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Whole-Plant Seedling Functional Traits Suggest Lianas Also Support "Fast-Slow" Plant Economics Spectrum

Zhenhua Sun [1,2,†], Nujaree Prachanun [1,3,†], Arunkamon Sonsuthi [1,3,†], Wirong Chanthorn [4,5], Warren Y. Brockelman [6,7], Anuttara Nathalang [6], Luxiang Lin [1,2,8,9,*] and Frans Bongers [10]

[1] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China; sunzhenhua@xtbg.ac.cn (Z.S.); gibbon.fr79@gmail.com (N.P.); hongza_hongzuza@icloud.com (A.S.)
[2] Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla 666303, China
[3] University of Chinese Academy of Sciences, Beijing 100049, China
[4] Department of Environmental Technology and Management, Faculty of Environment, Kasetsart University, 50 Ngamwongwan Road, Jatujak, Bangkok 10900, Thailand; Wirong.c@ku.th
[5] Department of Ecological Modelling, Helmholtz Centre for Environmental Research, UFZ, 04318 Leipzig, Germany
[6] National Biobank of Thailand (NBT), National Science and Technology Development Agency, Bangkok 12120, Thailand; wybrock@cscoms.com (W.Y.B.); anuttara.nat@nstda.or.th (A.N.)
[7] Institute of Molecular Biosciences, Mahidol University, Salaya, Nakhon Pathom 73170, Thailand
[8] National Forest Ecosystem Research Station at Xishuangbanna, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China
[9] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Naypyidaw 05282, Myanmar
[10] Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands; frans.bongers@wur.nl
* Correspondence: linluxa@xtbg.ac.cn
† These authors contributed equally to this work.

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Abstract: Lianas are predicted to perform better than trees during seasonal drought among tropical forests, which has substantial implications for tree and forest dynamics. Here, we use whole-plant trait comparison to test whether lianas allocated on the resource acquisitive end of the continuum of woody plant strategies. We measured morphological and biomass allocation traits for seedlings of 153 species of trees and lianas occurring in a tropical forest in Thailand during the dry season. We first compared trait differences between lianas and trees directly, and then classified all species based on their trait similarities. We found that liana seedlings had significantly higher specific leaf areas and specific stem lengths than co-occurring tree seedlings. Trait similarity classification resulted in a liana-dominated cluster and a tree-dominated cluster. Compared to the tree-dominated cluster, species in the liana-dominated cluster were characterized by a consistent pattern of lower dry matter content and cheaper and more efficient per dry mass unit investment in both above- and below-ground organs. The consistency of all organs operating in tandem for dry matter content, together with optimized investment in them per mass unit, implied that the lianas and trees can be highly overlapped on the strategy gradient of the resource acquisition continuum.

Keywords: 'fast–slow' plant economics spectrum; functional traits; lianas and trees; seasonal growth advantage (SGA); tropical forest

1. Introduction

Lianas (woody climbers) are an important component of tropical forests and they contribute a significant portion of both species diversity and biomass [1,2]. Evidence has mounted that lianas have proliferated at the expense of trees during the past few decades, possibly due to increasing forest fragmentation, logging, and the intensity and duration of seasonal drought [3–6], although the basic causes remain somewhat unclear. Schnitzer [7] posited that lianas have a seasonal growth advantage (SGA), which allows them to grow faster than most trees in seasonal drought. As the increase of lianas relative to co-occurring trees may exert negative effects on tree survival [8], regeneration [9], and growth [10,11], it has led to a serious concern over whether and how lianas are capable of having a growing advantage over trees in seasonal tropical forests globally [2].

Lianas use trees as hosts to develop and reach the top of the canopy, which makes the most distinct contrast between life forms [12,13], with implications for functional strategies in relation to biomass allocation and resource acquisition of different organs [14,15]. With the help of mechanical support from trees, adult lianas are believed to allocate more biomass to the photosynthetic leaf area and perhaps also the roots, and less to their elongated stems in comparison to trees [16–18]. These contrasting biomass allocation strategies in leaves, stems, and roots between lianas and trees may confer lianas the ability to absorb more carbon with given whole-plant biomass and grow faster than their tree counterparts [12]. In contrast, such allocation properties and the subsequent potential growth advantage for lianas may be less likely to be pronounced when they are juveniles and/or under a canopy with low light [19], since both of them need a vertical, self-supporting structure and comparable leaf area ratio for photosynthesis [20]. Yet, evidence for both the lianas' growth/survival advantage over trees and their relevant trait differences from trees in the juvenile life stage are mixed. For example, a 10-year demographic inventory in a Puerto Rican tropical forest implied dry conditions and disturbance promoted liana seedling survival and abundance [21], while seedling dynamics over 16 years in a tropical forest in Panama revealed liana seedlings decelerated increases in the relative abundance of lianas over time [22]. The resource acquisition between lianas and trees suggests lianas seedlings may also follow a "fast-slow" growth spectrum, defined by whether they are light-demanding or shade tolerant [18].

Together with biomass allocation properties, other functional traits, including morphological and physiological features, also affect plant growth, survival, and reproduction [23], and maintain species diversity [24,25]. These functional traits and the relevant trait-based approach allow ecologists to infer the functional or adaptive strategies of individuals and species. The past few decades have witnessed the coverage and usage of functional traits all across the biomes and have revealed the globally convergent patterns of trait covariations [26]. A single "fast-slow" plant economics spectrum integrating different organs of a plant has been proposed to explain species strategies for acquiring, investing, and retaining limited resources [27–30]. In this framework, species traits tend to co-vary along a continuum of a cheap to expensive organ dry mass investment of resources with returns of a fast growth rate (but short life-span) to slow the growth rate(but long-lived organs) [30,31]. For instance, the "leaf economics spectrum (LES)" illustrates how a suite of leaf traits consistently co-vary along a single axis of the resource use axis and form the resource acquisition−conservation trade-off [27,32,33]. A similar trait continuum also exists in stem and root traits separately. In the stem or wood trait economics spectrums (WES), the wood density leads to a trade-off between the growth and survival potential by determining the mechanical and hydraulic properties of the stem [34]. At the root level, root tissue density was reported to be most consistent with below-ground traits and associated with growth rate [35]. However, being fast at acquiring and processing resources is only paid off when all organs are operating simultaneously; otherwise, it would be functionally inefficient [30]. While the coordination of leaf, stem, and root traits in influencing the fitness of trees under stress is becoming increasingly clear [35], the picture of how traits coordinate among organs in lianas compared with co-occurring trees is not well understood.

Many have postulated that mature lianas may gain an ecological advantage over trees through leaf and root functional traits that offer quick acquisition and processing of limiting resources [30,36]. For example, lianas in climbing form depend on a tree as trellises to reach the canopy, and thus, they typically proportionally allocate more biomass on the canopy, resulting in lianas having greater specific leaf area (SLA) and photosynthetic rate (Amax) than trees [14,15,37,38]. Lianas tend to have wider and longer vessels than trees, which facilitate faster water transport and therefore, higher water usage efficiency [39,40]. These fast and acquisitive strategies in lianas help to explain why lianas outperform trees in seasonal dry forests and/or under higher light conditions [41]. However, some recent trait comparisons implied that lianas and trees may not differ as much as previously thought [36,42,43]. Lianas are not always located on the acquisitive side of the spectrum [38,44]. Furthermore, in the early life stage, seedlings of lianas and trees normally co-occur and survive for years within the low-light understory [45]; thus, they may be similar to each other in morphology and resource usage strategies [12,46]. Consequently, contrasting potential growth rate, resource uptake, and allocation may not occur in early ontogenetic stages where light remains the most limited resource, and lianas and trees may have overlapping strategies expressed in the functional traits dimension.

Here, we quantify morphological traits important for resource acquisition–conservation trade-offs of tropical lianas and tree seedlings that co-occur in a tropical, seasonal evergreen forest. We test the potential differences between the seedlings of lianas and trees to gain insight into the strategies that may drive the contrasting resource acquisition and growth under the forest canopy. A whole-plant analysis of the seedlings of 100 tree species (794 individuals) and 53 liana species (712 individuals) during the dry season in a seasonal, dry, tropical forest of Thailand helped us to address the following questions:

(1) Which traits or trait sets make lianas, as a whole, different from trees at the seedling stage?
(2) Are lianas, as a whole, represented by species with a higher resource acquisition strategy and alternatively, are tree species associated with a more conservative resource acquisition strategy?
(3) Do similar trait continuums exist among leaf, stem, and root traits?

2. Materials and Methods

2.1. Study site

This study was conducted in the 30-ha Mo Singto forest dynamics plot (MSP), 600 m × 500 m in size, which is a ForestGEO plot of the Center for Tropical Forest Science (CTFS) network [47]. The plot is located at 101°22′ E and 14°26′ N with an altitude range of 725–815 m asl in the central landscape of Khao Yai National Park, which is part of a UNESCO World Heritage Site. The dry season lasts from November to April, with some thunderstorms occurring during March and April. Average annual precipitation is ca. 2000 mm, and the average annual minimum−maximum temperature range is 19–28 °C [48]. The 2004–2005 census of all trees and shrubs yielded 262 tree species and a later liana survey found a total of ca. 150 liana species occurring in the plot W. Brockelman, unpublished data.

2.2. Species Selection

In May of 2018, we established 634 2 m × 2 m seedling plots arrayed in the center of every 20 m × 20 m quadrant of the MSP to monitor seedling dynamics. Based on a seedling census conducted in 2018, 33,490 seedlings with a height above 5 cm and dbh (diameter at breast height) less than 1 cm were tagged and identified as species, including 169 tree species and 105 liana species. We selected 153 species as target species for trait collection because they are more abundant in both the plot and nearby forest, including 100 tree species and 53 liana species. These 153 species covered 87 % of the seedling census observations. Considering that the total biomass differences of individuals may affect the comparison of interspecific differences in traits, we only sampled seedling individuals with a height less than 100 cm but above 10 cm. Nine individuals of each species were planned to be harvested outside of the plot. In total, 1206 individuals belonging to 153 woody seedling species were sampled, the minimum individuals of 3 and mean of 8. Quantification of morphological traits as well as plant allocation traits were conducted in the dry season of 2020. Considering the potential interactional effect on traits between light intensity and drought severity, all the sampled species and relevant individuals mostly occurred in low light intensity.

2.3. Trait Measurement

We separated each harvested individual into leaves, stem, and roots. All fully expanded leaves were scanned using a scanner (EPSON) V19 A4, Epson Co., Ltd., Bangkok, Thailand) for measurement of the leaf area (LA), specific leaf area (SLA), and total aggregate area. Fresh mass of all leaves, stems, and roots was measured using a 0.001 g precision balance (Ohaus® Pioneer® PX Analytical Balances, Cole-Parmer China). Stem length and root length were also measured. After these measurements, all leaf, stem, and root material of each individual was separately dried for 72 h at 65 °C in an oven (Binder ED 400, BINDER GmbH (Headquarters), Tuttlingen, Deutschland) and weighed to determine biomass allocation to their respective parts. We considered eleven leaf, three stem, and three root traits that describe biomass allocation and are important for resource acquisition or resource conservation: leaf area (LA), leaf dry mass content (LDMC), specific leaf area (SLA), leaf area ratio (LAR), leaf mass fraction (LMF), stem dry matter content (SDMC), specific stem length ratio (SLR), stem mass fraction (SMF), root dry matter content (RDMC), specific root length (SRL), and root mass fraction (RMF). All traits measured in this study and their ecological relevance are defined in Table 1.

Table 1. Trait overview with abbreviations, units, equations, and ecological relevance.

Trait	Abbr.	Unit	Equation	Ecological Relevance
Leaf area	LA	cm^2	-	Leaf temperatures and higher photosynthetic and water use efficiency under drought [13,49]
Specific leaf area	SLA	cm^2 g^{-1}	$\frac{\text{Leaf size}}{\text{Leaf dry weight}}$	Potential relative growth rate [31]
Leaf area ratio	LAR	cm^2 g^{-1}	$\frac{\text{Total leaf size}}{\text{Total biomass}}$	Per dry mass investment in leaf, light capture, and enhanced growth [50]
Leaf dry matter content	LDMC	g g^{-1}	$\frac{\text{Leaf dry weight}}{\text{Leaf fresh weight}}$	Cost of leaf construction and potential growth rate [51]
Leaf mass fraction	LMF	g g^{-1}	$\frac{\text{Leaf biomass}}{\text{Total biomass}}$	Per allocation of resources to optimize light capture [52]
Specific stem length	SSL	cm g^{-1}	$\frac{\text{Stem length}}{\text{Stem biomass}}$	Per dry mass stem investment in stem length, trade-off between stem expansion, and stability [53]
Stem dry matter content	SDMC	g g^{-1}	$\frac{\text{Stem dry weight}}{\text{Stem fresh weight}}$	Stem construction cost, xylem conductance, and photosynthetic potential [54]
Stem mass fraction	SMF	g g^{-1}	$\frac{\text{Stem biomass}}{\text{Total biomass}}$	Allocation of biomass to stem development and growth towards direct sunlight [52]
Specific root length	SRL	cm g^{-1}	$\frac{\text{Root length}}{\text{Root biomass}}$	Per dry mass root investment in root length and potential relative growth rate [33]
Root dry matter content	RDMC	g g^{-1}	$\frac{\text{Root dry weight}}{\text{Root fresh weight}}$	Cost of root construction, a proxy of root tissue density [55], related to potential relative growth rate [35]
Root mass fraction	RMF	g g^{-1}	$\frac{\text{Root biomass}}{\text{Total biomass}}$	Extract deeper soil water and avoid drought [52]

2.4. Statistical Analysis

In order to answer the first question, which traits or trait sets differentiate lianas from trees at the seedling stage, linear mixed models (lmer function of 'LME4′ package) were fitted with the functional group (liana or tree) as a categorical variable and the species as a random effect. To control the effect caused by plant size, we put individual total mass as a confounding effect in the model. Whenever a trait was found to be significantly different between lianas and trees, Tukey post-hoc tests were conducted with the R/EMMEANS package.

Considering that most traits were highly correlated (Table S1_1, Table S1_2 and Table S1_3) and the difference between lianas and trees may be species-specific [56], we then ran a principal component analysis (PCA) using species-level trait means. PCA scores of the first three axes accounting for 74% of the total variance, rather than the original trait values, were further used in a hierarchical clustering analysis to determine whether lianas and trees can be divided into two big clusters. The resulting clusters reflected species-level trait differences and differences between clusters are indicated by branch length.

After different clusters were identified, linear mixed models were fitted for each trait to examine trait differences among clusters. Within each single trait model, a trait was selected as the response variable, 'cluster' was the fixed effect, and species was a random effect. To control the effect caused by plant size, we also put individuals' total mass as a confounding effect in the model. Whenever a trait was found to be significantly different between clusters, we ran a Tukey's post-hoc test to identify the differences between clusters.

Species-specific traits are often related to their habitat specialization properties, e.g., early- versus late-successional species [57]. Thus, to further examine the differences between/among tree and liana species that fell into different clusters, we classified species into specialists of different regeneration guilds based on the methodology of [58]. This method requires species abundance in two habitats, e.g., old- and second-growth forests. Here we used the data of trees [59] and lianas (W. Chanthorn, unpublished data) from second-growth forest plots located in the same landscape as the MSP [60]. The species were classified into old-growth forest specialists (OG), second-growth forest specialists (SG) and Generalists occurring in both forest types, based on their relative abundance in secondary and old-growth forests, respectively. Compared to OG specialists, SG specialists are reported as shade intolerant species capable of growing faster with fast resource acquisition and rapid growth rates.

For all analyses, data were transformed when necessary to meet the assumptions of the statistical tests. All analyses were conducted using R v.3.6.0.

3. Results

When lianas and trees were treated as two separate functional groups, only two traits showed significant differences. Lianas had higher values for both SLA ($\chi^2 = 11.36$, $p \leq 0.001$, tree vs. liana, t = -3.370, $p = 0.0010$) and SSL ($\chi^2 = 54.46$, $p \leq 0.001$, tree. vs. liana, t = -7.378, $p \leq 0.001$) compared to trees (Table S2, Figure 1).

Clustering species based on the similarity of all considered traits (first three PC axes) resulted in two main clusters (Figure 2). One cluster was represented by 28 liana species (53% of all liana species) and 23 tree species, and the other was dominated by 77 tree species (77% of all tree species) and the remaining 25 liana species (Table 2). The clusters showed significant differences in eight of the eleven traits measured (Table S4). The tree-dominated cluster was characterized by significantly smaller SLA (182 ± 3.74 $cm^2\ g^{-1}$, marginal mean ± SE), LAR (50 ± 1.11 $cm^2\ g^{-1}$), SSL (18.0 ± 0.40 $cm\ g^{-1}$), SRL (12.3 ± 0.28 $cm\ g^{-1}$), but higher dry matter content (i.e. LDMC, SDMC, and RDMC) than those of the liana dominated cluster.

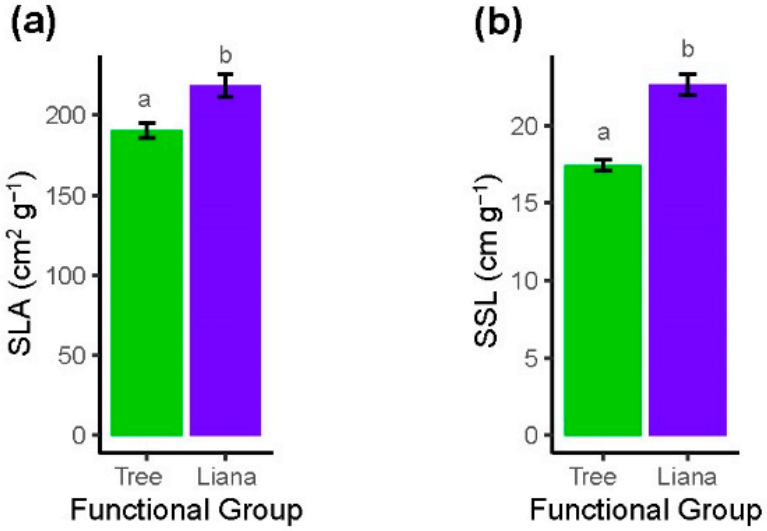

Figure 1. Trait averages of functional groups of lianas and trees. Bars represent marginal means and error bars show SE (95% confidence level) for (**a**) specific leaf area (SLA) and (**b**) specific stem length (SSL). Letters at the top of bars indicate significant ($p < 0.05$) differences among different clusters based on Tukey's HSD tests.

Table 2. Summary of species classification in two clusters. Cluster refers to the classification of species based on all traits. Habits refer to the functional group of trees or lianas, OG indicates species classified as specialists of old-growth forests, SG indicates species classified as specialists of secondary-growth forests, Generalist indicates species are specialists in both types of forests, Too-rare indicates species that do not have enough individuals for classification.

Cluster	Habits	Total No.	OG	SG	Generalist	Too-Rare
Tree-dominated	Tree	77	58	9	5	5
	Liana	25	10	4	7	4
Liana-dominated	Tree	23	13	1	6	3
	Liana	28	17	0	6	5

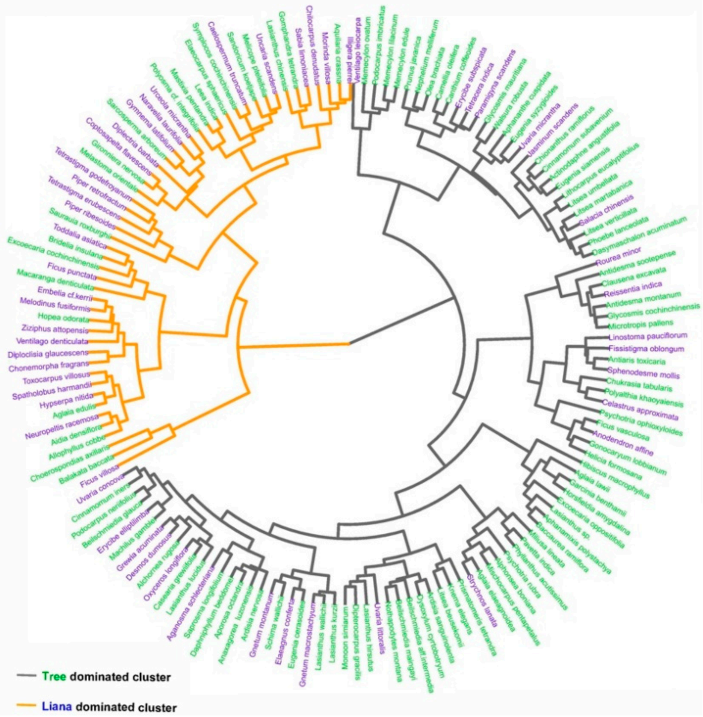

Figure 2. Clustering of species by all functional traits. Colors of branches indicate clusters: tree-dominated cluster in dark grey and liana-dominated cluster in brown. Species color indicates tree or liana: trees in green and lianas in blue.

Matter content among leaf (LDMC, 0.38 ± 0.01 g g^{-1}), stem (SDMC, 0.48 ± 0.01 g g^{-1}), and root (0.52 ± 0.01 g g^{-1}) and greater RMF (0.27 ± 0.01 g g^{-1}). The liana-dominated cluster was characterized by a far bigger SLA (243 ± 7.27 cm^2 g^{-1}), a much higher LAR (69.4 ± 2.37 cm2 g^{-1}), a greater SSL (21.8 ± 0.75 cm g^{-1}) and SRL (14.1 ± 0.75 cm g^{-1}), but a significantly lower LDMC (0.30 ± 0.01 g g^{-1}), SDMC (0.40 ± 0.01 g g^{-1}), RDMC (0.46 ± 0.01 g g^{-1}), and RMF (0.23 ± 0.01 g g^{-1}) (Figure 3).

The classification of species based on their habitat specialization revealed that the majority of old-forest specialist (OG) tree species (58 out of 71) fell in the tree-dominated cluster (Table 2). The same pattern was found for OG lianas and a larger number of them (17 out of 27) were found in the liana-dominated clusters. For the ten tree species that preferred secondary forest, nine fell in the tree-dominated cluster and one in the liana-dominated cluster. Only four liana species were classified as specialists of a secondary forest and they all fell in the tree-dominated cluster. The distribution of the generalist species of both lianas and trees in two clusters were almost the same. Five trees and six lianas were found in the tree-dominated cluster and six species of lianas and one tree fell in the liana-dominated cluster. The rest of the species failed to be classified due to low abundance, and thus, are referred to as too-rare species.

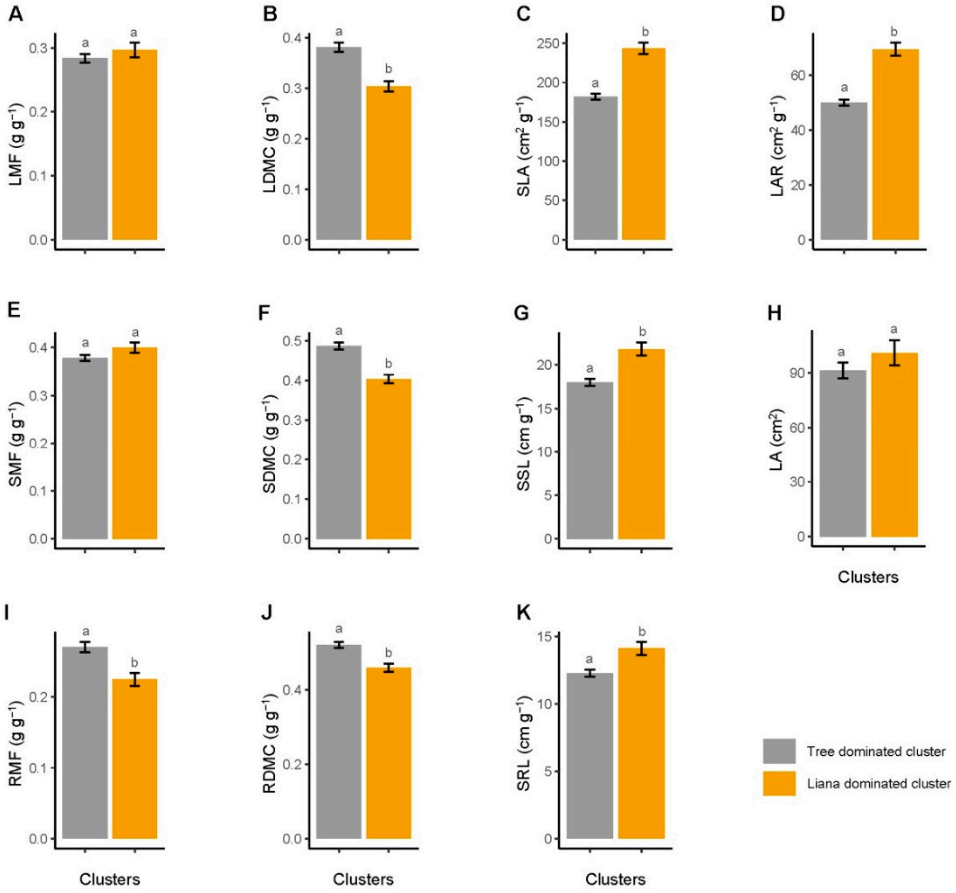

Figure 3. Trait averages of the species clusters as identified in Figure 2. Bars represent marginal means and error bars show SE (95% confidence level) for (**A**) leaf mass fraction (LMF), (**B**) leaf dry matter content (LDMC), (**C**) specific leaf area (SLA), (**D**) leaf area ratio (LAR), (**E**) stem mass fraction (SMF), (**F**) stem dry matter content (SDMC), (**G**) specific stem length(SSL), (**H**) leaf area size (LA), (**I**) root mass fraction (RMF), (**J**) root dry matter content (RDMC), and (**K**) specific root length (SRL). Letters at the top of bars indicate significant (p < 0.05) differences among different clusters based on Tukey's HSD test.

4. Discussion

We used a whole-plant analysis of a large number of liana and tree seedlings co-occurring in a single seedling assemblage to test whether liana seedlings possess a set of functional traits located on the resource acquisitive end of the "fast-slow" growth spectrum which may make them capable of outperforming trees in the dry season. Two key discoveries were made. First, consistent with current beliefs, lianas, as a whole, did have a few traits which suggested a high potential growth rate compared to trees; second, as a complement to common expectations, when most of the traits were considered, around half of liana species were located on the resource conservative end of the "fast-slow" growth spectrum. The observation that some trees shared the same trait strategies with these lianas and almost half of lianas were functionally similar to most trees implies that lianas' competitive advantages over trees are not universal but are species-dependent or species' life stage-dependent.

4.1. Direct Traits Comparison between Lianas and Trees

It has long been thought that lianas have evolved independently multiple times in ways which have led them to perform better than trees in dry tropical forest conditions [61].

For example, lianas tend to have a higher SLA than trees [14,37], which typically makes them fall on the acquisitive end of the resource use spectrum. Our finding that lianas had a higher SLA than co-occurring trees is consistent with this trend. Most lianas' full life cycle may only be completed when they reach the canopy [62], but they still have a self-supporting and free-standing early life stage [63]. Though little is known about the switch between the self-supporting and climbing phases, a fast pace of vertical expansion or bending is necessary in the search for support [64,65]. Having a higher SSL is an easy way to gain such support [66], although it may adversely affect its self-support and stem stability [67]; however, once support is gained, the longer stem or bigger SSL, as compared with trees, pays off.

4.2. Pattern of Biomass Allocation between Clusters

Strategies for avoiding or tolerating drought stress in the dry season are critical for plants to survive in seasonal tropical forests. Here, we found that most tree seedlings (77 of 100) allocated significantly more biomass to their roots in the dry season than to leaves and stems, which is consistent with the prediction of optimal partitioning theory [52] under a drought stress scenario [68]. Optimal partitioning theory suggests that allocation patterns of biomass to different organs reflect species strategies for optimizing performance [69]; thus, when water is limited, species should allocate more biomass to roots. A larger root biomass fraction leads to a longer root length and/or a bigger surface area in the soil profile [70], which helps plants strengthen their drought tolerance. For example, Markesteijn and Poorter [71] revealed that drought tolerance strategies involving a high investment in the root system may exist in other species of different life forms.

The findings that nearly half of liana species (25 of 53) shared the same pattern of biomass allocation to roots as most trees did (Table 2), together with the lack of difference found in the biomass allocation patterns between lianas and trees, may simply imply that partitioning more biomass to roots is a common strategy for most woody species to overcome drought challenges in seasonal tropical forests. Our finding that species in the liana-dominated cluster have lower RMF was contrary to previous findings that lianas were capable of accessing and efficiently using water [72], especially deep sources [73,74]; however, consistent with a recent finding of a lack of evidence of deeper root penetration by adult lianas as compared to trees, with no clear differences in root mass allocation [75].

4.3. Pattern of Dry Matter Content and per Dry Mass Unit Investment between Clusters

Dry matter content has been regarded as a key predictor of plant strategies [52,76]. Lower dry matter content enables rapid resource acquisition and processing and thus, promotes fast growth, as the construction cost is low [77]. Interestingly, we found that species in the liana-dominated cluster were characterized by correlated, lower dry matter content among leaf, stem, and root compared with those in the tree-dominated cluster, implying that these lianas (28 of 53 liana species, and 17 of 27 old-growth forest liana specialists) were indeed capable of growing faster than the majority of trees. Thus, this finding is partly consistent with predictions of the seasonal growth advantage hypothesis of lianas [55]. Yet, considering that almost the same number of lianas fell in the tree-dominated cluster, we propose that lianas may somehow also support the "fast–slow" plant spectrum hypothesis [78].

The majority of tree species fell in the tree-dominated cluster, characterized by a pattern of a high content of dry matter in both above- and below-ground organs, implying they were located on the slow end of the growth spectrum and being indicative of conservative resource use [79]. This finding was further confirmed by our classification of most of these species (58 of 71) as OG specialists (sensu [58]). A slow growth rate for OG specialists has been reported widely in seedlings [80] and saplings [81]. Interestingly, the majority of lianas in both clusters are also OG, not SG or generalists, as predicted by SGA [82]. This may suggest the current method of habitat specialization classification of lianas based on their occurrence in forest types needs to be carefully checked in the future, considering that lianas are mainly gap- or disturbance-preferred species, as previously suggested for adult lianas [55], and gaps are more characteristic of OG forests than of SG forests in the stem-exclusion stage [59].

Higher per unit of dry mass used in organs (leaves, stems, and roots) indicates strategies of resource optimization. Both higher SLA and LAR in species of the liana-dominated cluster suggested they optimized their already limited dry leaf mass to capture light [67]. SLA and LAR are classic traits which are thought to be of paramount importance for plant performance [49]. The higher SLA and LAR of lianas in this cluster enhanced their resource acquisition and resource use efficiency, and thus, were associated with fast growth, which has been found for both adult [15,83] and seedling lianas [18]. SRL is the below-ground analogue of SLA [84,85], reflecting the per mass unit of dry root mass used to uptake soil nutrients and water [86]. Positive correlations that have been found between SRL and relative growth rates [32,33] suggests that SRL also played a role in whole-plant economics.

We acknowledge the limitations of our focus on the seedling stage and the classification of species based on habitat affinities. Trait values are likely to differ between seedlings and adults, but seedlings are a gateway to future development and performance, and so this stage must have implications for forest dynamics. Nevertheless, as our trait data were based on a comprehensive seedling dynamic monitoring network, any differences observed should indicate evolutionarily driven intrinsic trait differences between lianas and trees.

5. Conclusions

This study has demonstrated that liana seedlings, as a whole, were significantly different from trees with regard to two traits: one indicating light capture optimization (SLA) and the other indicating a stem length−stability trade-off (SSL). Taking all traits under consideration, we found that slightly more than half the lianas, together with a few trees, fell into a "fast" cluster. The majority of trees and few lianas fell into a "slow" cluster. Thus, lianas and trees had a considerable overlap in characteristics, implying both tree and liana species can fall in a major trait spectrum, represented by species with acquisitive trait values on one end versus conservative traits values on the other end of the spectrum. The seasonal growth advantage of lianas over trees, based on the fact that lianas are supposed to be "fast" and trees are supposed to be "slow", may therefore not apply to all lianas and all tree species at least at the seedling stage. Lastly, our study suggests that there is an acute need to better understand liana life histories, especially at the early free-standing stage.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13070990/s1, Table S1_1 Rho values of Spearman's correlations between seedling traits of all woody species (liana and tree combined). Table S1_2 Rho values of Spearman's correlations between seedling traits of tree species. Table S1_3 Rho values of Spearman's correlations between seedling traits of liana species. Table S2 linear mixed model results for the differences between lianas and trees. Table S3 linear mixed model results for the differences between multivariate clusters. Table S4 summaries of species collected for functional traits. Figure S1. PCA analysis of traits for both lianas and tree seedling spcies. Names indicated species of lianas and trees.

Author Contributions: Conceptualization, Z.S., N.P., A.S. and L.L.; methodology, Z.S., N.P., A.S. and L.L.; writing—original draft preparation, Z.S.; writing—review and editing, Z.S., N.P., A.S., L.L., W.C., W.Y.B., A.N. and F.B. All authors have read and agreed to the published version of the manuscript.

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