

# Tropical Fern Flora of Brunei Shows Entire Fronds in Epiphytic Species and Divided Fronds in Terrestrial Species: Two Working Hypotheses to Explain Such Morphological Differences

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## Abstract

Fern species are famous for their frond division, often used as a fractal representation. Fronds can be entire, or divided into first, second and third orders of division. In general, fern species tend to have divided fronds, while species with entire fronds are less common. In tropical regions, where fern species reach their highest richness and morphological diversity, the frequency of entire fronds versus divided fronds has rarely been studied. In this study, I present the frond division pattern for the fern flora of Brunei Darussalam. I use the recently published checklist of the ferns of Brunei Darussalam, which lists 341 species. I also divided the species by their life form: terrestrial and epiphytic. Terrestrial species represent 60% of the Brunei fern diversity, while epiphytes represent the remaining 40%. I find that terrestrial species have the highest proportion of first-order frond division, followed by entire fronds, second-order fronds, and third-order fronds. In contrast, the epiphyte species are predominantly represented by entire fronds, followed by first-order frond division. I conclude this article with two working hypotheses to explain this remarkable morphological difference between the two tropical life forms.

*Index Terms:* ferns, frond division, Brunei Darussalam

## 1. Introduction

Fern species reach their peak diversity in tropical regions, and the highest levels of endemism are found on tropical islands.<sup>1,2</sup> This species diversity is mirrored by high phylogenetic and life-form diversity. Fern life forms can be summarized as (1) terrestrial, anchored to the ground and self-supporting, (2) climbers, anchored to the ground but requiring a host tree to climb, (3) aquatic, plant species that float on water, and (4) epiphytic, species that grow on other plants and are not anchored to the ground. Within this group is often included the saxicolous species, which grow exclusively on rocks. This large phylogenetic and life form diversity is also represented by a high variability in fern frond morphology. In fact, fern species are probably the group of vascular plants with the greatest morphological diversification of fronds.<sup>3</sup> The

tropics and tropical islands, particularly with their high level of endemism, have an exceptional and complete array of fern frond morphological diversity.

Fern fronds can be described in the following terms. Entire fronds have the main central vein without a secondary vein forming an independent pinna. The margin of the entire fronds can be undulate or deeply lobate (see *Figure 1*). Fronds can be described in terms of their divisions. The first order of division is when the fronds are pinnate, when the pinna lamina is not connected with the primary frond vein (see *Figure 2*). The second order of division is when the fronds are bi-pinnate. The third order of division is when the pinnule has a further division with small leaflets (see *Figure 2*). With increase in the number of frond divisions, the size of the frond

lamina is reduced, and the veins play an important role in frond blade integrity. Species with all these morphological structures are adapted to diverse habitats, such as shady

understory forests, open fields, and forest canopies.



**Figure 1.** Example of fern species with entire and divided fronds. (A) Epiphytic species *Asplenium nidus* with entire fronds and a continuous margin. (B) Epiphytic species of *Drynaria quercifolia* with entire fronds and lobate margin. (C) Terrestrial species of *Diplazium cordifolium* with entire fronds, and the base of the lamina with a cordate shape. (E) Epiphytic species of *Davallia denticulata* with divided fronds up to the third order of division; the smaller image shows the finer division of the pinna. (F) Epiphytic species of *Abocopteris nitida* with divided fronds with a first order of division (Pinnate). (D) Terrestrial species of *Cystodium sorbifolium* with bi-pinnate fronds.

The island of Borneo is divided into three independent countries. The Indonesian part of the island (Kalimantan) represents nearly 73% of the entire area of the island, followed by the states of Sabah, Sarawak and the Federal Territory of Labuan in Malaysia, and the Sultanate of Brunei Darussalam. Despite Brunei being the smallest state on the island, its tropical forest remains in relatively good condition. However, deforestation and climate change remain the most important drivers of biodiversity degradation, particularly in Brunei and Sarawak.<sup>4</sup> The majority of Brunei is represented by lowland tropical forest with seven recognised forest types. A small portion of the country is mountainous, with Bukit Pagon in the Temburong district as its highest peak. The lowland forest, with its high diversity of habitats, creates a matrix landscape that contributes to overall plant species diversity.<sup>5-9</sup> In this mainly lowland forest ecosystem in Brunei, the fern and Lycophyte species diversity has been reported at 364 species.<sup>10</sup> In the tropical island of Borneo, a recent assessment estimated the total fern diversity of 1139 species.<sup>11</sup> Whereas, at the global level, this diversity is estimated at around 11,000 species,<sup>12</sup> with Borneo representing 10% of the world's fern richness and Brunei 3.3%.

In this paper, I use a recently published checklist of ferns and lycophytes of Brunei<sup>10</sup> to assess the proportion of epiphytic versus terrestrial species and the relative difference in leaf morphology. Specifically, I ask the following questions: 1) How many species have epiphytic and terrestrial life forms? 2) How many fern species have entire versus divided fronds? 3) What is the difference in the ratio of entire and divided fronds for terrestrial and epiphytic species?

## 2. Methods

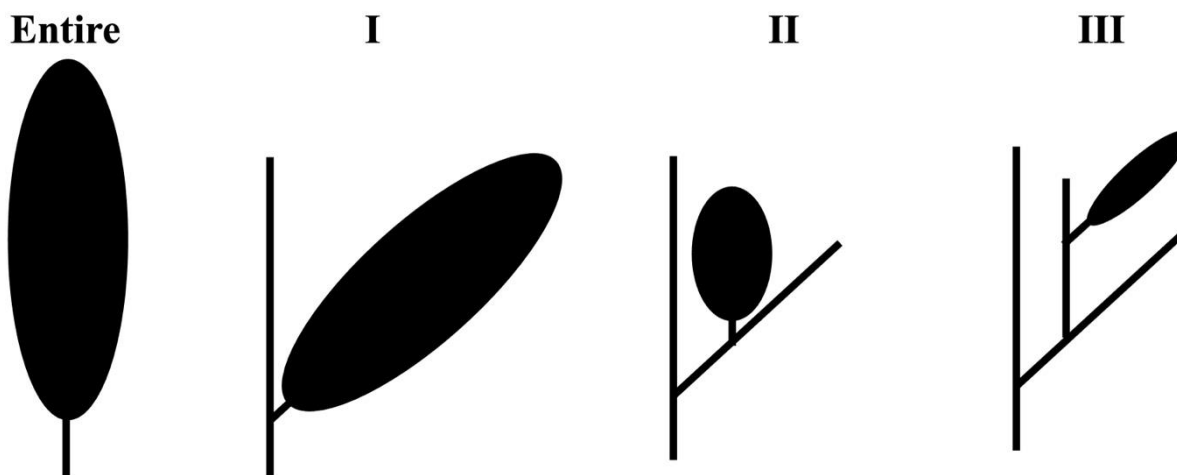
This study is based on the recently published checklist of fern and Lycophyte species from Brunei Darussalam.<sup>10</sup> The checklist reported 364 species, of which 23 belong to the Lycophyta group, Lycopodiaceae and Selaginellaceae. In this study, the Lycophyta were not considered

because of their distinctive leaf shapes, which do not fit into the divided/entire category. The new list, without the Lycophyta, included 341 fern species, 101 genera, and 30 families.

Each species was compared with herbarium specimens from the Brunei National Herbarium (BRUN) and the UBD Herbarium (UBDH). The vouchers were assessed in terms of three life forms: 1) terrestrial, if the species was anchored to soil, and growing independently; 2) climber, if the species was anchored to the ground but used host tree to climb upwards; 3) epiphyte, if the species lived on and was anchored to a tree, either on the lower part of the trunk or on the canopy branches. In the last category, I also included saxicolous species, which are anchored to and live on or among rocks.

After this first life form classification, the fronds of each species were classified into one of four categories. 1) Entire fronds, fronds with an oval shape, where the frond lamina is always in contact with the central vein. In this category, I included species with entire and undulate margins. Among the undulate margin type, it is important to mention species with very deeply lobate fronds, such as *Drynaria quercifolia* or the genus *Grammitis* (see **Figure 1**). 2) First order of division, species with pinnate fronds (see **Figure 1**), 3) second order of division, species with bipinnate fronds (see **Figure 1**) and lastly, 4) third order of division, species with pinnules subdivided in a further division (see **Figure 1**). A schematic representation of these four categories is represented in **Figure 2**.

In the final analysis, I combined the climber species among the terrestrial ones, as they are still anchored to the ground and can absorb nutrients from it. I used two categories for the life forms (terrestrial versus epiphytic) and two large categories for the fronds division (entire versus divided fronds). Chi-square test was used to assess the differences between terrestrial and epiphytic species.



**Figure 2.** Schematic representation of fern fronds among the 341 species of Brunei flora. Entire, with or without petiole, with continuous or lobate margin; I, first order of division or Pinnate fronds; II, second order of division or Pinnulate fronds; III, third order of division or three-pinnate fronds.

### 3. Results

The fern flora of Brunei Darussalam, excluding the Lycophyta group, comprise 341 species. The terrestrial and climber species together represent 203 species, whereas the epiphytic species represent 138 species. Terrestrial species thus account for 59.5% of the fern diversity in Brunei, while epiphytes account for the remaining 40.5%. The difference between terrestrial and epiphytic was statistically significant, with a Chi-squared = 107.51,  $df = 3$ ,  $p$ -value = 0.0005. Entire fronds account for 40.2% of the fern diversity, while species with divided fronds are 59.8%.

The results showed that based on the proportion of each life form, we found that of the 203 terrestrial species, 54.7% had fronds with the first order of division, 23.2% had fronds with the second order of division, 4.4% had fronds with the third order of division, and 18% had entire fronds. It shows that fern species with a terrestrial life form have significantly more divided fronds. Whereas epiphytic species had 73.2% of species with entire fronds, followed by a 18.1%, 5.1% and 3.6% for the first, second and third orders of division, respectively (see **Table I**).

### 4. Discussion

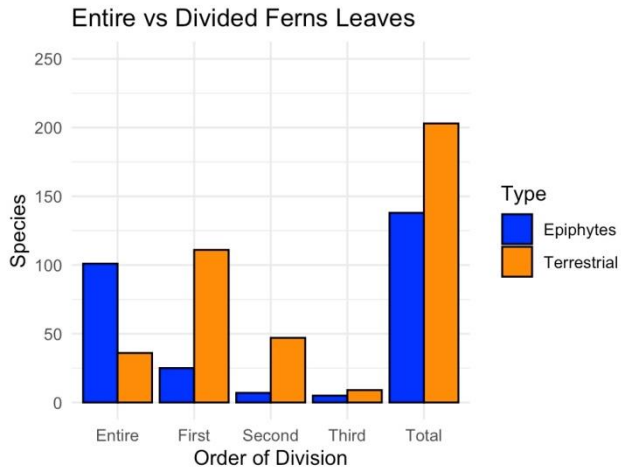
Four out of five terrestrial ferns have some degree of divided fronds, while three out of four

of the epiphytic species have entire fronds. The significant difference between the morphological traits of epiphytic versus terrestrial fern species raises the question about this difference in frond morphology. It is indeed challenging to propose a single explanation of this complex evolutionary adaptation. However, I present two possible interpretations that warrant further study in future research.

The majority of terrestrial species have a divided frond; 82.3% at the first, second and third orders of division. In comparison, the species with entire fronds are just at 17.7%. Morphologically, we can describe that the majority of terrestrial fern species have pinnate or bi-pinnate fronds, with a significantly lower proportion having entire fronds with linear or undulate margins.

The epiphytic species have, on the contrary, 73.2% of the species richness, with entire fronds, and 26.8% with first-, second- or third-order divisions. Fronds that can have an entire margin, such as the common *Asplenium nidus*, to the more deeply lobate *Drynaria quercifolia*, however, are still considered entire (see **Figure I**). Among the epiphytic fern life forms, it is important to note the highly divided fronds, up to the third level of division, of many *Davallia* species. The Davalliaceae family is well known for its very high leaf morphological diversity,

from the fine third order of leaf division, pinnate and species with entire fronds.



**Figure 3.** The number of species of terrestrial and epiphytic fern life forms and their frond category: Entire, First, Second and Third orders of division. The Total represents the difference between epiphytes and terrestrial species in the fern flora of Brunei Darussalam.

#### FronD morphology and evolutionary adaptations, two working hypotheses

- 1) *Entire fronds can be used to accumulate plant debris and associated nutrients in epiphytic ferns*

Epiphytic evolution has occurred in approximately 9 families among the 51 families of extant lycophytes and ferns.<sup>12</sup> In Brunei's flora, eight of 30 families (27%) have species with an epiphytic life form. A group of species with entire fronds is represented by those species that are able to accumulate debris and aerial soil, facilitated by the leaf morphology and arrangement. They represent only 13 species, all of which lack a petiole. The frond blade develops directly at the base of the primary veins, often forming a cordate base (see **Figure 1**). The fronds of these species are arranged with a specific phyllotaxy starting from the rhizome and are closely attached to the tree trunk. In this position, they can capture the stem flow from the tree trunk and debris falling from the canopy level.<sup>13</sup> Typical examples of Brunei flora with this adaptation are the common *Asplenium nidus* and *Drynaria quercifolia* (see **Figure 1**). They

can accumulate large amounts of debris that decompose into aerial soil.<sup>14</sup>

Furthermore, these epiphytic habitats, with aerial soil, constant humidity, and the presence of temporary water, host a community of several animal species. Invertebrates are the most common (Ellwood & Foster, 2002);<sup>14</sup> however, some canopy frog species complete their life cycles in the temporary water of the *Asplenium* nest.<sup>15</sup> This growth form is represented in different families such as Aspleniaceae and Polypodiaceae. This convergent morphological adaptation, despite being present in only 13 species of the Brunei fern flora, can be a successful trait in epiphytic species that generally live on nutrient depleted substrates. It is indeed an open question whether they share similar morphological and physiological traits, such as stomatal density, modified leaf tissue and rhizome anatomy for nutrient accumulation, and thermotolerance.<sup>16</sup> Although most species lack a proper soil-capture strategy, many fern species have developed other adaptations to absorb and accumulate nutrients in the canopy.<sup>13</sup> The majority of epiphytic species, such as the *Haplopteris* genus, have medium- to small-sized fronds, some of them grass-like, with a thin rhizome, or a more normal fibrous root system. However, in Brunei, a species of this genus is terrestrial.<sup>17</sup> Furthermore, the genus *Pyrrosia* has large, oval to narrow, elongate fronds, often thick, with a wiry rhizome. These rhizomes and fibrous roots are tightly attached to the trunk and can cover the whole circumference of a trunk of 30 cm in diameter.<sup>18</sup> Although the fronds are entire and petiolate, and no structure to capture debris is present, at the root level, there is always a certain amount of soil held by the petioles of the fronds. The quantity of soil is not comparable to that captured by the *Drynaria* or *Asplenium* species; however, we can certainly say that it is relevant for the nutrient needs of the species.

The epiphytic genus *Leucanopteris* has a symbiotic relationship with ants that transport soil inside and around the rhizome. This interaction provides the plant with rare and poorly accessible nutrients in the canopy.<sup>19</sup> The

ants build their nest inside the rhizome, which, during development, expands to provide space for the nest. In general, epiphytic fern species have higher concentrations of N, P, K, Ca, and Mg in their fronds compared with the terrestrial fern species.<sup>20</sup> This trait, with different stoichiometry between terrestrial and epiphytic species, has been considered a form of luxury consumption.<sup>21</sup> Epiphytic species tend to accumulate more nutrients in their fronds than are needed for their daily metabolic activity. This is explained as the capacity to sustain a long period of stress due to drought or high temperatures by the reserve accumulated in the frond tissues.<sup>21</sup>

The species with entire fronds, able to capture stem flow and accumulate aerial soil, generally have a larger frond area than species that are not. This suggests that epiphytic species with aerial soil allocate more energy to developing larger fronds and therefore accumulate more soil, thereby sustaining the positive feedback. Whereas the fronds without this adaptation, despite their high proportion of nutrients accumulated in their fronds, do not allocate high nutrients to the development of larger fronds. *Asplenium nidus*, *Asplenium phyllitidis*, *Drynaria quercifolia*, or *Platynerium coronarium*, common in Brunei, have significantly larger fronds than epiphytic species of *Asplenium belangeri* or *Haplopteris scolopendrina*, among others. Larger fronds, with ample leaf tissue, require more primary and secondary veins; therefore, more nutrients are required in the developmental process. At the same time, the frond size and the mechanical structure, vein density and average vein size, can be a parameter to consider when testing differences between the species with these two morphological traits. I acknowledge that every family has an evolutionarily independent path and evolutionary constraints;<sup>12</sup> therefore, the categories can be a misleading interpretation of plant evolution and function. However, the convergence of different families to similar strategies, accumulating soil and no petiole, or not accumulating soil and having fronds with petioles, entire or primary divided lamina, and

different rhizome traits, can be considered a working hypothesis to test.

**Table 1.** Summary of epiphyte and terrestrial fern species of Brunei Darussalam. Entire: Entire fronds, FOD: First Order of Division, SOD: Second Order of Division, and TOD: Third Order of Division.

	Epiphytes	Terrestrial	Life Forms	
			% Epiphyte	% Terrestrial
Total Species	138	203	40.5	59.5
Entire	101	36	73.2	17.7
FOD	25	111	18.1	54.7
SOD	7	47	5.1	23.2
TOD	5	9	3.6	4.4

2) *Divided fronds increase spore dispersal distance for terrestrial ferns*

The second hypothesis that I want to present here is the dispersal limitation of fern species. Fern species, compared with flowering plants, do not suffer from dispersal limitation. Ferns produce thousands, if not millions, of spores per individual, and the spores can survive long journeys and germinate when microclimate and light availability are appropriate.<sup>22</sup> The dispersal of fern spores has been studied with many fern species models, and the results show that the distance range is between 3 meters for *Botrychium virginianum* to 30 meters for the tree fern *Cyathea arborea*.<sup>23</sup> At the same time, if the species is mature and spores are released on a windy day (for example, during the monsoon season in tropical southeast Asia), the spores can reach high elevations and travel for thousands of kilometres. This also explains why fern species have a lower level of endemism compared with flowering plant species.<sup>24,25</sup> Although these studies are limited to a few species and often conducted in botanic gardens rather than in the habitats where the species occur, they nonetheless provide a range of spore-dispersal abilities.

These empirical studies, however, need to be integrated with the ecosystem in which most of these species occur. For example, in a tropical lowland forest, terrestrial species have a forest habitat; therefore, they are adapted to live in the forest understory. The usual tropical forest structure comprises layers, from the canopy, with thick tree crowns, to the lower part with tree saplings, shrubs, and lianas, followed by terrestrial herbs, among which are fern species. The tree crown and the woody species above the understory species shield the herbs from the wind. In this low-wind-exposure habitat, fern species with entire and divided fronds have to disperse spores away from the mother plant. In general, the vibration of plant fronds is associated with the need to reduce internal leaf temperature, maintain internal homeostasis, and protect the cells and organelles that would otherwise be damaged by high temperature.<sup>26</sup> This applies to all vascular plants, including ferns.

In angiosperm plants, leaves perform photosynthesis, thermoregulation, and gas exchange; in fern species, fronds also have a second function. This second function, unique to fern species, is to provide space for the reproductive part, called sori. Biomechanical studies on flowering plants' leaves have demonstrated that leaves with lobate margins have a more dynamic vibration in windy conditions.<sup>27</sup> In the dispersal process of fern spores, a frond with a divided lamina can have a higher level of vibration due to the increase in the reduction ratio between area and perimeter. As with divided fronds, the perimeter increases considerably. Therefore, more divided fronds, which still allow a sufficient space to accommodate the fern reproductive part, can vibrate more and disperse the spores further away from the mother plant, on a forest floor, where the wind speed is usually low. A single pinna has the lamina not attached to the primary vein (see *Figure 1*); therefore, it is more independent and can vibrate with a small wind speed. The vibration of the pinna, independently from the others, can facilitate the spore dispersion and requires a lower wind speed, typical of ground-floor understory habitats. This hypothesis could

explain why the division of fern fronds is significantly higher in terrestrial species than in epiphytic species. This hypothesis suggests a trade-off between the fronds' lamina for photosynthesis and thermoregulation, and the fronds' division to allocate space for the reproductive part and spore dispersion.

In epiphytic species, which are already several meters above the ground, it is easy to disperse the spores away from the mother plant. However, this contradicts the number of epiphyte species in the first order of division, such as *Asplenium*, and even more the third order of division of many *Davallia*.

To my knowledge, this is the first attempt to describe the morphological diversity of fern fronds in a tropical region based on a complete fern checklist. Although Brunei represents a small proportion of the Borneo area, the complete checklist of species allowed us to draw some initial morphological descriptions of this flora. The striking difference between entire and divided fronds in two major life forms has raised fundamental questions that I am trying to interpret here and suggest some future working hypotheses.

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Dr David Edwards has contributed to the establishment of the major holding of Brunei fern voucher species in the Brunei National Herbarium (BRUN) and in the Universiti Brunei Darussalam Herbarium (UBDH). The elaboration and the interpretation presented in this paper are a direct result of these contributions of Dr D. Edward's, which also served the basis of a publication of a checklist of the Ferns and Lycophytes of Brunei Darussalam. I would like to acknowledge my student, Goh Hui Ting, for her contribution to the description of species frond division and Prof Harald Schneider, with whom I conversed on this topic.

## References

- [1] H. Kreft *et al.*, “Global diversity of island floras from a macroecological perspective”, *Ecology Letters*, 11, 116-127, 2008.
- [2] A. Taylor *et al.*, “The contribution of plant life and growth forms to global gradients of vascular plant diversity”, *New Phytologist*, 240, 1548-1560, 2023.
- [3] A. Vasco *et al.*, “The evolution, morphology, and development of fern leaves”, *Frontiers in Plant Science*, 4 (September), 345, 2023.
- [4] R. N. Zulkarnaen *et al.*, “Trends and Patterns of Plant Conservation Research in Borneo: A Review”, *ASEAN Journal on Science and Technology for Development*, 42, 90-103, 2025.
- [5] D. Cicuzza *et al.*, “Fern diversity and distribution in the UBD campus”, *Scientia Bruneiana*, 19 (1), 1-18, 2020.
- [6] D. Cicuzza *et al.*, “Variation in fern species richness, assemblages and morphology along a tropical riparian humidity gradient: an example from Borneo”, *Botany Letters*, 171, 319-327, 2024.
- [7] K. M. Wong *et al.*, “Where are Sabah’s plant biodiversity hotspots and what are our remaining conservation options?” *Sandakanian*, 26, 129-151, 2025.
- [8] B. Zoletto *et al.*, “Fern communities in lowland tropical forests of Brunei Darussalam, Borneo: Diversity, indicator species, and environmental drivers across forest types”, *Biotropica*, 57, 1-12, 2025.
- [9] B. Zoletto and D. Cicuzza, “Heath forest in tropical Southeast Asia: Its ecology and conservation risk”, in *Imperiled: The Encyclopedia of Conservation* (pp. 114-128), Elsevier, 2022.
- [10] D. Cicuzza *et al.*, “Novitates Bruneienses, 11. A Checklist of the Ferns and Lycophytes of Brunei Darussalam (In continuation of studies of Brunei pteridophytes initiated by David S. Edwards)”, *Webbia*, 80, 125-200, 2025.
- [11] S. Y. Wong, “Flora of Borneo: The vascular plant genera”, *Webbia*, 78, 5-309, 2023.
- [12] PPGL, “A community-derived classification for extant lycophytes and ferns,” *Journal of Systematics and Evolution*, 54, 563-603, 2016.
- [13] J. Dubuisson *et al.*, (2009). “Epiphytism in ferns: diversity and history”, *C. R. Biologies*, 332, 120-128, 2009.
- [14] M. D. F. Ellwood and W. A. Foster, “Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites, and other invertebrates”, *Biotropica*, 34, 575-583, 2002.
- [15] B. R. Scheffers *et al.*, “*Asplenium* bird’s nest ferns in rainforest canopies are climate-contingent refuges for frogs”, *Global Ecology and Conservation*, 2, 37-46, 2014.
- [16] T. M. Perez and K. J. Feeley, “Weak phylogenetic and climatic signals in plant heat tolerance”, *Journal of Biogeography*, 48, 91-100, 2021.

- [17] C. W. Chen *et al.*, “*Haplopteris palustris*, a new terrestrial vittarioid fern (Pteridaceae; Polypodiales) from Western Malaysia. *Systematic Botany*, 49, 227-235, 2024.
- [18] D. Cicuzza, personal observation.
- [19] J. E. Watkins *et al.*, “Ants mediate nitrogen relations of an epiphytic fern”, *New Phytologist*, 180, 5-8, 2008.
- [20] S. P. Sulaiman *et al.*, “Tropical terrestrial and epiphytic ferns have different leaf stoichiometry with ecological implications”, *Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology*, 157, 899-906, 2023.
- [21] U. Winkler and G. Zotz, “‘And then there were three’: Highly efficient uptake of potassium by foliar trichomes of epiphytic bromeliads”, *Annals of Botany*, 106(3), 421-427, 2010.
- [22] J. Suo *et al.*, “Fern spore germination in response to environmental factors”, *Frontiers in Biology*, 10, 358-376, 2015.
- [23] K. A. Penrod and L. H. McCormick, “Abundance of viable hay-scented fern spores germinated from hardwood forest soils at various distances from a source”, *American Fern Journal*, 86, 69-79, 1996.
- [24] D. N. Karger *et al.*, “Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago”, *Journal of Biogeography*, 41, 250-260, 2014.
- [25] H. Kreft *et al.*, “Contrasting environmental and regional effects on global pteridophyte and seed plant diversity”, *Ecography*, 33, 408-419, 2010.
- [26] O. Tserej and K. J. Feeley, “Variation in leaf temperatures of tropical and subtropical trees are related to leaf thermoregulatory traits and not geographic distributions”, *Biotropica*, 53, 868-878, 2021.
- [27] S. Vogel, “Leaves in the lowest and highest winds: Temperature, force and shape: Tansley review”, *New Phytologist*, 183, 13-26, 2009.