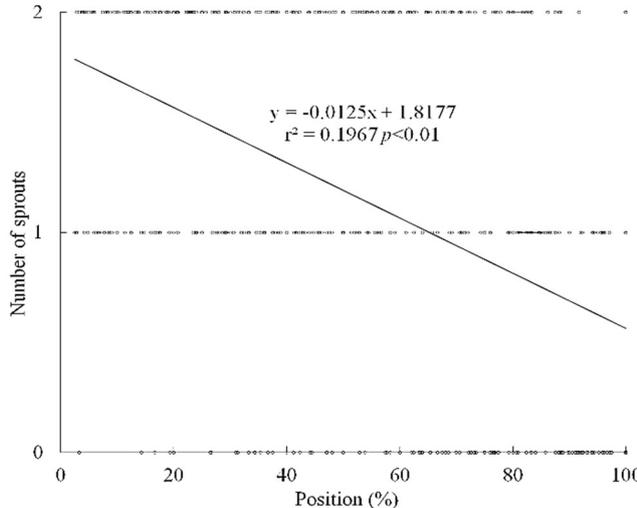
Statuses	n	Position	Age	Width	Weight	Sprouting time
2-sprout	220 (43.0%)	40.1±25.2 ^a	5.5±3.8 ^a	17.1±4.4 ^a	2.8±1.3 ^a	15.2±3.5 ^a
1-sprout	157 (30.6%)	51.2±29.0 ^b	7.0±4.4 ^b	17.1±3.6 ^a	2.7±1.1 ^a	15.9±3.3 ^a
Arrested	115 (22.5%)	69.5±21.9 ^c	9.7±3.9 ^c	16.8±4.0 ^a	2.6±1.3 ^a	--
Deceased	20 (3.9%)	87.7±22.2 ^d	12.4±4.2 ^d	13.9±4.1 ^b	1.7±1.2 ^b	--

Data represent the mean ± s.e. * Different letters in the same column indicate significant difference. (One-way ANOVA with post-hoc Tukey HSD test, $p < 0.05$)

Table 3. The correlations between sprouting parameters (numbers and time) and phenotypic traits (position, age, width, and weight) of stipules of *Angiopteris somae* based on multiple linear regression analysis.

	Coefficient	Std. Error	t	p	VIF
Sprouting numbers					
Constant	1.5890	0.1580	10.061	<0.001	--
Position	-0.0087	0.0026	-3.386	<0.001	5.302
Age	-0.027	0.0168	-1.621	0.106	5.210
Width	0.0114	0.0123	0.931	0.352	2.414
Weight	0.0138	0.0409	0.337	0.736	2.568
Sprouting time (weeks)					
Constant	14.903	0.720	20.708	<0.001	--
Position	0.0035	0.0124	0.279	0.780	5.368
Age	0.0310	0.0815	0.380	0.7040	5.275
Weight	-0.1240	0.1830	-0.679	0.4980	2.179
Width	0.0240	0.0542	0.444	0.6570	2.145

Note: Position and age of stipules have a collinear relationship, as indicated by the variance inflation factors (VIFs) greater than 5.0. Of the four phenotypic traits, only position had the ability to predict stipule sprouting ($p < 0.05$).

**Fig. 2.** The correlation between stipule positions and numbers of sprouts of *Angiopteris somae*.

but weak negative relationship with the corresponding position on the rhizome (Table 3, Fig. 2). In other words, stipules closer to the apex of the rhizome tend to generate more sprouts, whereas those located closer to the base demonstrate a reduced ability for sprouting. Sprouting times of stipules were not significantly correlated with the four phenotypic traits (Table 3).

DISCUSSION

The effect of the age of the tree on the sprouting (rooting) process of cuttings is noted for flowering plants (Altoé *et al.*, 2011; Wendling *et al.*, 2014); however, this correlation had not yet been investigated for marattioid ferns. In this study, we found that sprouting percentages were not correlated with the age of plants. Additionally, the sizes of the plants (stem diameters) have also been documented that did not significantly affect sprouting percentages (Chiou *et al.*, 2006).

The sprouting ability of cuttings is influenced by multiple factors, including the age and position of the cutting as well as the concentrations of both exogenous and endogenous hormones (Pandey and Husen, 2022). For flowering plants, the effect of the cutting position on sprouting has been widely discussed (e.g., Kraiem *et al.*, 2010). The probability of a cutting to form roots (analogous to sprouting in this study), would decrease with increasing distance from the apical shoot (Wilson, 1993; Hartmann *et al.*, 2002) due to differences in the type and quantity of carbohydrates and other stored materials (Hartmann *et al.*, 2002). Consequently, juvenile branches that are in optimal nutritional condition tend to root better (Wendling *et al.*, 2014). We also found that the number of sprouts per stipule in *Angiopteris somae* correlates with their position on the rhizome. To maximize cost-benefit efficiency and minimize damage to mother plants, young stipules near the apex of rhizome are better candidates for culture than those near the base of rhizome. Chiou *et al.* (2006) collected stipules near the base of rhizomes of *A. somae* from Wulai population for cultivation. After one year of culture, the sprouting percentage reached only 40%. The sprouting percentage of basal-part-rhizome stipules of *A. itoi*, at the same Wulai site, reached 90%. This significant disparity suggests that the influence of stipule position on sprouting percentage may also be species-dependent.

When the primary function of the leaf blade transitions away from photosynthesis, other parts may assume the role of storing photosynthetic products in some ferns. Trophopods of *Osmunda*, *Onoclea*, *Matteuccia*, *Plagiogyria*, *Athyrium*, and *Dryopteris* species, which are expansions of the petiole, serve as storage organs by accumulating nutrients and persist long after the leaves have withered and decayed (Wagner and Johnson, 1981). Stipules of *A. somae* may fulfill a role



analogous to trophopods. This study found that basal stipules were smaller and lighter than those located toward the apex. We proposed that starch, which is converted into soluble sugars for sprouting, may be more prevalent in juvenile stipules, located closer to the shoot apex, and gradually diminishing in older stipules. Deceased and arrested stipules are typically found on the basal part of the rhizome, suggesting that they have aged and may have depleted their photosynthetic products, leading to tissue softening. Alternatively, the products may have decomposed, resulting in insufficient quantities to support sprouting, despite the stipules still exhibiting firm tissue.

Certain factors may influence meristematic activities in flowering plants. Researches indicated that the synthesis of nitric oxide (NO) is more pronounced in juvenile tissues compared to mature tissues following excision from the plant (Abu-Abied *et al.*, 2012; Legué *et al.*, 2014; Rousson *et al.*, 2023). The production of NO at the sites of root formation is critical for cell division and the subsequent expansion necessary for the development root primordia (Xu *et al.*, 2017). However, it remains undocumented whether the juvenile stipules of *A. somae* are capable of synthesizing higher quantities of nitric oxide. Additionally, the process of root formation from cuttings in flowering plants is regulated by phytohormones (De Klerk *et al.*, 1999; Druge *et al.*, 2016; Rousson, 2023). Future research should focus on the selection of appropriate phytohormones to enhance the sprouting percentage of *A. somae* stipules, especially for those located on the base of rhizome.

Sprouting of stipules could spontaneously but scarcely be found in the natural forest (e.g., Huang *et al.* 2010). Sharpe and Jernstedt (1991) conducted an experiment for *Danaea wendlandii* Rehb. f. (Marattiaceae) in a natural forest in Costa Rica and found that the number of sprouts on decapitated plants was 27 times higher than that observed on intact plants. In an extreme case, spontaneous sprouting was not observed on the stipules attached to plants in *A. somae* (Huang *et al.*, 2010). This suggests that certain inhibitory mechanisms are present in this fern under natural conditions.

The genetic diversity observed within populations of *An. somae* is surprisingly high based on a study of the *atpB-rbcL* intergenic spacer of chloroplast DNA (Chiang *et al.*, 2002). Consequently, propagating sprouts from the stipules of various individual plants are essential for preserving a significant proportion of the genetic diversity within each population. To mitigate the risk of excessive stipule collection, which may lead to damage to the plants, it is imperative to implement stringent controls on the collection process. Our study provides valuable insights, demonstrating that stipules located closer to the apex are capable of producing a substantial number of sprouts within a relatively short period.

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