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Leaf Nitrogen and Phosphorus Stoichiometry and Its Response to Geographical and Climatic Factors in a Tropical Region: Evidence from Hainan Island

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Abstract: Leaf stoichiometry effectively indicates the response and adaptation of plants to environmental changes. Although numerous studies on leaf stoichiometry patterns have focused on the mid-latitudes and specific species of plants, these patterns and the effect of the climate change on them across a broad range of plants have remained poorly characterized in hot and humid regions at low latitudes. In the present study, leaf N, P, N:P, C:N, and C:P ratios, were determined from 345 plant leaf samples of 268 species at four forest sites in Hainan Island, China. For all plants, leaf N (3.80 ± 0.20 mg g^{-1}) and P (1.82 ± 0.07 mg g^{-1}) were negatively correlated with latitude and mean annual temperature (MAT) but were positively correlated with longitude. Leaf N was found to be positively correlated with altitude (ALT), and leaf P was positively correlated with mean annual precipitation (MAP). The leaf C:N ratio (278.77 ± 15.86) was significantly correlated with longitude and ALT, leaf C:P ratio (390.69 ± 15.15) was significantly correlated with all factors except ALT, and leaf N:P ratio (2.25 ± 0.10) was significantly correlated with ALT, MAT, and MAP. Comparable results were observed for woody plants. The results suggest that leaf stoichiometry on Hainan Island is affected by changes in geographical and climatic factors. In addition, the low N:P ratio indicates that plant growth may be limited by N availability. Moreover, the significant correlation between leaf N and P implies a possible synergistic relationship between N and P uptake efficiency in the plants of this region. This study helps to reveal the spatial patterns of leaf stoichiometry and their response to global climate change in a variety of plants in tropical regions with hot and humid environments, which may provide an insight in nutrient management in tropical rainforest.

Keywords: leaf stoichiometry; climate; geography; life form; Hainan Island

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1. Introduction

Leaf stoichiometry can indicate plant nutrient status, community composition, and ecosystem functions, and drives fundamental physiological and ecological processes in plants [1,2]. Essential nutrients for plants, such as carbon, nitrogen, and phosphorus, affect plant growth and adaptation to terrestrial habitats and are closely related to global biochemical cycles [3]. N and P are closely related to plant photosynthesis, genetic material composition, energy storage, and are the most important limiting nutrients in terrestrial ecosystems [4–6]. In particular, the stoichiometry of N and P is closely related to plant ecological strategies [7–11]. For example, as important indicators of leaf nutrient usage efficiency, higher leaf C:N and C:P ratios indicate a more efficient usage of N and P [4,6,12,13]. Research has shown that climate change considerably affects matter and energy cycles, both regionally and globally, thereby affecting vegetation activity and ecosystem function [11,14–17]. For instance, warming can affect the rate of alter litter decomposition and organic matter mineralization via changes in the soil's physicochemical properties and microbial activity, ultimately leading to changes in plant nutrient availability and leaf stoichiometry [4,11,14]. Therefore, understanding the effects of geographical and climatic factors on the leaf N and P contents, as well as on the C:N, C:P, and N:P ratios, plays a vital role in discerning the plant response and adaptation to environmental changes.

Ecosystem functions and processes are regulated by both biotic and abiotic factors [18–21]. The former includes plant functional traits, whereas the latter includes edaphic, geographic, and climatic features. Thus, spatial variations in plant leaf chemometrics are influenced by various factors. Changes in climate and geomorphology, including air temperature, precipitation, and latitude, have significant impacts on plant physiology and soil biogeochemistry, which affects the nutrient cycling in ecosystems [22,23]. Reich and Oleksyn [4] described global patterns in leaf N and P stoichiometry of terrestrial plants across latitudinal and temperature gradients. They proposed that leaf N and P concentrations rise from the tropics to the mid-latitude regions and remain stable or decline at high-latitude regions. Additionally, they reported that the leaf N:P ratio increases with temperature [4]. Previous studies have shown that tropical climate and soil nutrient changes may lead to different spatial patterns of leaf C, N, and P stoichiometry and nutrient resorption [8,24]. Han et al. [25] analyzed leaf data from 753 terrestrial plants in China and found that the variations in leaf N and P concentrations showed an opposite trend to the mean annual temperature (MAT), but leaf N:P did not show significant changes. However, when additional species in China were considered, they found that plant functional type exhibited the greatest impact on most leaf nutrients. Additionally, the variation in leaf N and lack thereof in leaf P was better explained by changes in precipitation, rather than temperature [26]. Possibly due to the low availability of soil P in China, the previous two reports found that the leaf N:P ratio of Chinese flora was higher than the global average [25,26]. Other studies found that intense precipitation can exacerbate soil nutrient loss, resulting in reduced leaf P concentration [27].

The relationship between leaf stoichiometry and environmental factors has become a research hotspot in ecology and earth sciences [4]. The concentrations of leaf N and P can be used as indicators of how plants use nutrients and respond to environmental changes, as they are associated with many key aspects of plant growth, reproduction, and ecosystem functions [3,28]. Therefore, current studies on leaf stoichiometry mainly focus on N and P. This is especially true for studies exploring leaf stoichiometry models in the mid-latitude regions and under specific conditions [11,29–35]. However, leaf stoichiometry patterns of various plants in areas with elevated temperatures and humidity at low latitudes, such as tropical regions, are poorly understood, limiting understanding of plant growth strategies in these areas under severe climate change conditions.

Tropical forests are the terrestrial ecosystems with the highest biodiversity and strongest ecological functions, causing them to be very significant to the global C budget. They account for 70% and approximately 55% of the gross global forest C sink and C pool, respectively [36,37]. Hainan Island is the largest and most diverse tropical-type forest in China. Owing to their high diversity, endemism, and complexity, tropical forests on Hainan Island are of great significance at both the national and global protection levels [38]. Here, we hypothesized the leaf N and P stoichiometry patterns would be affected by geographical and climatic factors in Hainan Island with high temperature and high humidity. To test our hypothesis, we selected the four areas of Danzhou, Tunchang, Changjiang, and Wuzhishan on Hainan Island as sampling points and analyzed the leaf nutrients of 345 leaf samples from 268 species. First, this study aimed to measure the leaf N and P content of all plants at four sampling sites on Hainan Island. Next, the relationship between leaf N, P concentration, C:N, C:P, and N:P ratios; and climatic and geographical factors were analyzed. This report provides better evidence of the patterns and drivers of leaf N and P stoichiometry and nutrient uptake on Hainan Island, which is important for discovering plant growth strategies in the tropical region under drastic environmental changes, and for guiding the nutrient management in tropical rainforests.

2. Materials and Methods

2.1. Site Description

Our study was conducted at four forest sites (Wuzhishan, Danzhou, Changjiang and Tunchang) in the western central region of Hainan Island. These forest sites are geographically located from 109°2′ to 110°6′ E and 18°47′ to 19°22′ N (Figure 1). There were two plots (18°55′45.46″ N, 109°28′7.83″ E; 18°47′40.22″ N, 109°38′54.94″ E) in Wuzhshang, and only one plot in Danzhou (19°30′50.94″ N, 109°29′58.70″ E). Changjiang (19°07′21.87″ N, 109°04′45.63″ E) and Tunchang (19°27′48.29″ N, 110°05′52.77″ E). The study area is a humid tropical region, where the climate type is tropical monsoon and tropical alpine climate, with a MAT of 22 to 25 °C. The average annual temperature of Wuzhishan, Danzhou, Changjiang, and Tunchang is 22.80, 23.70, 24.33, and 23.13 °C, respectively. Mean annual precipitation (MAP) in the whole study region is 1400 to 2100 mm, with 70% to 90% of the precipitation concentrated in the rainy season from May to October. The total precipitation in the rainy season is >1500 mm. The MAP of Wuzhishan, Danzhou, Changjiang, and Tunchang is 2080.95 mm, 1934.99 mm, 1563.12 mm, and 2105.15 mm, respectively. The altitude (ALT) of the research area ranges from 135 to 660 m above sea level. The major soil types are laterite and yellow. The main soil types in Wuzhishan are yellow soil and latosol, while the main soil types in Danzhou, Changjiang and Tunchang are latosol. The dominant climate type in Wuzhishan is tropical alpine climate and in Danzhou, Changjiang, and Tunchang is tropical monsoon climate. Specific information regarding the study area is presented in Table 1.

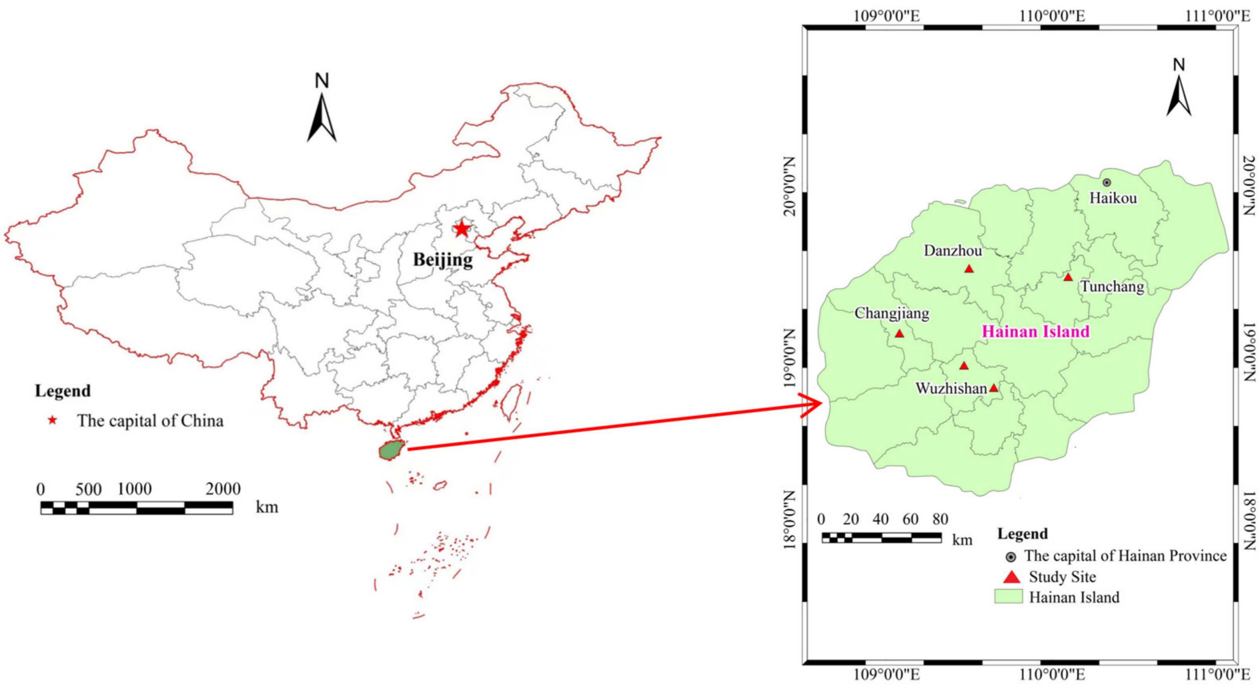

Figure 1. Location of the study area. Danzhou, Tunchang, Changjiang, and Wuzhishan on Hainan Island were selected as the sampling points. There were two sampling points in Wuzhishan, resulting in a total of five sampling points.

Table 1. Overview of the study area.

Study Area	Wuzhishan		Danzhou	Changjiang	Tunchang
Latitude	18°55′45.46″ N	18°47′40.22″ N	19°30′50.94″ N	19°07′21.87″ N	19°27′48.29″ N
Longitude	109°28′7.83″ E	109°38′54.94″ E	109°29′58.70″ E	109°04′45.63″ E	110°05′52.77″ E
Average Altitude (m)	260	505	137	660	135
MAT (°C)	22.80	22.80	23.70	24.33	23.13
MAP (mm)	2080.95	2080.95	1934.99	1563.12	2105.15
Average Sunshine Time (h)	2000		1900	2300	2000
Soil Types	Yellow soil, Latosol		Latosol		
Climate Type	Tropical alpine climate		Tropical monsoon climate		

MAP and MAT represent the mean annual precipitation and mean annual temperature, respectively.

2.2. Plant Sampling and Chemical Analysis

Leaf samples were collected from the study sites between August and September 2017. A healthy plant community was selected for each site in this study. More than three individuals from each species were selected and fully expanded healthy leaves were collected from shoots in different directions in areas of sun-exposed (total fresh mass > 100 g for each species). In total, we collected 345 leaf samples from 268 species. A total of 102 samples from different species were collected from Wuzhishan; 83 samples came from Danzhou; 83 samples were collected from Changjiang; and 77 samples were from Tunchang. Sample statistics were listed in Table 2, and the species of all samples were listed in Table A1.

Table 2. Sample statistics.

Study Area		Wuzhishan	Danzhou	Changjiang	Tunchang
Life form	Woody plants	58	83	62	44
	Herbs	37	0	8	28
	Vines	7	0	13	5
Evergreen sample		47	77	72	40
Deciduous plant sample		18	6	3	9
Sample size		102	83	83	77

Sample size refers to the total number of woody plants, herbs, and vines samples.

All leaf samples were placed in sealed plastic bags and transported to the laboratory. The leaf samples were rinsed with distilled water before being oven-dried at 105 °C for 30 min to denature the enzymes. Next, the samples were dried at 75 °C for approximately 48 h to a consistent weight and were finely ground. Leaf N and P concentrations were determined after sample digestion in H_2SO_4-H_2O_2, using a flow analyzer (Proxima1022/1/1, Alliance, France).

2.3. Accessing Data

The MAT, MAP, and other meteorological data of Hainan Island from 1959 to 2019 were obtained from the National Meteorological Science Data Center (Beijing, China). For research areas lacking climate data, the Inverse Distance Weighted method was used to fit the spatial variation map of Hainan climate data according to data from the Hainan Island meteorological station, producing climate data of the research area. Additionally, leaf C concentration data were obtained in another part of this project, a report on "Effects of geographical and climatic factors on the intrinsic water use efficiency of tropical plants: evidence from leaf ^{13}C" (unpublished results).

2.4. Statistical Analysis

The inverse distance weight interpolation method of ArcGIS 10.6 was used to obtain the climatic data from each study site from 1959 to 2019. IBM SPSS Statistics 25 was used to conduct single-factor analysis of variance and Spearman correlation analysis.

3. Results

3.1. Leaf Stoichiometry Characteristics in Hainan Island

In this study, the mean leaf N and P concentrations were 3.80 and 1.82 mg g^{-1} respectively, ranging from 0.16 to 16.39 mg g^{-1} and 0.24 to 7.18 mg g^{-1}, respectively. The coefficient of variation (CV) for leaf N and P concentrations ranged from 5.36 to 3.85, in which the leaf N concentration CV was the highest (Table 3). In this study, there was a significant positive correlation between leaf N and P concentrations in Hainan Island. ($p < 0.01$; Figure 2). The average leaf C:N, C:P, and N:P ratios and ranges can be found in Table 3.

Table 3. Statistics of N and P concentrations and stoichiometric ratios in leaves.

Items	Mean	SD	Minimum	Maximum	CV (%)
N (mg g^{-1})	3.80	0.20	0.16	16.39	5.26
P (mg g^{-1})	1.82	0.07	0.24	7.18	3.85
C:N ratio (C:N)	278.77	15.86	20.59	2865.25	5.69
C:P ratio (C:P)	390.69	15.15	47.47	1756.33	3.88
N:P ratio (N:P)	2.25	0.10	0.14	14.70	4.44

SD represents standard deviation, CV indicates coefficient of variation.

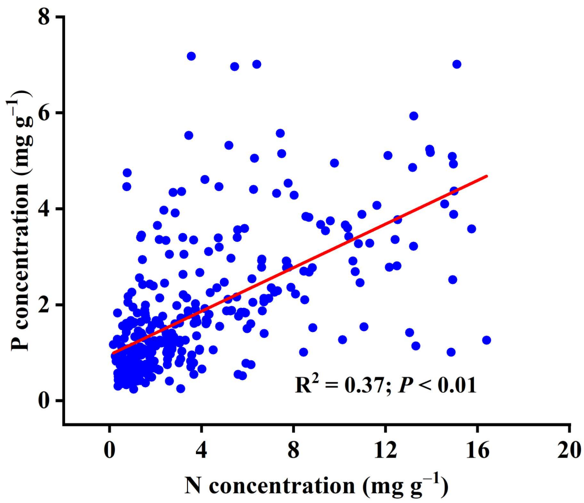

Figure 2. Correlation of N and P concentrations in leaves. Red solid line represents the significant correlation between leaf stoichiometry and geographical factors ($p < 0.05$, $p < 0.01$).

3.2. Variations in Leaf Stoichiometry alongside Geographical and Climatic Variables

At the spatial scale, both leaf N and P concentrations decreased with latitude, and the C:N and C:P ratios increased with latitude ($p < 0.01$, Figure 3a,b), whereas the leaf N:P ratio did not change with latitude (Figure 3c). With increasing longitude, both leaf N ($p < 0.05$) and P ($p < 0.01$) concentrations increased, but the C:P ratio decreased ($p < 0.01$, Figure 3d,e). The C:N and N:P ratios did not change with longitude (Figure 3e,f). The leaf N concentration and N:P ratio (Figure 3g,i) significantly increased with altitude ($p < 0.05$, and $p < 0.01$, respectively). Meanwhile, the leaf C:N ratio decreased with increasing ALT, and the leaf P concentration ($p < 0.01$, Figure 3g,h) and C:P ratio (Figure 3h) showed no marked changes along ALT.

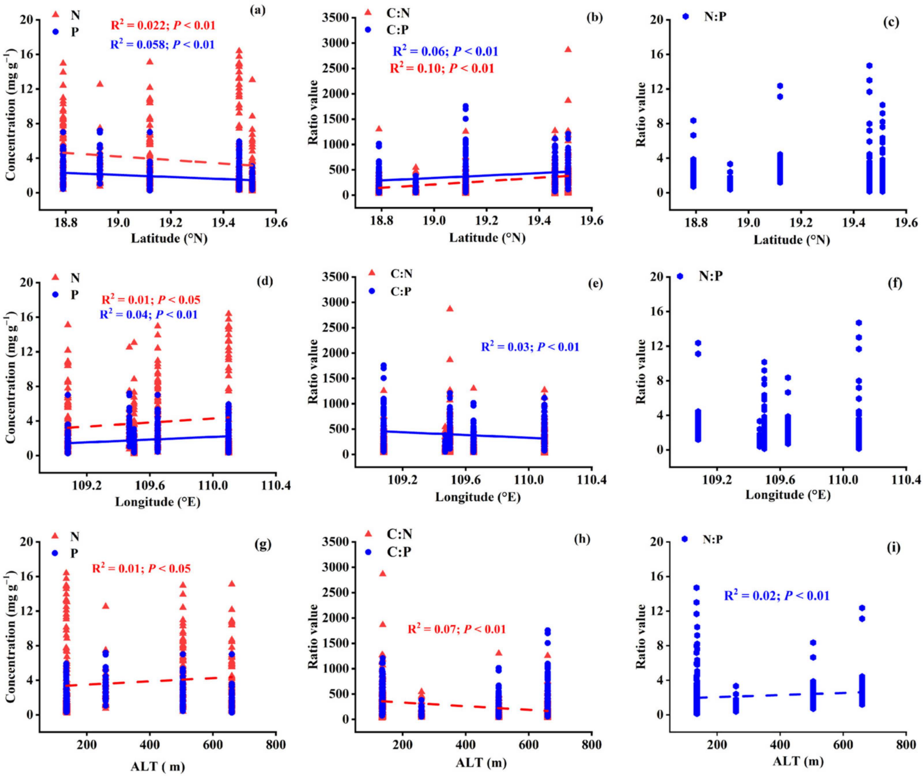

Figure 3. Correlation between leaf stoichiometry and geographical factors. Both the red dotted and blue solid lines represent significant correlations between leaf stoichiometry and geographical factors ($p < 0.05$, $p < 0.01$). No line indicates the absence of a significant correlation between leaf stoichiometry and geographical factors. ALT: altitude.

The leaf P concentration increased, and the C:P and N:P ratios decreased with increasing MAP; however, the leaf N concentration and C:N and N:P ratios did not change with MAP ($p < 0.01$, Figure 4a–c). Both leaf N and P concentrations decreased with increasing MAT; however, the C:P and N:P ratios increased with increasing MAT, whereas the leaf C:N ratio was not affected by MAT ($p < 0.01$, Figure 4d–f).

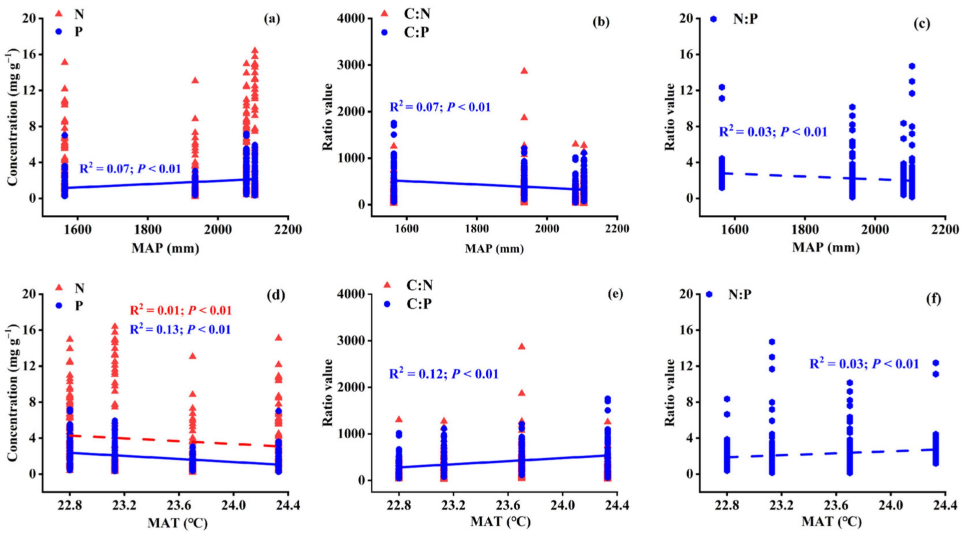

Figure 4. Correlation between leaf stoichiometry and climatic factors. Both the red dotted and blue solid lines represent significant correlations between leaf stoichiometry and climatic factors ($p < 0.05$, $p < 0.01$). No line indicates the absence of a significant correlation between leaf stoichiometry and climatic factors. MAP and MAT represent the mean annual precipitation and temperature, respectively.

3.3. Characteristics of Leaf Stoichiometry among Different Life Forms

There was no significant difference ($p < 0.05$) in the N concentration in the leaf of different life forms. The leaf N concentration of each life form was in the following order: herbs (4.34 mg g^{-1}), woody plants (3.73 mg g^{-1}), and vines (2.94 mg g^{-1}). In contrast, the leaf P concentration of herbs (2.35 mg g^{-1}) was significantly higher than that of woody plants and vines (1.68 and 1.54 mg g^{-1}, respectively) ($p < 0.05$). There were no significant differences in leaf P content among the remaining life forms (Figure 5a, $p < 0.05$).

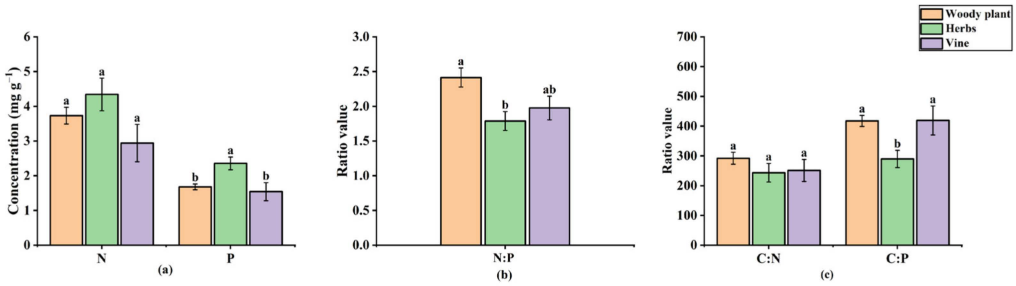

Figure 5. (**a**) Variance of N and P concentrations and (**b**,**c**) their stoichiometric ratios among different life forms (woody plants, herbs, and vines). Different lowercase letters above the bar indicate significant differences among the life forms for the same element, concentration, or ratio. (**a**) Description of N and P concentrations in the leaves of the different plant life forms. (**b**,**c**) description of stoichiometric ratios among the different life forms.

Among the different life forms, the C:N ratio was the highest in woody plants, followed by vines and herbs; however, there were no significant differences among the ratios of the different life forms. The C:P ratio in herb leaves was significantly lower than that in woody plants ($p < 0.05$). In descending order, the C:P ratio was the highest in woody plants, vines, and herbs (Figure 5c). The N:P ratio was significantly higher in the leaves of woody plants than in herbs ($p < 0.05$). No significant differences were observed between the ratios of the leaves of the other life forms. In descending order, the N:P ratio was the highest in woody plants, vines, and herbs (Figure 5b).

3.4. Leaf Stoichiometry in Different Life Forms Response to Environmental Factors

3.4.1. Variations in Leaf Stoichiometry in Different Life Forms: Geographical Variables

The average leaf N and P concentrations in woody plant leaves are negative correlated with latitude, whereas the average leaf N and P concentrations of herbs and vines were not significantly correlated with latitude ($p < 0.05$). Both leaf N and P concentrations of woody plants showed a positive correlation with longitude. Meanwhile, the average leaf N and P concentrations of herbs and vines were not significantly correlated with longitude ($p < 0.05$). The average leaf N concentrations of woody plants showed a positive correlation with ALT, whereas the other plant life forms and their elemental concentrations had no significant correlation with this parameter (Figure 6, $p < 0.05$).

The average leaf C:N and C:P ratios of woody plants showed a positive correlation with latitude, whereas the ratios of herb and vine leaves were not significantly correlated with latitude ($p < 0.05$). The average leaf C:P ratio of woody plants and average leaf N:P ratio of vines showed a negative correlation with longitude, whereas the average leaf C:N ratio of herbs showed a positive correlation with longitude. No significant correlations were found between the stoichiometric ratios of the other life forms and longitude. The average leaf C:P ratio of woody plants and herbs showed a negative correlation with altitude, whereas the average leaf N:P ratio of woody plants and herbs showed a positive correlation with ALT. The stoichiometric ratios of other life forms were not significantly correlated with the change in ALT levels (Figure 6, $p < 0.05$).

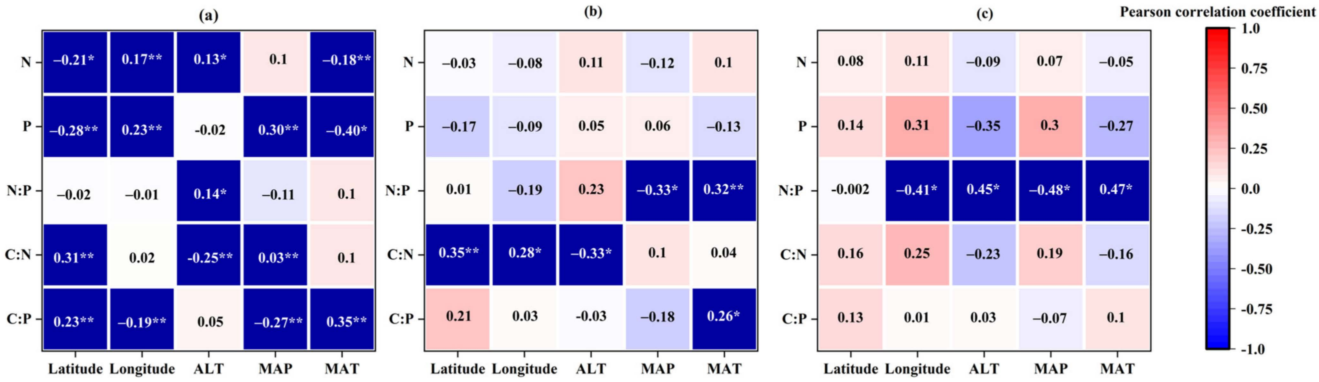

Figure 6. Heat map of Pearson's matrix of correlation coefficients between leaf stoichiometry and geographical and climatic factors for different life forms. (**a**–**c**) represent the correlations of woody plants, herbs, vines with geographical and climatic factors, respectively. * and ** represent significant correlations at $p < 0.05$ and $p < 0.01$, respectively. ALT, MAP, and MAT represent altitude, mean annual precipitation, and mean annual temperature, respectively.

3.4.2. Variations in Leaf Stoichiometry in Different Life Forms: Climatic Variables

The average leaf N concentration of woody plants showed a positive correlation with MAP, whereas the average leaf N and P concentrations of herbs and vines were not significantly correlated with MAP ($p < 0.05$). In terms of temperature variation, the average leaf N and P concentrations of woody plants were negatively correlated with MAT, whereas the average leaf N and P concentrations of herbs and vines were not significantly correlated with MAT (Figure 6, $p < 0.05$).

The average leaf C:P ratio of woody plants and average leaf N:P ratio of herbs and vines were negatively correlated with MAP, whereas the stoichiometric ratios of the other life forms were not significantly correlated with MAP ($p < 0.05$). The average leaf C:P ratio of woody plants, C:P and N:P ratios of herbs, and N:P ratio of vines were positively correlated with MAT. The stoichiometric ratios of the other life forms were not significantly correlated with MAT (Figure 6, $p < 0.05$).

4. Discussion

4.1. Patterns of Leaf Stoichiometry in Hainan Island

Leaf stoichiometry is used as an important indicator to study plant nutrient limitation, nutrient cycling, and plant response to climate change [39,40]. The present study showed that the average leaf N concentration of 268 species on Hainan Island was 3.80 mg g^{-1} (Table 3), which was lower than that reported in global and other regional scale [4,25,41]. Compared with other regions, higher precipitation and temperature in Hainan Island may promote enzymatic activity and photosynthesis, thereby accelerating nutrient cycling and leading to relatively lower leaf N concentrations [42]. In addition, evergreen woody plants accounted for more than two-thirds of the total plant samples in this study (Tables 2 and A1). Lower N concentrations in evergreen species is suggested to facilitate the adaptation to a wide range of conditions in different habitats [43]. Moreover, there is tight coupling between soil and plant nutrients [44]. Soil acidification is evident on Hainan Island [45], which inhibits microbial activity and the decomposition of organic matter, slowing the release of soil nutrients and thus affecting the uptake of soil N nutrients by plants. The mean leaf P concentration in Hainan Island was 1.82 mg g^{-1}, which was slightly higher than that reported in previous studies [4,25,41]. Different from soil-available nitrogen, which comes from decomposition of organic matter, soil-available phosphorus is mainly derived from the weathering of rocks [46,47]. In the tropics and subtropics, geochemical and biological processes are expected to occur at faster rates, resulting in intense soil weathering [48–50]. Previous studies have shown that the soil P concentration tends to increase, and the N:P ratio tends to decrease on Hainan Island [51]. In addition, enhanced precipitation can increase the soil P uptake by plants [47,52]. Consequently, leaf P concentrations of plants in our study were higher than those in previous studies. The average leaf C:N and C:P ratios were 278.77 and 390.60, respectively (Table 3), which were higher than those in global scale [4,53]. The suitable moisture and temperature conditions in Hainan Island may accelerate the photosynthetic C assimilation in plants, resulting in higher N, P utilization, and thus higher C:N and C:P ratios [23,54]. The average leaf N:P ratio was 2.25, which was lower than global research [4]. The average leaf P concentration in this study was slightly higher than that in previous studies, whereas the leaf N concentration was lower, causing the lower N:P ratio in Hainan Island.

For plants of different life forms, the average leaf N and P concentrations of the herbs were the highest. According to the growth rate hypothesis [55,56], leaf N and P concentrations in short-lived and fast-growing species (e.g., annual herbaceous plants) are always higher than those in long-lived and slow-growing species (e.g., evergreen woody plants). Herbs have a shorter life span than woody plants [57,58]; therefore, they have higher leaf N and P concentrations. The homeostasis system of herbs is weaker than that of vines, resulting in a more quickly stoichiometric change under environmental shifts, and thus higher leaf N and P concentrations.

The stoichiometric ratio can objectively reflect the distribution and trade-offs of the restrictive elements of the plant during the growth process [59,60]. A previous study suggested that the C:N, C:P, and N:P ratios play a significant role in the determination of the plant nutrient limitation [61]. According to Verhoeven et al. [62], when N:P is less than 14, plant growth is mainly restricted by N; meanwhile, N:P greater than 16 results in the restriction of plant growth mainly by P. As mentioned above, the average leaf N:P ratio of the 268 plants in this study was 2.25, suggesting that plant growth on Hainan Island may be limited by N. This conclusion has also been proved by some previous studies [51,63]. N limitation is widespread among different habitats [64]. According to our results, N is also a key factor limiting plant growth in temperate and tropical forests. In addition, there was a close link between leaf N and P concentrations (Figure 2), which is consistent with several previous studies conducted at national and global scales [4,25]. This result suggests that there may be a synergistic relationship between the N and P absorption efficiency of plants on Hainan Island [65].

4.2. Influence of Geographical and Climatic Factors on Leaf Stoichiometry

The present study found that leaf N, P stoichiometry had significant correlation with latitude, longitude, altitude, MAT and MAP, which confirmed our hypothesis that leaf N and P stoichiometry patterns in Hainan Island would be affected by geographical and climatic factors. Changes in temperature and precipitation can affect plant growth and nutrient metabolism, consequently affecting the nutrient cycling of ecosystems [20,25,65,66]. The leaf N and P concentrations were significantly negatively correlated with MAT (Figure 4d), which were also observed in mainland China and on a global scale [4,25,41]. The temperature–plant physiology hypothesis [4] suggests that due to physiological acclimation (i.e., plants regulate N, P levels to counteract the effects of temperature) and the adaptation to temperature (i.e., temperature regulates N, P levels by affecting plant metabolism), N and P decline monotonically with increasing temperature. In general, temperature decreases with increasing latitude, resulting in a positive relationship between leaf N, P concentrations and latitude [4,25,41]. However, a negative correlation has been found between leaf N, P concentrations and latitude in Hainan Island (Figure 3a). This may be because the latitudinal range of our study area (18.79° to 19.51° N, Table 1) is smaller than those of the previous studies in global scale (43 to 70° N) [4], the Chinese mainland (18° to 48° N) [25], and the north–south transect of eastern China (18° to 52° N) [41]. At a smaller gradient, the leaf N and P concentrations showed weak geographical patterns and even decreased with latitude [3,67,68]. C:N and C:P ratios are important physiological indices of plants growth rate [56,69,70]. Our results showed that the leaf C:N and C:P ratios increased with latitude and MAT (Figures 3b and 4b), implying that nutrient utilization and C assimilation rates increased in high-latitude regions [11,23,54,71]. Leaf N:P ratios reflect the relative availability of N [72]. Owing to the limited latitudinal range of the study area, no significant correlation between leaf N:P and latitude was observed (Figure 3f), this indicates that N availability does not vary with latitudinal gradient.

In this study, the leaf P concentration showed a significantly positive correlation with MAP (Figure 4a), which was consistent with the results of Sardans et al. [73]. High precipitation may enhance the nutrient uptake capacity of plants [74–76], resulting in a positive relationship between leaf P concentration and MAP. However, there was no significant correlation between leaf N concentration and MAP (Figure 4a), which differs from the results of a previous report [25]. This may be caused by the high nitrogen deposition in China over the last 30 years [6,77,78]. N deposition exacerbates the nutrient imbalance and disturb the C, N, and P cycles in tropical ecosystem [79]. A study in a tropical forest in China showed that large amounts of reactive atmospheric N deposition were absorbed and transported into plant tissues [80], which might have led to weak relationships between the leaf N concentration and MAP. In addition, Hui et al. [51] showed that the soil N availability on Hainan Island was lower, which might be due to the leaching of N modulated by the high annual precipitation. Therefore, the impact of soil N availability on the leaf N content on Hainan Island may be higher than the effect of MAP, resulting in the observed insignificance between leaf N concentration and MAP. The leaf N and P concentrations were positively correlated with longitude (Figure 3d), which is consistent with the findings of Han et al. [26]. The distribution of precipitation in China gradually decreases from the southeast coast to the northwest inland region. Therefore, the longitudinal zonality of leaf stoichiometry in China is mainly affected by precipitation. The ratio of leaf C:P and N:P in leaf are vital indicators of plant growth because the distribution and variation in P-rich RNA occur at different growth rates [55,81,82]. In our study, the leaf C:P and N:P ratios decreased with increasing MAP, which may have been influenced by the relationship between leaf N and P concentrations and climate (Figure 4a–c). These correlations indicate that along with longitude, high MAP promotes the utilization efficiency of P, improving the growth rate of plants [4,83].

The leaf N concentration and N:P ratio in Hainan Island were significantly positively associated with the altitude (Figure 3g,i), whereas the trend of the C:N ratio exhibited the opposite behavior (Figure 3h), and there was no significant correlation between P concentration and altitude, and between C:P and altitude (Figure 3g,i). Climatic and soil factors change along the altitudinal gradients, leading to the variation in plant functional traits and nutrient composition [84–87]; thereby, leaf stoichiometry changes with altitude [88–94]. Temperature decreases monotonically with increasing altitude, and leaf N concentration has a negative relationship with temperature. Therefore, leaf N, even N:P ratio increased, and C:N ratio decreased with increasing altitude in Hainan Island. No correlation between leaf P concentration and altitude, and between C:P ratio and altitude may be associated with the disturbance of soil phosphorus availability, which may also change along altitude.

In order to reduce interspecific competition [24], plants of different life forms have different resource utilization efficiencies and environmental adaptation strategies. Therefore, leaf element concentrations and their correlation with geographical and climatic factors change across life forms. The leaf stoichiometric characteristics of woody plants were consistent with those of the entire study area, whereas the leaf N and P concentrations and stoichiometric ratios of herbs and vine were almost not significantly related to geographical and climatic factors (Figure 6a,b). Limited by relatively shallow root depth more than woody plants, nutrient state in herbs is more sensitive to the change in soil nutrient availability. Thereby, leaf stoichiometry of herbs may be less affected by graphical and climatic factors. Vines have faster resource acquisition strategy than woody plants [95]; thus, their nutrient concentration may also be less sensitive to climatic change. However, the leaf N:P ratio was relatively stable and significant correlation with climatic and geographical variables across the different life forms (Figure 6c), which is inconsistent with the trends found in recent studies [4,25,96]. This inconsistency again suggested that study of biogeographic patterns of leaf nutrients at regional scales is increasingly important to accurately understand the relationship between vegetation and climate at the global scale.

5. Conclusions

The present study showed that average N, P concentration and N, P stoichiometric ratio of 345 plant samples from 268 species in Hainan Island were different from global scale and other regions, suggesting that plant stoichiometric pattern is unique in tropical regions. Leaf N concentration was negatively correlated with latitude and MAT, but was positively related to longitude and ALT; leaf P concentration was negatively associated with latitude and MAT, but was positively correlated with MAP; and leaf C:N, C:P, and N:P ratio was also related to some geographical and climatic factors. These results confirmed our hypothesis and suggest that geographical and climatic factors have great effect on plant stoichiometry in Hainan Island. In addition, the correlation between plant stoichiometry and geographical and climatic factors changed across life forms, indicating that plants of different life forms have different resource utilization efficiencies and environmental adaptation strategies. Our results contribute to the understanding of the spatial patterns of leaf stoichiometry in a wide variety of tropical plants and their response to global climate change, which may play a crucial role in guiding the nutrient management in tropical rainforest.

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Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Plant species status.

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
1	*Alangium chinense*	Woody plant	Deciduous plant
2	*Artocarpus hypargyreus*	Woody plant	Evergreen
3	*Abelmoschus esculentus*	Herbs	/
4	*Acacia confusa*	Woody plant	Evergreen
5	*Acalypha wikesiana*	Woody plant	Evergreen
6	*Acanthopanax senticosus*	Woody plant	Evergreen
7	*Acer buergerianum*	Woody plant	Deciduous plant
8	*Achyranthes bidentata*	Herbs	/
9	*Acmena acuminatissima*	Woody plant	Evergreen
10	*Acronychia pedunculata*	Woody plant	Evergreen
11	*Actinidia chinensis*	Vine	Deciduous plant
12	*Adenanthera pavonlna*	Woody plant	Deciduous plant
13	*Aeschynomene indica*	Herbs	/
14	*Aidia cochinchinensis*	Woody plant	Evergreen
15	*Alangium salviifolium*	Woody plant	Deciduous plant
16	*Albizia chinensis*	Woody plant	Evergreen
17	*Albizzia corniculata*	Vine	Evergreen
18	*Albizzia procera*	Woody plant	Deciduous plant
19	*Alchornea davidii*	Woody plant	Deciduous plant
20	*Alchornea trewioides*	Woody plant	Evergreen

Table A1. *Cont.*

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
21	*Aleurites moluccana*	Woody plant	Evergreen
22	*Allamanda cathartica*	Woody plant	Evergreen
23	*Alocasia macrorrhiza*	Herbs	/
24	*Alpinia japonica*	Herbs	/
25	*Alpinia zerumbet*	Herbs	/
26	*Alseodaphne rugosa*	Woody plant	Evergreen
27	*Alstonia scholaris*	Woody plant	Evergreen
28	*Annona glabra*	Woody plant	Evergreen
29	*Annona montana*	Woody plant	Evergreen
30	*Aphanamixis polystachya*	Woody plant	Evergreen
31	*Aporosa dioica*	Woody plant	Evergreen
32	*Aquilaria sinensis*	Woody plant	Evergreen
33	*Araucaria cunninghamii*	Woody plant	Evergreen
34	*Ardisia japonica*	Woody plant	Evergreen
35	*Areca catechu*	Woody plant	Evergreen
36	*Areca triandra*	Woody plant	Evergreen
37	*Arenga pinnata*	Woody plant	Evergreen
38	*Bambusa textilis*	Herbs	/
39	*Bidens pilosa*	Herbs	/
40	*Blastus cochinchinensis*	Woody plant	Evergreen
41	*Bombax malabaricum*	Woody plant	Deciduous plant
42	*Bowringia callicarpa*	Woody plant	Evergreen
43	*Brucea javanica*	Woody plant	Evergreen
44	*Buxus megistophylla*	Woody plant	Evergreen
45	*Byttneria aspere*	Vine	Evergreen
46	*Caesalpinia pulcherrima*	Woody plant	Evergreen
47	*Calliandra haematocephala*	Woody plant	Deciduous plant
48	*Callistemon rigidus*	Woody plant	Evergreen
49	*Camptotheca acuminata*	Woody plant	Deciduous plant
50	*Canarium pimela*	Woody plant	Evergreen
51	*Carica papaya*	Herbs	/
52	*Carmona microphylla*	Woody plant	Evergreen
53	*Carvota mitis*	Woody plant	Evergreen
54	*Caryota mitis*	Woody plant	Evergreen
55	*Caryota ochlandra*	Woody plant	Evergreen
56	*Cayratia japonica*	Vine	Evergreen
57	*Cecropia peltata*	Woody plant	Evergreen
58	*Ceiba pentandra*	Woody plant	Deciduous plant
59	*Ceiba speciosa*	Woody plant	Deciduous plant
60	*Celosia argentea*	Herbs	/
61	*Cerbera manghas*	Woody plant	Evergreen
62	*Chamaedorea erumpens*	Woody plant	Evergreen
63	*Choerospondias axillaris*	Woody plant	Deciduous plant
64	*Chromolaene odorata*	Herbs	/
65	*Chrysalidocarpus lutescens*	Woody plant	Evergreen
66	*Chukrasia tabularis*	Woody plant	Evergreen
67	*Cinnamomum bodinieri*	Woody plant	Evergreen
68	*Cinnamomum pedunculatum*	Woody plant	Evergreen
69	*Citrus maxima*	Woody plant	Evergreen
70	*Clerodendrum trichotomum*	Woody plant	Evergreen
71	*Cocos uncifera*	Woody plant	Evergreen
72	*Codiaeum variegatum*	Woody plant	Evergreen
73	*Cola acuminata*	Woody plant	Evergreen
74	*Conyza canadensis*	Herbs	/
75	*Cordyline fruticosa*	Woody plant	Evergreen
76	*Costus speciosus*	Herbs	/
77	*Crassocephalum crepidioides*	Herbs	/
78	*Cratoxylum cochin chinense*	Woody plant	Deciduous plant

Table A1. *Cont.*

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
79	*Croton laevigatus*	Woody plant	Evergreen
80	*Cudrania cochin chinensis*	Woody plant	Evergreen
81	*Curculigo orchioides*	Herbs	/
82	*Dalbergia hupeana*	Woody plant	Evergreen
83	*Delonix regia*	Woody plant	Deciduous plant
84	*Grona heterocarpos*	Woody plant	Evergreen
85	*Desmos chinensis*	Woody plant	Evergreen
86	*Dianella ensifolia*	Herbs	/
87	*Digitaria sanguinalis*	Herbs	/
88	*Dimocarpus longan*	Woody plant	Evergreen
89	*Dioscorea opposita*	Vine	Evergreen
90	*Diospyros ebenum*	Woody plant	Evergreen
91	*Dolichandrone stipulata*	Woody plant	Evergreen
92	*Dracaena angustifolia*	Woody plant	Evergreen
93	*Dracontomelon duperreanum*	Woody plant	Evergreen
94	*Duranta repens*	Woody plant	Evergreen
95	*Elaeagnus pungens*	Woody plant	Evergreen
96	*Elaeis guineensis*	Woody plant	Evergreen
97	*Elephantopus scaber*	Herbs	/
98	*Elephantopus tomentosus*	Herbs	/
99	*Eleusine indica*	Herbs	/
100	*Elsholtzia ciliata*	Herbs	/
101	*Engelhardtia roxburghiana*	Woody plant	Evergreen
102	*Erythrophleum fordii*	Woody plant	Evergreen
103	*Eugenia uniflora*	Woody plant	Evergreen
104	*Euphorbia humifusa*	Herbs	/
105	*Evodia glabrifolia*	Woody plant	Evergreen
106	*Evodia lepta*	Woody plant	Evergreen
107	*Fagraea ceilanica*	Woody plant	Evergreen
108	*Ficus altissima*	Woody plant	Evergreen
109	*Ficus auriculata*	Woody plant	Evergreen
110	*Ficus benjamina*	Woody plant	Evergreen
111	*Ficus fistulosa*	Woody plant	Evergreen
112	*Ficus hirta*	Woody plant	Evergreen
113	*Ficus hispida*	Woody plant	Evergreen
114	*Ficus microcarpa*	Woody plant	Evergreen
115	*Ficus subpisocarpa*	Woody plant	Evergreen
116	*Ficus tinctoria*	Woody plant	Evergreen
117	*Fissistigma oldhamii*	Woody plant	Evergreen
118	*Garcia nutans*	Woody plant	Evergreen
119	*Garcinia oblongifolia*	Woody plant	Evergreen
120	*Gardenia jasminoides*	Woody plant	Evergreen
121	*Gleditsia sinensis*	Woody plant	Deciduous plant
122	*Gleditsia vestita*	Woody plant	Evergreen
123	*Gmelina arborea*	Woody plant	Evergreen
124	*Gnetum parvifolium*	Vine	Evergreen
125	*Grevillea banksii*	Woody plant	Evergreen
126	*Gynura segetum*	Herbs	/
127	*Hamelia patens*	Woody plant	Evergreen
128	*Hedera nepalensis*	Woody plant	Evergreen
129	*Hedyotis auricularia*	Herbs	/
130	*Hedyotis hedyotidea*	Vine	Evergreen
131	*Heritiera angustata*	Woody plant	Evergreen
132	*Heritiera parvifolia*	Woody plant	Evergreen
133	*Hernandia sonora*	Woody plant	Evergreen
134	*Hevea brasiliensis*	Woody plant	Deciduous plant
135	*Hibiscus mutabilis*	Woody plant	Deciduous plant
136	*Hibiscus rosa-sinensis*	Woody plant	Evergreen

Table A1. *Cont.*

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
137	*Hibiscus schizopetalus*	Woody plant	Evergreen
138	*Holmskioldia sanguinea*	Woody plant	Evergreen
139	*Holarrhena antidysenterica*	Woody plant	Evergreen
140	*Homalium cochinchinense*	Woody plant	Evergreen
141	*Homalium hainanense*	Woody plant	Evergreen
142	*Hopea exalata*	Woody plant	Evergreen
143	*Hoya carnosa*	Vine	Evergreen
144	*Hymenaea courbaril*	Woody plant	Evergreen
145	*Ilex asprella*	Woody plant	Deciduous plant
146	*Ipomoea biflora*	Herbs	/
147	*Ixora chinensis*	Woody plant	Evergreen
148	*Jasminum lanceolarium*	Woody plant	Evergreen
149	*Juncellus serotinus*	Herbs	/
150	*Kigelia pinnata*	Woody plant	Deciduous plant
151	*Lantana camara*	Herbs	/
152	*Lasianthus chinensis*	Woody plant	Evergreen
153	*Lasianthus japonicus*	Woody plant	Evergreen
154	*Leptodermis parkeri*	Woody plant	Evergreen
155	*Ligustrum vicaryi*	Woody plant	Deciduous plant
156	*Litchi chinensis*	Woody plant	Evergreen
157	*Lithocarpus corneus*	Woody plant	Evergreen
158	*Litsea monopetala*	Herbs	/
159	*Litsea pungens*	Woody plant	Deciduous plant
160	*Lophatherum*	Woody plant	Evergreen
161	*Lucuma nervosa*	Woody plant	Evergreen
162	*Machilus salicina*	Woody plant	Evergreen
163	*Maesa japonica*	Woody plant	Evergreen
164	*Magnolia coco*	Woody plant	Evergreen
165	*Magnolia denudata*	Woody plant	Deciduous plant
166	*Magnolia liliflora*	Woody plant	Evergreen
167	*Mallotus apelta*	Woody plant	Evergreen
168	*Mallotus hookerianus*	Woody plant	Evergreen
169	*Malvastrum coromandelianum*	Herbs	/
170	*Manihot esculenta*	Woody plant	Evergreen
171	*Manilkara zapota*	Woody plant	Evergreen
172	*Melastoma candidum*	Herbs	/
173	*Melastoma sanguineum*	Herbs	/
174	*Mesua ferrea*	Woody plant	Evergreen
175	*Michelia odora*	Woody plant	Evergreen
176	*Mimosa pudica*	Herbs	/
177	*Mimosa sepiaria*	Herbs	/
178	*Mimusops elengi*	Woody plant	Evergreen
179	*Miscanthus sinensis*	Herbs	/
180	*Moghania macrophylla*	Woody plant	Evergreen
181	*Mucuna sempervirens*	Vine	Evergreen
182	*Muntingia calabura*	Woody plant	Evergreen
183	*Musa nana*	Herbs	/
184	*Nephelium lappceum*	Woody plant	Evergreen
185	*Pacrydium pierrei*	Woody plant	Evergreen
186	*Paederia scandens*	Vine	Evergreen
187	*Paeonia suffruticosa*	Woody plant	Deciduous plant
188	*Pandanus tectorius*	Woody plant	Evergreen
189	*Parakmeria lotungensis*	Woody plant	Evergreen
190	*Passiflora foetida*	Vine	Evergreen
191	*Pharbitis nil*	Herbs	/
192	*Photinia serrulata*	Woody plant	Evergreen
193	*Phragmites australias*	Herbs	/
194	*Phyllanthus emblica*	Woody plant	Evergreen

Table A1. *Cont.*

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
195	*Phyllanthus urinaria*	Herbs	/
196	*Pittosporum tobira*	Woody plant	Evergreen
197	*Platycladus orientalis*	Woody plant	Evergreen
198	*Plumeria rubra*	Woody plant	Deciduous plant
199	*Podocarpus imbricatus*	Woody plant	Evergreen
200	*Pollia japonica*	Herbs	/
201	*Polyalthia longifolia*	Woody plant	Evergreen
202	*Polyalthia rumphii*	Woody plant	Evergreen
203	*Polygala japonica*	Herbs	/
204	*Polygonatum odoratum*	Herbs	/
205	*Polygonatum sibiricum*	Herbs	/
206	*Pongamia pinnata*	Woody plant	Evergreen
207	*Portulaca grandiflora*	Herbs	/
208	*Pothos chinensis*	Vine	Evergreen
209	*Pouzolzia zeylanica*	Herbs	/
210	*Psychotria rubra*	Woody plant	Evergreen
211	*Pterocarpus marsupium*	Woody plant	Evergreen
212	*Pterolobium punctatum*	Vine	Evergreen
213	*Pterospermum heterophyllum*	Woody plant	Evergreen
214	*Ptychosperma macarthurii*	Woody plant	Evergreen
215	*Pueraria lobata*	Vine	Evergreen
216	*Quercus variabilis*	Woody plant	Evergreen
217	*Quisqualis indica*	Woody plant	Evergreen
218	*Rhaphidophora hongkongensis*	Vine	Evergreen
219	*Rhapis excelsa*	Woody plant	Evergreen
220	*Rhodomyrtus tomentosa*	Woody plant	Evergreen
221	*Rhopalostylis sapida*	Woody plant	Evergreen
222	*Richardia scabra*	Herbs	/
223	*Rourea microphylla*	Woody plant	Evergreen
224	*Rubus corchorifolius*	Woody plant	Evergreen
225	*Russelia equisetiformis*	Woody plant	Evergreen
226	*Schinus terebinthifolius*	Woody plant	Evergreen
227	*Sabal mauritiformis*	Woody plant	Evergreen
228	*Sanchezia speciosa*	Woody plant	Evergreen
229	*Sapium sebiferum*	Woody plant	Deciduous plant
230	*Sarcandra glabra*	Herbs	/
231	*Schefflera octophylla*	Woody plant	Evergreen
232	*Setaria viridis*	Herbs	/
233	*Sida acuta*	Herbs	/
234	*Sida rhombifolia*	Woody plant	Evergreen
235	*Sindora glabra*	Woody plant	Evergreen
236	*Sinomenium acutum*	Vine	Evergreen
237	*Sloanea hemsleyana*	Woody plant	Evergreen
238	*Smilax china*	Vine	Evergreen
239	*Spathodea campanulata*	Woody plant	Deciduous plant
240	*Spermacoce latifolia*	Herbs	/
241	*Spondias lakonensis*	Woody plant	Evergreen
242	*Styrax suberifolius*	Woody plant	Evergreen
243	*Swietenia macrophylla*	Woody plant	Evergreen
244	*Symplocos caudata*	Woody plant	Evergreen
245	*Symplocos congesta*	Woody plant	Evergreen
246	*Synedrellanodiflora*	Herbs	/
247	*Synsepalum dulcificum*	Woody plant	Evergreen
248	*Syzygium buxifolium*	Woody plant	Evergreen
249	*Syzyglum hancei*	Woody plant	Evergreen
250	*Tectona grandis*	Woody plant	Evergreen
251	*Terminalia arjuna*	Woody plant	Evergreen
252	*Terminalia catappa*	Woody plant	Evergreen

Table A1. *Cont.*

Serial Number	Plant Name	Life Form	Evergreen/Deciduous Plant
253	*Tetracera asiatica*	Vine	Evergreen
254	*Thunbergia erecta*	Woody plant	Evergreen
255	*Tithonia diversifolia*	Herbs	/
256	*Toddalia asiatica*	Woody plant	Evergreen
257	*Toona sinensis*	Woody plant	Deciduous plant
258	*Trachelospermum jasminoides*	Vine	Evergreen
259	*Triumfetta rhomboidea*	Woody plant	Evergreen
260	*Urena lobata*	Herbs	/
261	*Uvaria boniana*	Woody plant	Evergreen
262	*Veitchia merrillii*	Woody plant	Evergreen
263	*Viburnum odoratissimum*	Woody plant	Evergreen
264	*Vitex quinata*	Woody plant	Evergreen
265	*Wedelia chinensis*	Herbs	/
266	*Zanthoxylum avicennae*	Woody plant	Deciduous plant
267	*Zanthoxylum bungeanum*	Woody plant	Deciduous plant
268	*Zingiber zerumbet*	Herbs	/

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