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# A BACKGROUND ABOUT LEAF ECONOMIC SPECTRUM IN TROPICAL VEGETATION

# UM PANORAMA SOBRE O ESPECTRO ECONÔMICO DAS FOLHAS NA VEGETAÇÃO TROPICAL

# UN PANORAMA SOBRE EL ESPECTRO ECONÓMICO DE LAS HOJAS EN LA VEGETACIÓN TROPICAL

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## ABSTRACT

The Leaf Economic Spectrum (LES) describes the different strategies of leaves in capturing and using resources, ranging from fast-growing species with short-lived leaves to those that adopt a more conservative approach, investing in durable and efficient leaves in the use of resources. The objective of this systematic review is to quantify and investigate studies on the Leaf Economic Spectrum (LES) in tropical vegetation, analyzing the association with functional traits, their geographic distribution, vegetation types, plant life habits and the main biotic and abiotic factors that shape these characteristics. The current study performed a systematic review of the indexed databases (Web of Science, Scopus) in the last 20 years (2004-2024). We identified 160 publications. The discovery of articles investigating leaf functional properties and the leaf economic spectrum in the tropics, the topic of our systematic review, has grown considerably over the past eight years. We identified a dominant association of studies published with the Neotropical region. The most common functional leaf attributes studied in the framework of LES (e.g. specific leaf area, leaf nitrogen concentration and photosynthetic capacity) were all found to be associated with the plant growth rate in our research. The distribution of LES research shows that LES studies of tropical vegetation cover a relatively higher amount of sampling for tropical and subtropical dry and moist broadleaf forests than others. Despite the advances, significant knowledge gaps remain, particularly regarding physiological traits and understudied plant groups such as lianas, epiphytes, and bryophytes. Future research efforts must prioritize a broader range of life forms and functional traits, integrating eco-physiological and biogeochemical approaches to better predict the responses of tropical vegetation to environmental changes and to support more effective conservation and restoration strategies.

**Keywords:** Environmental Filters. Functional Traits. Nitrogen. Phosphorus. Specific Leaf Area. Systematic Review. Tropical Forests.

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**RESUMO**
O Espectro Econômico das Folhas (Leaf Economic Spectrum – LES) descreve as diferentes estratégias das folhas na captura e no uso de recursos, variando desde espécies de crescimento rápido, com folhas de curta duração, até aquelas que adotam uma abordagem mais conservadora, investindo em folhas duráveis e eficientes no uso de recursos. O objetivo desta revisão sistemática é quantificar e investigar estudos sobre o Espectro Econômico das Folhas (LES) na vegetação tropical, analisando sua associação com atributos funcionais, a distribuição geográfica, os tipos de vegetação, os hábitos de vida das plantas e os principais fatores bióticos e abióticos que moldam essas características. O presente estudo realizou uma revisão sistemática em bases de dados indexadas (Web of Science, Scopus) nos últimos 20 anos (2004–2024). Foram identificadas 160 publicações. A produção de artigos que investigam propriedades funcionais das folhas e o espectro econômico das folhas nos trópicos, tema desta revisão sistemática, cresceu consideravelmente nos últimos oito anos. Identificou-se uma associação dominante de estudos publicados com a região Neotropical. Os atributos funcionais foliares mais comumente estudados no âmbito do LES (por exemplo, área foliar específica, concentração de nitrogênio foliar e capacidade fotossintética) mostraram-se associados à taxa de crescimento das plantas em nossa análise. A distribuição das pesquisas sobre o LES indica que os estudos em vegetação tropical apresentam maior esforço amostral em florestas tropicais e subtropicais secas e úmidas de folhas largas em comparação com outros tipos de vegetação. Apesar dos avanços, permanecem lacunas significativas de conhecimento, especialmente no que se refere a atributos fisiológicos e a grupos vegetais pouco estudados, como lianas, epífitas e briófitas. Pesquisas futuras devem priorizar uma gama mais ampla de formas de vida e atributos funcionais, integrando abordagens ecofisiológicas e biogeoquímicas para melhor prever as respostas da vegetação tropical às mudanças ambientais e apoiar estratégias mais eficazes de conservação e restauração.

**Palavras-chave:** Filtros Ambientais. Atributos Funcionais. Nitrogênio. Fósforo. Área Foliar Específica. Revisão Sistemática. Florestas Tropicais.

**RESUMEN**
El Espectro Económico de las Hojas (Leaf Economic Spectrum – LES) describe las diferentes estrategias de las hojas para capturar y utilizar recursos, que van desde especies de rápido crecimiento con hojas de corta vida hasta aquellas que adoptan un enfoque más conservador, invirtiendo en hojas duraderas y eficientes en el uso de recursos. El objetivo de esta revisión sistemática es cuantificar e investigar los estudios sobre el Espectro Económico de las Hojas (LES) en la vegetación tropical, analizando su asociación con rasgos funcionales, la distribución geográfica, los tipos de vegetación, los hábitos de vida de las plantas y los principales factores bióticos y abióticos que configuran estas características. El presente estudio realizó una revisión sistemática de bases de datos indexadas (Web of Science, Scopus) de los últimos 20 años (2004–2024). Se identificaron 160 publicaciones. La producción de artículos que investigan las propiedades funcionales de las hojas y el espectro económico de las hojas en los trópicos, tema de esta revisión sistemática, ha crecido considerablemente en los últimos ocho años. Se identificó una asociación dominante de los estudios publicados con la región Neotropical. Los atributos funcionales foliares más comúnmente estudiados en el marco del LES (por ejemplo, área foliar específica, concentración de nitrógeno foliar y capacidad fotosintética) se encontraron asociados con la tasa de crecimiento de las plantas en nuestro análisis. La distribución de la investigación sobre el LES muestra que los estudios de vegetación tropical presentan un mayor esfuerzo de muestreo en bosques tropicales y subtropicales secos y húmedos de hojas anchas en

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comparación con otros tipos de vegetación. A pesar de los avances, persisten importantes vacíos de conocimiento, especialmente en relación con los rasgos fisiológicos y con grupos vegetales poco estudiados, como lianas, epífitas y briófitas. Los esfuerzos de investigación futuros deben priorizar una gama más amplia de formas de vida y rasgos funcionales, integrando enfoques ecofisiológicos y biogeoquímicos para predecir mejor las respuestas de la vegetación tropical a los cambios ambientales y apoyar estrategias más eficaces de conservación y restauración.

**Palabras clave:** Filtros Ambientales. Rasgos Funcionales. Nitrógeno. Fósforo. Área Foliar Específica. Revisión Sistemática. Bosques Tropicales.

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## 1 INTRODUCTION

Plants exhibit high phenotypic plasticity, developing effective adaptive strategies to tolerate environmental variations and unfavorable ecological interactions (Niijhout, 2003; Schneider, 2022). Within this context, the Leaf Economic Spectrum (LES) has emerged as a fundamental theoretical framework for understanding how leaf functional strategies mediate resource acquisition and conservation in response to environmental variations (Wright et al., 2004; Díaz et al., 2016). LES describes a continuous gradient of leaf attributes reflecting a trade-off between in obtaining resources, ranging from species with short-lived leaves, high photosynthesis rates, and fast growth that are less conservative to more conservative species with more durable leaves and greater efficiency in resource use over time (Wright et al., 2004).

In tropical ecosystems, where high environmental variability directly influences species' adaptation strategies, this concept is particularly relevant (Braga et al., 2016; Vlemincky et al., 2021; Ferrero et al., 2022). The diversity of tropical vegetation, including forests (dry and wet), savannas, and wetlands (Barlow et al., 2018), provides an ideal setting to investigate how biotic and abiotic factors shape plant functional traits (Malhi et al., 2014; Lapola et al., 2023). Functional traits associated across the LES continuum are influenced by environmental gradients such as temperature, water availability, soil fertility, and altitudinal elevation, which act as selective pressures on plant strategies (Götzenberger et al., 2011; Garnier et al., 2016; de Bello et al., 2021). In low-temperature, high-altitude environments, for example, plants typically have a low rate of photosynthesis, low nitrogen concentration, small specific leaf area, and slow growth to minimize water loss and merit resource use efficiency (van der Sande et al., 2016; Matesanz et al., 2021; Sanaphre-Villanueva et al., 2022). In hot and humid regions, plants present inverse characteristics, with more delicate leaves and higher photosynthetic rates, which promotes growth and light capture (Wright et al., 2004).

Functional traits of leaves can vary between individuals of different species (interspecific variation), reflecting distinct evolutionary adaptations, and between groups of individuals within the same species (intraspecific variation), reflecting changes in local conditions and/or ecological interactions (Araujo et al., 2021; Ferrero et al., 2022). Studies on the variation of functional traits in individuals of the same species have been widely studied, especially in tropical ecosystems, where competition for resources and microclimatic variations in the environment cause these individuals to develop different adaptive strategies to ensure the survival and perpetuation of their descendants (Albert et al., 2010; Hulshof &

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Swenson, 2010). For example, individuals of the same species may have thicker leaves rich in secondary compounds in areas with high herbivory pressure, while in environments with greater availability of light and nutrients, they may develop thinner leaves with a high specific leaf area (Lambers et al., 2008; Aguilar-Peralta et al., 2022).

The objective of this systematic review is to quantify and investigate studies on the leaf economic spectrum (LES) in tropical vegetation. Specifically, we aim to identify studies that focus on LES and its associated functional traits, considering their geographic distribution, vegetation type, plant life habits, and key biotic and abiotic factors influencing these traits. By bringing together this information, we aim to provide a comprehensive overview of how LES-related traits have been studied in tropical ecosystems. Ultimately, we hope that this will contribute to a better understanding of plant ecological strategies and their potential responses to environmental change.

## 2 METHODOLOGY

### 2.1 SYSTEMATIC LITERATURE SEARCH

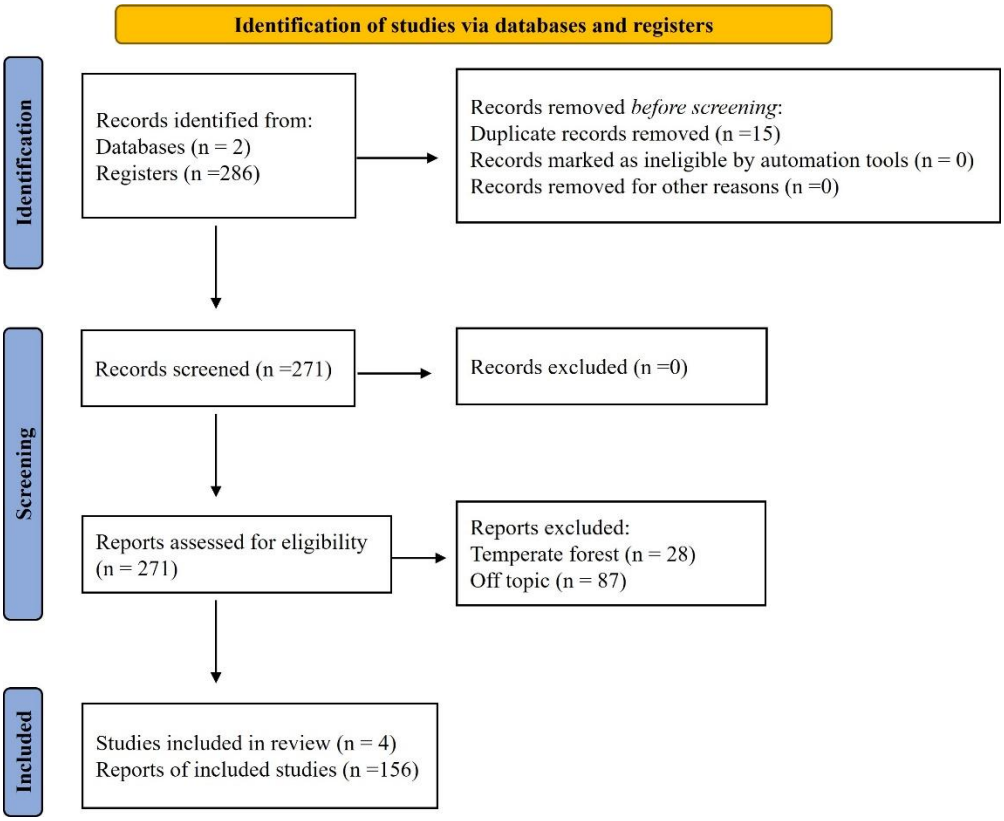
The bibliographic search was conducted in January 2025, targeting articles indexed in the Web of Science and Scopus databases. We employed the search terms: “Leaf economic* spectrum” AND “Tropical Forest” across titles, abstracts, and keywords. We did not limit the chronological period of the search. All selected articles were written in English and presented results that address the functional characteristics related to the leaf economic spectrum (both at the species and community levels) and community assembly in tropical forests. In the second stage, the retrieved articles were screened to ensure relevance. Duplicate records and studies that did not meet the pre-established inclusion criteria were removed using the Rayyan platform (Ouzzani et al., 2016) and the Mendeley reference manager. Articles that did not have LES as their central theme were excluded.

In total, 286 publications were collected, from which, after the screening process, a set of 160 articles were selected for analysis (Figure 1, Appendix S1). Data were extracted from these scientific articles, such as: year of publication, authors, the country where the study was conducted, area of knowledge, vegetation type, life form (wood or herbaceous), ecological group (tree, shrub, liana, fern) and results regarding the economic spectrum of the leaf (specific leaf area, leaf nitrogen concentration, leaf phosphorus concentration, leaf lifespan, photosynthetic capacity, and nocturnal respiration rate).

The annual publication growth rate was calculated based on the percentage change between the current number of publications and the previous number. The following formula was used: Publication growth rate=(current value- previous value)/( previous value)*100.

**Figure 1**

*Flowchart of the research protocol and articles included in the systematic literature review on the economic spectrum of leaves in tropical forests (adapted from Haddaway et al., 2022), from 2009 to 2024*




## 3 RESULTS AND DISCUSSION

### 3.1 CHRONOLOGICAL EVOLUTION OF STUDIES ON LES

Over the last ten years (2014 – 2024), there has been a gradual increase in the number of scientific publications evaluating leaf functional traits through a multidimensional approach and their relationship with LES in tropical vegetation (Figure 2). This growth trend has intensified since 2015, with the highest number of publications recorded in 2022.

However, the annual growth rate for publications changes throughout the years explored, with alternating phases of exponential growth and sharp drops in the relative number of scientific publications. Notably, 2010 is the year with the greatest relative increase,

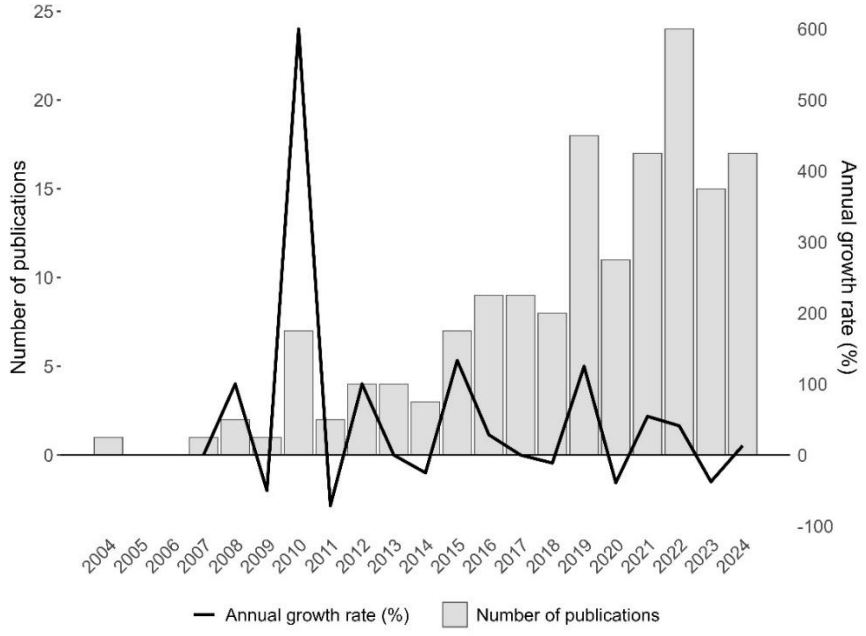
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while subsequent years show smaller differences, thereby indicating the gradual concentration of the research field.

Overall, the results suggest a progressive increase in scientific production, with occasional fluctuations, possibly associated with external factors, such as research funding, academic interest in the topic, and changes in research funding (Millones-Gómez et al., 2021; Ou et al., 2024). Although studies addressing different resource trade-off strategies have been ongoing since the 1970s - when Grime defined the competitive, stress-tolerant, ruderal (CSR) theory (Grime, 1974, 1977, 2001) (reviewed by Grime & Pierce, 2012). It was not until 2004 that Wright and collaborators related the functional characteristics of leaves and resource trade-off strategies to this central idea of “economy” for resource allocation, grouping the characteristics that are correlated into groups with different strategies for resource investment (Wright et al., 2004; Reich, 2014; Pierce et al., 2017). The growing volume of publications observed in recent years underscores the increasing relevance of the LES framework and suggests a continued expansion of research on plant resource-use strategies in tropical ecosystems.

**Figure 2**

*Number of published scientific articles about the leaf economic spectrum in tropical vegetation from 2004 to 2024. The gray bars represent the absolute count of publications per year, while the black line indicates the percentage change from the previous year (N=160)*



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### 3.2 GLOBAL DISTRIBUTION OF STUDIES ON LES

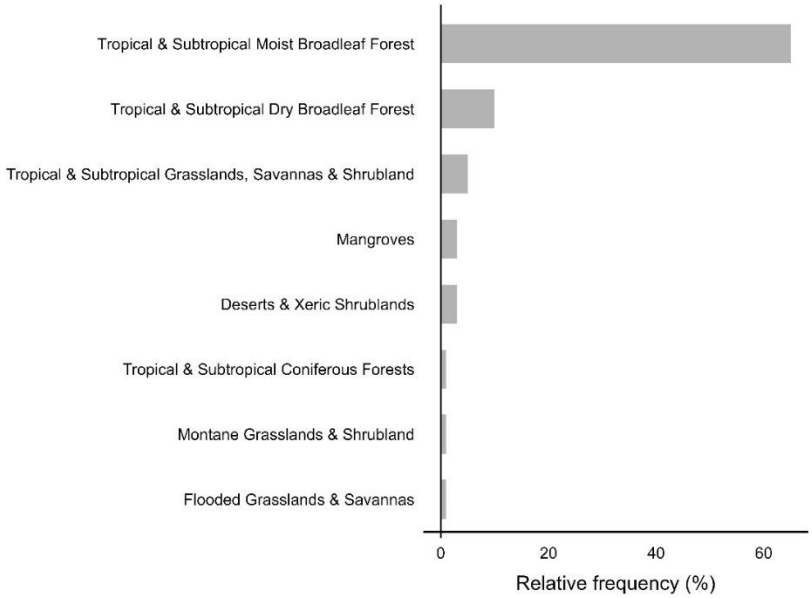
On the global scale, scientific publications did not show a homogeneous distribution among countries with tropical vegetation. Research efforts were mainly focused on the tropical part of the Asian continent, which played a significant role, representing 33.5% of the total data, and in the Neotropical region, with substantial contributions from Brazil (15%), Panama (9.5%) and Mexico (7.7%). In contrast, the low occurrence of researched areas in the African continent and Oceania is notable, representing only 6% to 2.4% of the total. This imbalance in research coverage is not exclusive to studies on functional attributes. When analyzing the anthropogenic influence on tropical forests, Malhi et al. (2014) already highlighted this disparity in forest types and emphasized the need to expand study areas. Similarly, Loureiro et al. (2023), identified the same pattern in scientific research distribution when assessing the functional traits of plants in forest restoration areas, suggesting that this research gap extends beyond leaf economics studies to the broader spectrum of functional data.

When examining the distribution of studies across the different ecoregions, we observed that 68% of the scientific articles were conducted in tropical and subtropical moist broadleaf forests, while just over 23% occurred in dry, desert, and floodplain (Figure 3). The greater concentration of studies in humid ecoregions can be explained by two factors: the inhomogeneous distribution of research areas since more than 58% (n=68) of these studies were conducted in Brazil, China, and Panama; and/or the strong interest of the academic community in the high diversity, adaptation, and resilience of the species present in these environments (Malhi et al., 2014; Zhang et al., 2022).

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**Figure 3**

*Relative frequency of ecoregions (N= 173) reported in studies on the leaf economic spectrum in tropical vegetation published between the years 2004 and 2024*




In monodominant forests, in which a single tree species represents more than 50% proportion of basal area and abundance (Hart et al., 1989; Peh et al., 2011), the factors that modulate leaf functional traits are not fully understood, but there is evidence that they are related to the absence of disturbance, shade tolerance, soil nutrient availability, as well as evolutionary and spatial characteristics (Connell & Lowman, 1989; Hart et al., 1989; Peh et al., 2011; Brookshire & Thomas, 2013; Nascimento et al., 2017; Araújo et al., 2022).

Despite the ecological importance of these forest formations, the literature on the subject remains limited. In our research, only one study appeared that explicitly examined the functional leaf characteristics related to LES in monodominant species. When evaluating the functional leaf characteristics of Brosimum rubescens Taub. (Moraceae), Araújo et al. (2022) observed that, in monodominant forests in the Amazon, this species presents functional characteristics that favor the acquisition of resources, such as larger specific leaf area, stomatal size, and maximum stomatal aperture. These attributes promote high photosynthetic rates and faster growth, favoring its dominance. On the other hand, in mixed forests, B. rubescens adopts an opposite strategy, characterized by functional traits associated with resource conservation, such as thicker adaxial cuticle, palisade and spongy parenchyma, and thicker leaves. These adaptations are often related to drought resistance and greater water use efficiency (Gratani et al. 2006). The ability of this species to adjust its

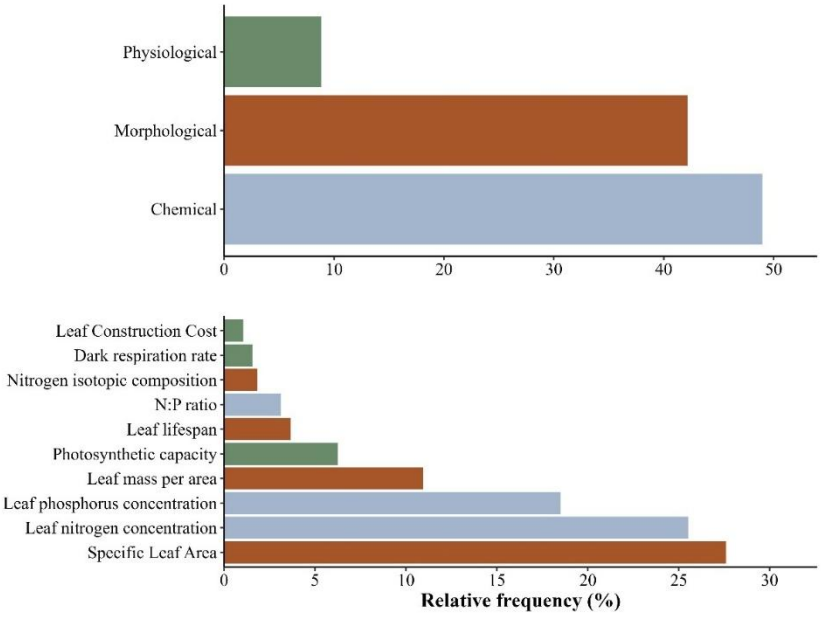
functional traits according to the environment reflects its high phenotypic plasticity, allowing it to adapt to different ecological conditions and contributing to its persistence and dominance in certain areas (Araújo et al., 2022).

### 3.3 FUNCTIONAL TRAITS ASSOCIATED WITH LES

Our data indicates that studies on LES prioritize the evaluation of structural traits and nutritional composition, representing more than 90% of the attributes analyzed (Figure 4A). This discrepancy may be directly related to the specific objectives of each research or the difficulty and high experimental costs involved in providing physiological data. The predominance of chemicals and morphological traits - particularly specific leaf area and nitrogen and phosphorus concentrations (Figure 4B) in scientific literature can be explained by their strong relationship with plant productivity and resource use efficiency. These variables are widely used to assess plant growth strategies and adaptation to varying environmental conditions (Wright et al., 2004; Reich et al., 2014; Cheng et al., 2016) and are highly responsive to environmental gradients (Wright & Westoby, 2001; Wright et al., 2004; Reich & Oleksy, 2004).

**Figure 4**

*Relative frequency of leaf functional traits (N=384) in studies on the leaf economic spectrum. The top graphic (A) shows the frequency of traits grouped into three categories: physiological (green), morphological (brown) and chemical (blue). The bottom graphic (B) details the frequency of specific traits within each of those categories*



Although the key attributes proposed in the LES model (Wright et al., 2004) offer valuable insights into plant resource acquisition strategies, numerous other traits also contribute substantially to plant functioning. Of the total number of leaf attributes evaluated in the articles surveyed in this review, 54% (N=453) refer to attributes that are not directly linked to LES. Attributes such as leaf hardness and density, dark respiration rate, efficiency in the use of photosynthetic nitrogen and phosphorus, among others, are not part of the main axis of LES (Kikuzawa et al., 2006; Chen et al., 2020), but many studies add these variables to the methodology because they are important in adding biochemical, physiological and defense information as they play roles correlated with the main variables of the model (Loureiro et al., 2023; Freitas et al., 2024).

Notably, traits related to leaf construction cost, dark respiration, and nitrogen isotopic composition monitoring indicate a gap in the understanding of plant energy efficiency and metabolism. This knowledge gap is particularly relevant considering that several studies suggest that traits such as photosynthetic capacity, nitrogen and phosphorus concentrations, specific leaf area, and leaf lifespan are governed by LES and guide leaf trait combinations in an economic spectrum (Wright et al., 2004; Chen et al., 2020). Nutrient concentrations and photosynthetic rate are positively correlated with specific leaf areas and negatively related to leaf lifespan (Wright et al., 2004; Díaz et al., 2016). Thus, species with larger, thinner leaves tend to exhibit higher resource acquisition and growth rates over shorter lifespans, whereas species with conservative traits typically show slower growth rates and higher investment in leaf construction (Reich et al., 1997; Wright et al., 2004; Díaz et al., 2016).

Despite being less frequently studied, leaf construction cost is a fundamental functional trait, as it determines the energy spent by plants to synthesize carbon skeletons and nitrogen compounds (Eamus et al., 1999; Xiao et al., 2018). Fast-growing species tend to have a larger specific leaf area, thinner blades, and lower leaf construction costs compared to slower-growing plants (Li et al., 2011). Such characteristics can be good predictors for evaluating plant resistance to environmental stress (Suárez, 2003, 2005), growth, and survival (Baruch & Goldstein, 1999; Liao et al., 2007; Song et al., 2007; Feng et al., 2008).

Nitrogen is strongly correlated with plant growth and photosynthetic processes, including carboxylation, bioenergetics, and light-harvesting components (Poorter & Evans, 1998), so it is positively related to photosynthetic capacity and photosynthetic nitrogen use efficiency (Feng et al., 2008; Hikosaka, 2014). Xiao et al. (2018) observed that in early successional forests, the cost of leaf construction is lower and inversely proportional to photosynthetic capacity, specific leaf area, and photosynthetic nitrogen use efficiency

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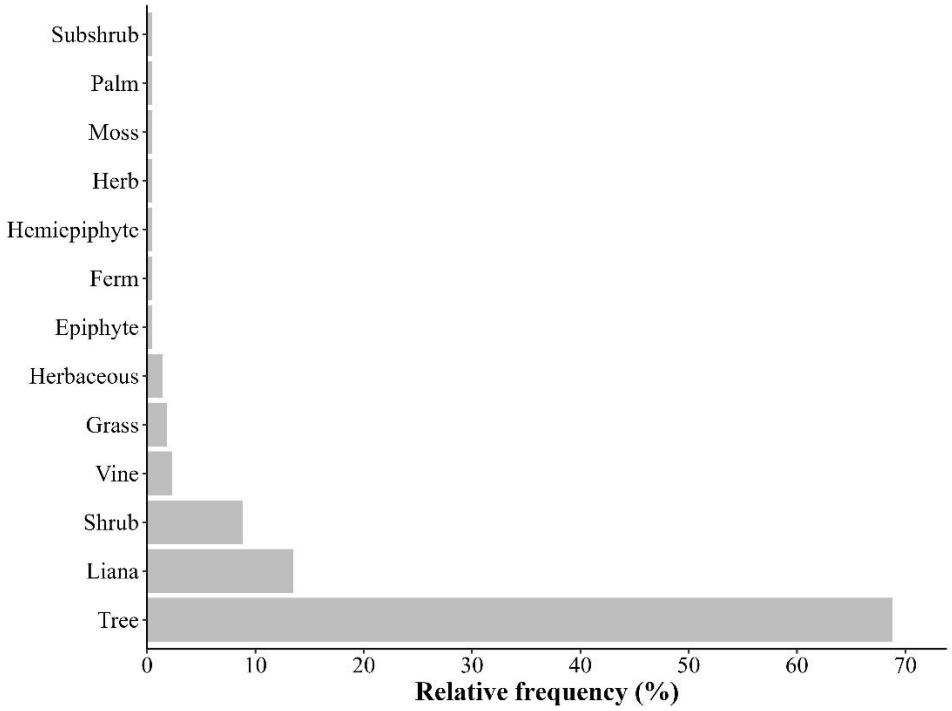
compared to late successional forests. This trend may be related to the change in floristic composition and, consequently, to changes in the functional characteristics of the community.

### 3.4 HOW PLANT LIFE HABIT CHANGES THE TRAITS OF THE LES

Sampling effort and data availability for LES vary considerably among different plant life habits. Arboreal individuals (n= 148) were recorded in approximately 70% of the total articles, wood lianas (climbers; n= 24) and shrubs (n= 19) (Figure 5) accounted for only 14% and 9% of the records, respectively. This discrepancy is mainly due to the greater abundance of trees and the facility of data collection, as the arboreal stratum of a community is widely studied in several fields of plant ecology and physiology.

**Figure 5**

*Relative frequency of plant growth habit (N= 212) reported in studies on the leaf economic spectrum in tropical vegetation published between the years 2004 and 2024*




In contrast, other life forms, such as subshrubs, palms, and non-wood species, were markedly underrepresented in datasets, with the last seven being recorded only once in the research. This low representation may be related to the difficulty in collecting data or to methodological limitations of leaf attributes in these life habits. Bryophytes have often been ignored in conservation actions because they are seen as plants of lesser relevance and complex to identify (Goffinet et al., 2009; Glime, 2017). In addition, groups such as mosses,

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hemiepiphytes and epiphytes have distinct ecological strategies, which may make it difficult for them to adapt to the traditional LES axes (Petter et al., 2015; Wuyun et al., 2024).

Among these underrepresented groups, wood lianas are particularly noteworthy. Their climbing growth form allows them to reach the forest canopy while bypassing the structural constraints faced by understory plants (Wyka et al., 2013; Smith-Martin et al., 2022). Although this group has low diversity and contributes relatively little to the wood biomass of the forest (van der Heijden et al., 2013; Gianoli, 2015; Slot & Winter, 2017), their ecological role is significant. Lianas are often dominant in more open habitats, such as clearings, forest edges, and human-disturbed areas, where their growth strategies give them competitive advantages (Laurence et al., 2001; Schnitzer & Bongers, 2002; Schnitzer, 2005). Understanding how their functional traits influence their growth strategies may help explain the recent increase in their abundance in tropical forests (Schnitzer & Bongers, 2011), especially in disturbed areas and in the process of succession. Regardless of forest type, lianas tend to adopt more acquisitive strategies for resource capture, positioning themselves at the fast end of the LES. (Zhu & Cao, 2010). Typically, lianas are characteristics such as high specific leaf area (low LMA), high nutrient concentrations, higher photosynthetic and respiration rates, lower leaf construction cost per unit area and useful lifespan (Paul & Yavitt, 2011; Zhu & Cao, 2010; Asner & Martin, 2012).

Differences in leaf economic strategies are also observed between plant species with distinct leaf habitats, such as decidual and evergreen trees. Plants with different growth forms exhibit distinct ecophysiological strategies even when coexisting in the same environment (Pimentel et al., 2004; Shi et al., 2015; Yan et al., 2016, Vitória et al., 2018). Regardless of the forest type or growth habit, plant species with deciduous or evergreen leaf habits that coexist have distinct leaf functional characteristics (Huang et al., 2015). Evergreen species generally display lower photosynthetic efficiency, reduced nutrient concentration, smaller specific leaf area, and longer useful lifespan (Reich et al., 1997; Tomlinson et al., 2013; Silva et al., 2019). In contrast, deciduous species are more efficient in capturing resources, with higher efficiency in the photosynthetic rate, larger specific leaf area, lower leaf construction cost, and shorter useful lifespan (Wright et al., 2004; Kröber et al., 2015; de Souza et al., 2020). According to Pandi et al. (2023), deciduous trees, by adopting acquisitive resource-use strategy, exhibit greater competitive advantage over evergreen species in environments without liana colonization (greater specific leaf area and mass-based nitrogen concentration), while evergreen species were more shade tolerant and acclimated better in shaded environments.

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3.5 ENVIRONMENTAL FACTORS SHAPE FOLIAR STRATEGIES

Soil fertility results from the combined effects of physical, chemical, and biological factors that regulate nutrient mobilization and directly influence plant metabolism (Shen et al., 2019; Vitória et al. 2019; Delpiano et al. 2020). In tropical ecosystems, fertile soils favour species with rapid resource-acquisition strategies, while nutrient-poor soils select for species exhibiting more conservative functional traits (Freitas et al., 2024). A study conducted in a subtropical evergreen broadleaves forest in China demonstrated that soil fertility is one of the main factors that influenced the functional response of plants (Shen et al., 2019). The results showed that species adapted to rapid resource acquisition are more abundant in soils rich in phosphorus and potassium, but poor in nitrogen and organic matter. In contrast, species with conservative strategies predominate in soils with high nitrogen and organic matter contents, but low in phosphorus and potassium (Shen et al., 2019).

In addition to soil fertility, water availability is one of the main limiting factors for plant performance in natural ecosystems (Pinheiro & Chaves, 2011). In dry tropical forests, water availability acts as an environmental filter, selecting functional leaf traits that enhance species survival under drought conditions (Lebrija-Trejos et al., 2010). Under these conditions, plants adopt different strategies to minimize water loss through stomata and, at the same time, maintain efficient $CO_2$ assimilation (Falcão et al., 2017). In areas with greater water availability, a pattern characterized by larger specific leaf area, higher nitrogen and phosphorus concentrations, thinner leaves, and lower water-use efficiency is observed (Appendix S2). On the other hand, in environments with water restriction, thicker leaves and greater water use efficiency prevail, reflecting adaptations to drought conditions (Schönbeck et al., 2015; Ouédraogo et al., 2016; Wang et al., 2021).

Although Wright et al. (2004) demonstrated that mean annual precipitation is not a strong global predictor of measuring leaf characteristics related to LES. Martinelli et al. (2021) observed that, across evaluating the elemental and isotopic concentration of carbon and nitrogen, soil and climate conditions showed a strong relationship with leaf functional characteristics in different Brazilian biomes. Species sampled in the Caatinga, vegetation located in dry environments, presented more conservative characteristics, with higher values in leaf N concentration and $\delta^{15}N$, and lower C:N ratio, indicating a longer nitrogen residence time in the soil due to low leaching and lower absorption by plants (Martinelli et al., 2021). In contrast, species sampled in areas with higher average annual precipitation, such as evergreen forests of the Atlantic Forest and the Amazon Rainforest, present low levels of leaf

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nitrogen and a high C:N ratio, indicating a greater dependence on an acquisition strategy to obtain and use resources efficiently (Martinelli et al., 2021, Freitas et al., 2024).

Temperature and solar radiation intensity are two strongly correlated environmental variables within the LES that influence the adaptive leaf characteristics of plants. Most studies found in the literature relate leaf functional characteristics with the different adaptive ways of the plant to deal with thermal and light stress (Appendix S2). In general, plants in environments with high light intensity tend to present lower SLA, high photosynthetic rate and consequently, higher nitrogen concentrations, and lower leaf longevity (Wright et al., 2004; Gotsch et al., 2015; Falcão et al., 2017; Limberger et al., 2021).

Changes in temperature, climate and rainfall regime caused by climate change can negatively affect the fitness of acquisitive species, since these species are more dependent on resources and in conditions of drought and rising temperatures, these resources can become scarce, compromising the survival of these species (Wright et al., 2004; Lavergne et al., 2010; Reich, 2014; Anderegg et al., 2019). In addition, increased CO2 concentration in the atmosphere can affect the balance between carbon absorption and water loss, impacting the efficiency of photosynthesis and modifying the functional characteristics of leaves over time (Way & Oren, 2010; Dusenge et al., 2019).

These changes in LES parameters can directly impact on the dynamics of tropical forests, affecting ecological succession, plant biomass and the carbon cycle. Constant monitoring of leaf functional traits and LES in different ecosystems is essential to understand how plants react to climate change and the effects that these reactions will have on the resilience of tropical ecosystems.

Leaf functional adaptations associated with the les through ecological succession

At both local and regional scales, the distribution of plant communities is influenced by adaptations to variations in biotic conditions, such as competition and herbivory, and abiotic conditions, such as temperature and precipitation (Veenendaal et al., 1998; Webb & Peart, 2000; Harms et al., 2001; Ter Steege et al., 2003). These environmental filters play a central role in the selecting traits associated with plant adaptive strategies (Lavorel et al., 1997; Lavorel & Garnier, 2002; Zakharova et al., 2019; Baraloto et al., 2012). Understanding how these functional traits link physiological mechanisms to community assembly processes is fundamental to ecology. (McGill et al., 2006; Bernard-Verdier et al., 2012; Mason et al., 2012).

Among the studies reviewed leaf functional traits associated with LES, 55% (n=88) analyzed the influence of these traits on species success along successional gradients (Appendix S2). The drivers ecological successions vary across forest type, community

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structure, and composition. However, predictable patterns in leaf economic spectrum emerge along the LES continuum in response to changing environmental conditions and resource availability (Wright et al., 2004). This pattern reflects a fundamental ecological trade-off: in early successional stages, pioneer species tend to invest in thin, highly photosynthetic leaves to maximize light and nutrient capture, whereas later-successional species develop thicker, more durable leaves that enhance resource conservation and longevity (Reich, 2014).

Areas undergoing forest succession often reflect a history of disturbance or degradation, and their functional attributes indicate the current phase of the succession process (Reich et al., 2004). In areas where succession occurs without external influences that alter the structure of the vegetation, the community typically follows the theoretical model proposed by Grime's C-S-R strategy (Grime et al., 1974, 1997; 2001; Grime & Pierce, 2012; Cintra et al., 2024). In the initial stages, such as in pastures and early regeneration areas, species with acquisitive functional traits predominate, which favor rapid growth and reproduction in environments with highlight availability (Cintra et al., 2024). As regeneration progresses and the structure of the vegetation becomes more complex, the environment acts as a filter, favoring species adapted to resource limitations and more conservative strategies (Cintra et al., 2024).

Different approaches associated with LES have been used to explain species success along successional gradients (Lohbeck et al., 2015). Studies on LES in wet and dry vegetation have revealed contrasting patterns in species' leaf strategies (Wright et al., 2004; Díaz et al., 2016). Studies comparing moist and dry tropical vegetation reveal contrasting successional dynamics. In tropical moist forests, succession is primarily driven by decreasing light availability due to canopy closure, whereas in tropical dry forests, it is closely linked to progressive increases in water availability over time (Nicotra et al., 1999; Lebrija-Trejos et al., 2011; Pineda-García et al., 2013).

Direct variations in leaf functional traits and LES of species throughout ecological succession have implications for forest preservation and recovery strategies (Werden et al., 2018; Carlucci et al., 2020; Loureiro et al., 2023). The advancement of deforestation and climate change can significantly alter the expected patterns of forest succession, directly influencing the adaptive characteristics of the plant (Reich et al., 2003; Wallwork et al., 2023; Cintra et al., 2024). Furthermore, understanding the variation in functional traits throughout ecological succession can provide support for more effective restoration strategies, especially in degraded areas, where natural succession may be limited by resource availability (Loureiro et al., 2023).

## 4 FINAL CONSIDERATIONS AND PERSPECTIVE

This systematic review allowed us to quantify and investigate studies on the Leaf Economic Spectrum (LES) in tropical vegetation, providing an overview of the progress of research in this field. The increase in the growth rate of scientific publications in recent decades reinforces the relevance of the topic. However, the variation in the number of publications in different years, as shown in Figure 4, suggests that external factors, such as funding and academic interests, determine the total number of articles written on the subject, influencing the scientific pace.

The results suggest that most studies focus on the evaluation of chemical and morphological functional attributes, meaning that functional attributes related to plant physiological processes, such as leaf construction cost and respiration rates, remain little explored. This gap highlights the need to expand methodological approaches to obtain more comprehensive information on leaf functioning, particularly about energy efficiency and plant metabolism. Furthermore, some life forms, such as lianas, epiphytes and bryophytes, remain underrepresented in literature, which limits the understanding of the functional diversity of tropical plants. Future studies should focus on the inclusion of these groups to improve knowledge about the traits that structure the functional continuum of LES, particularly those that mediate the response of sensitive species to variations in environmental variables.

Environmental factors stand out as key elements in the configuration of foliar strategies. Variations in soil fertility, water availability, temperature and light intensity act as ecological filters, selecting species with more acquisitive or conservative strategies, depending on the supply of resources. In addition, changes throughout ecological succession directly influence the distribution of functional traits, reflecting predictable patterns of adaptation of species to environmental conditions and interactions with other plants.

The geographic distribution of LES studies reveals a significant bias, with most research concentrated on humid tropical forests in Asia and the Neotropics, while drier regions such as savannas and seasonal forests, as well as continents such as Africa and Oceania, remain underexplored. This inequality raises a critical point: much of the current knowledge may be limited to specific environmental conditions, hindering broader predictions about leaf functionality in different tropical ecosystems.

By bringing together and analyzing the current state of the art on LES, this review provides a solid foundation for future investigations, highlighting the need for integrated approaches that combine ecophysiology, biogeochemistry, and functional modeling. Progress in this field is essential to understanding the economic trade-offs of leaves,

predicting how plants will respond to environmental changes, and improving conservation, management, and ecological restoration strategies in tropical ecosystems in a changing world.

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## APPENDIX

**Table 1**

*Selected articles addressing leaf functional diversity associated with the LES in tropical ecosystems*

| D | MAIN AUTHOR | CO-AUTHORS | YEAR | TITLE | DOI |
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| 1 | Baraloto, C. | Marcon, E.; Morneau, F.; Pavoine, S.; Roggy, J. | 2010 | Integrating functional diversity into tropical forest plantation designs to study ecosystem processes | 10.1051/forest/2009110 |
| 2 | Liu, X. | Swenson, N. G.; Zhang, J.; Ma, K. | 2013 | The environment and space, not phylogeny, determine trait dispersion in a subtropical forest | 10.1111/1365-2435.12018 |
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| 5 | Liu, Q. | Sterck, F. J.; Zhang, J.; Scheire, A.; Konings, E.; Cao, M.; Sha, L.; Poorter, L. | 2021 | Traits, strategies, and niches of liana species in a tropical seasonal rainforest | 10.1007/s00442-021-04937-4 |
| 6 | Yi, R. | Xu, X.; Huang, Y.; Zhu, S.; Xu, C.; Zhang, Y. | 2022 | Tropical plant species living under P limitation show signs of greater resistance to drought | 10.1029/2021GL096686 |
| 7 | Li, Y. | Feng, Y.; Li, W.; Tomlinson, K.; Liao, Z.; Zheng, Y.; Zhang, J. | 2022 | Leaf trait association in relation to herbivore defense, drought resistance, and economics in a tropical invasive plant | 10.1002/ajb2.1858 |
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| 14 | Wallwork, A. | Castro-Trujillo, B.; Banin, L. F.; Dent, D. H.; Skiba, U.; Kerdraon, D.; Sayer, E. J. | 2023 | Soil carbon dynamics are linked to tree species growth strategy in a naturally regenerating tropical forest | 10.3389/ffgc.2023.1232694 |
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**Table 2**

*Leaf functional traits evaluated in studies on the Leaf Economic Spectrum in tropical vegetation*

| ID | $A_{mass}$ | CCL | LL | LNC | LPC | N:P ratio | $R_{mass}$ | SLA | LMA | $\delta^{15}N$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ✓ | | | ✓ | | | | ✓ | | ✓ |
| 2 | | | | | | | | ✓ | | |
| 3 | | | | ✓ | | | | ✓ | | |
| 4 | | | | ✓ | ✓ | | | ✓ | | |
| 5 | | | | ✓ | ✓ | ✓ | | ✓ | | |
| 6 | | | | ✓ | | | | ✓ | | |
| 7 | ✓ | | ✓ | ✓ | | | | | ✓ | |
| 8 | | | | ✓ | | | | ✓ | | ✓ |

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| 9 | | | | ✓ | | | | ✓ | | |
| 10 | | | | ✓ | | | | ✓ | | |
| 11 | | | | ✓ | ✓ | | | ✓ | | |
| 12 | | | | ✓ | | | | ✓ | | |
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| 14 | | | | ✓ | | | | ✓ | | |
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| 17 | | | | | | | | | | ✓ |
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| 19 | | | | ✓ | ✓ | | | ✓ | | ✓ |
| 20 | | | | ✓ | | | | ✓ | | |
| 21 | | | | | | | | | ✓ | |
| 22 | | | | ✓ | ✓ | | | | ✓ | |
| 23 | ✓ | | | ✓ | ✓ | | | ✓ | | |
| 24 | | | | ✓ | ✓ | ✓ | | ✓ | | |
| 25 | ✓ | | | ✓ | ✓ | | | ✓ | | |
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| 27 | | | | | | | | | ✓ | |
| 28 | | | | | | | | ✓ | | |
| 29 | ✓ | | | ✓ | ✓ | | | ✓ | | |
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| 106 | ✓ | | | | | | | ✓ | | |
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| 115 | ✓ | | | | ✓ | | ✓ | | ✓ | |
| 117 | | | | ✓ | ✓ | | | ✓ | | |
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| 121 | | | | ✓ | ✓ | | | ✓ | | |
| 122 | | | | ✓ | ✓ | | | ✓ | | |
| 123 | ✓ | | ✓ | ✓ | ✓ | | ✓ | | ✓ | |
| 124 | | | | ✓ | ✓ | | | ✓ | | |
| 125 | | | | ✓ | ✓ | ✓ | | ✓ | | |
| 126 | | | ✓ | | | | | | | |
| 127 | | | ✓ | | | | | | ✓ | |
| 128 | | | | ✓ | ✓ | | | ✓ | | |
| 129 | | | | ✓ | | | | ✓ | | |
| 130 | | | | | | | | ✓ | | |
| 131 | | | | ✓ | ✓ | ✓ | | ✓ | | |
| 132 | | | | ✓ | ✓ | | | | ✓ | |
| 133 | | | | ✓ | ✓ | | | | ✓ | |
| 134 | | | | ✓ | ✓ | | | ✓ | | |
| 139 | | | | | | | | ✓ | | |
| 140 | | | | ✓ | ✓ | | | ✓ | | |
| 141 | | | | ✓ | | | | ✓ | | |
| 142 | | | | ✓ | ✓ | | | ✓ | | |
| 143 | | | | ✓ | ✓ | | | ✓ | | |
| 144 | | | | ✓ | | | | | | |
| 145 | | | | | | | | ✓ | | |
| 146 | | | | ✓ | | | | | ✓ | |
| 147 | ✓ | | | | | | | ✓ | | |

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|---|---|---|---|---|---|---|---|---|---|---|
| 148 | | | | ✓ | ✓ | | | ✓ | | |
| 149 | | | | ✓ | ✓ | | | ✓ | | |
| 150 | ✓ | | | ✓ | ✓ | | | | ✓ | |
| 151 | | | | ✓ | ✓ | | | ✓ | | |
| 152 | | | ✓ | ✓ | ✓ | | | ✓ | | |
| 153 | | ✓ | | ✓ | ✓ | | | ✓ | | |
| 154 | | | | ✓ | ✓ | | | ✓ | | |
| 155 | | | | ✓ | ✓ | | | ✓ | | |
| 156 | | | | ✓ | | | | | ✓ | |
| 157 | | | ✓ | | | | | | | |
| 158 | | | | ✓ | ✓ | ✓ | | | ✓ | |
| 159 | ✓ | | ✓ | ✓ | ✓ | | ✓ | | ✓ | |
| 160 | | | ✓ | ✓ | ✓ | | | | ✓ | |
| **Total Geral** | **24** | **4** | **14** | **98** | **71** | **12** | **6** | **106** | **42** | **7** |

Amass - Photosynthetic assimilation rates, CCL - Construction cost leaf, LL - Leaf lifespan, LNC - leaf nitrogen concentrations, LPC- leaf phosphorus concentrations, N:P ratio - molar or mass-based ratio between nitrogen (N) and phosphorus (P) concentrations, Rmass - Dark respiration rate, SLA - Specific Leaf Area, LMA - Leaf mass per area, δ15N - stable nitrogen isotopes ($^{15}N/^{14}N$).