

# **IDENTIFYING INTER-GROWTH FORM DIFFERENCES AND SEASONAL DYNAMICS IN LEAF SPECTRAL AND FUNCTIONAL TRAITS OF LIANAS AND TREES IN A TROPICAL FOREST**

**Elise Huysman**

Student ID: 01900317

Promotors: prof. dr. ir. Hans Verbeeck, dr. ir. Félicien Meunier

Tutor: ir. Kasper Coppieters

A dissertation submitted to Ghent University in partial fulfilment of the requirements for the degree of master in Bioscience Engineering.

Academic year: 2023 - 2024

De auteur en promotor geven de toelating deze scriptie voor consultatie beschikbaar te stellen en delen ervan te kopiëren voor persoonlijk gebruik. Elk ander gebruik valt onder de beperkingen van het auteursrecht, in het bijzonder met betrekking tot de verplichting uitdrukkelijk de bron te vermelden bij het aanhalen van resultaten uit deze scriptie.

The author and promoter give the permission to use this thesis for consultation and to copy parts of it for personal use. Every other use is subject to the copyright laws, more specifically the source must be extensively specified when using results from this thesis.

Gent, June 4, 2024

The promoters,

The author,

prof. dr. ir. Hans Verbeeck  
dr. ir. Félicien Meunier

Elise Huysman

# **ACKNOWLEDGEMENTS**

This thesis beautifully marks the conclusion of my five years as a student at 'het Boerenkot'. I want to express my gratitude to everyone who made this project not only possible, but also enjoyable and educational. It will always hold a special place in my memories. First, I would like to thank both my promotors. Prof. dr. ir. Hans Verbeeck, thank you for allowing me to work on this fascinating topic and for the opportunity to participate in the field campaign abroad. Dr. ir. Félicien Meunier, your constant enthusiasm and assistance during data analysis, even on Saturdays, was invaluable. A special thank you to ir. Kasper Coppieters, who was a fantastic tutor from start to finish. Your guidance and passion during the fieldwork made it an unforgettable experience that I will cherish for years to come. Manon, we only met a few months before becoming roommates, but you were an amazing friend to share adventures with during our free time.

I want to thank my parents and sister for their support throughout my academic journey as well as my personal one. I also want to thank Naima for immediately agreeing to fly across the ocean to embark on a great adventure with me, as well as for dealing with all the emotions during our many hangouts in the past five years. Eef, Justine, Lien, Lies, Lotte, and Sarah, the friendship we share is one I dreamed of five years ago. I'm sure we will continue to add to our stories in the coming decades. And last but certainly not least, Zias, your support and love means the world to me. The different time zones were challenging, but even the smallest 'slaapwel' when I returned from the fieldwork made me smile. While we may not know all the intricate details of each other's studies, you were always there to listen to my struggles and validate my feelings. I hope to be as helpful to you next year when it's your turn.



# **CONTENTS**

|                                                                  |            |
|------------------------------------------------------------------|------------|
| <b>Acknowledgements</b>                                          | <b>i</b>   |
| <b>Contents</b>                                                  | <b>iv</b>  |
| <b>Samenvatting</b>                                              | <b>v</b>   |
| <b>Abstract</b>                                                  | <b>vii</b> |
| <b>List of abbreviations</b>                                     | <b>ix</b>  |
| <b>1 Introduction</b>                                            | <b>1</b>   |
| <b>2 Literature review</b>                                       | <b>3</b>   |
| 2.1 (Neo)tropical forests . . . . .                              | 3          |
| 2.1.1 General info . . . . .                                     | 3          |
| 2.1.2 The forest's processes . . . . .                           | 4          |
| Tropical forest in the global carbon cycle . . . . .             | 4          |
| The nutrient cycles in (tropical) forests . . . . .              | 5          |
| The water cycle in tropical forests . . . . .                    | 6          |
| 2.1.3 Ecosystem services . . . . .                               | 6          |
| 2.2 The Earth's Radiation Balance and Climate Forcing . . . . .  | 8          |
| 2.2.1 The radiation balance . . . . .                            | 8          |
| 2.2.2 Radiative forcing . . . . .                                | 9          |
| 2.2.3 Tropical forests and the radiation balance . . . . .       | 10         |
| Reflective properties of forest canopies . . . . .               | 10         |
| Impacts of radiative forcing on the Neotropical forest . . . . . | 11         |
| 2.3 Lianas . . . . .                                             | 13         |
| 2.3.1 Differences with trees . . . . .                           | 13         |
| Growth strategy/structural tissues . . . . .                     | 13         |
| Optical and structural leaf properties . . . . .                 | 14         |
| 2.3.2 Impact of lianas on forest functioning . . . . .           | 15         |
| Carbon cycle . . . . .                                           | 15         |
| Nutrient cycle . . . . .                                         | 17         |
| Water cycle . . . . .                                            | 18         |
| 2.3.3 Increasing abundance . . . . .                             | 19         |
| <b>3 Materials and methods</b>                                   | <b>23</b>  |
| 3.1 Description of the studied site . . . . .                    | 23         |
| 3.2 Data collection . . . . .                                    | 24         |
| 3.2.1 Leaf reflectance measurements . . . . .                    | 25         |
| 3.2.2 Leaf structural and biochemical traits . . . . .           | 26         |
| 3.3 Data pre-processing . . . . .                                | 27         |
| 3.4 Data analysis . . . . .                                      | 29         |
| 3.4.1 Comparing leaf traits and reflectance bands . . . . .      | 29         |
| 3.4.2 Linear mixed-effects models . . . . .                      | 30         |
| 3.4.3 Partial least squares regression (PLSR) . . . . .          | 32         |
| 3.4.4 Discrimination hyperspectral data . . . . .                | 33         |

|                                                                                                        |           |
|--------------------------------------------------------------------------------------------------------|-----------|
| <b>4 Results</b>                                                                                       | <b>35</b> |
| 4.1 Comparing leaf traits and reflectance bands . . . . .                                              | 35        |
| 4.2 Linear mixed-effects models . . . . .                                                              | 40        |
| 4.3 Partial least squares regression (PLSR) . . . . .                                                  | 42        |
| 4.4 Discrimination hyperspectral data . . . . .                                                        | 44        |
| <b>5 Discussion</b>                                                                                    | <b>49</b> |
| 5.1 Differences between growth forms . . . . .                                                         | 49        |
| 5.1.1 Differences in leaf structural and biochemical traits. . . . .                                   | 49        |
| 5.1.2 Differences in reflectance . . . . .                                                             | 50        |
| 5.2 Seasonality in both growth forms . . . . .                                                         | 52        |
| 5.3 Reflective spectra as proxy indicators for leaf structural and biochemical traits (PLSR) . . . . . | 53        |
| 5.4 Further research opportunities . . . . .                                                           | 54        |
| <b>6 Conclusion</b>                                                                                    | <b>57</b> |
| <b>Bibliografie</b>                                                                                    | <b>59</b> |
| <b>Appendix A</b>                                                                                      | <b>79</b> |
| <b>Appendix B</b>                                                                                      | <b>81</b> |
| B.1 Comparing leaf traits and reflectance bands . . . . .                                              | 81        |
| B.2 Linear mixed-effects models . . . . .                                                              | 85        |
| B.3 Partial least squares regression . . . . .                                                         | 87        |

# SAMENVATTING

Lianen zijn structurele parasieten die bomen beklimmen om toegang te krijgen tot de bovenste bladerdaklaag. Hun abundantie en biomassa nemen toe in de Neotropen, wat waarschijnlijk de werking van deze tropische gebieden beïnvloedt. Lianen hebben minder structureel weefsel en beperken de groei van bomen, waardoor de aangetaste bossen minder koolstof vastleggen. Hun bladreflectie is gemiddeld hoger dan die van bomen, wat de spectrale signatuur van de tropische bossen verandert.

Deze studie onderzoekt de structurele en biochemische bladkenmerken van lianen en bomen in een secundair tropisch regenwoud in Panama. De onderzochte kenmerken omvatten bladdikte, equivalente waterdikte ( $C_w$ ), bladmassadichtheid (LMA) en koolstof- en stikstofgehalte, evenals hun stabiele isotopen  $\delta^{13}\text{C}$  en  $\delta^{15}\text{N}$ . Daarnaast wordt de bladreflectie tussen 350 en 2500 nm onderzocht, met de focus op verschillen tussen de twee groeivormen en hoe deze kenmerken variëren met seizoensveranderingen. Door een combinatie van bladkenmerkmetingen en hyperspectrale reflectiegegevens, werden statistische testen en lineaire gemengde-effectenmodellen gebruikt om de gegevens te analyseren.

De resultaten onthullen significant lagere LMA,  $C_w$  en  $\delta^{13}\text{C}$ -gehalte voor lianen dan voor bomen. Seizoensgebondenheid heeft geen significant effect op de bladkenmerken. De reflectie van lianenbladeren is significant hoger dan die van bomen in twee van de vier waterbanden in het kortgolvig infraroodgebied en het groene gebied. Daarnaast beïnvloeden seizoensvariaties de reflectie-eigenschappen van bomen. Ze blijken significant verschillende reflecties te hebben tussen seizoenen in de twee overgebleven waterbanden en het nabij-infraroodgebied. Lianen daarentegen worden niet significant beïnvloed door seizoensgebondenheid in de vooraf bepaalde banden. De Kullback-Leiber divergentie van de reflectiespectra tussen seizoenen is meer dan 4 keer groter voor bomen dan voor lianen. Deze bevindingen suggereren dat onderzoek naar de reflectie van boombladeren seizoensgebondenheid in aanmerking moet nemen. Voor lianen daarentegen lijkt de reflectie weinig beïnvloed door seizoensgebondenheid. Zowel de bladkenmerken als de reflectie van lianen lijken stabiel te zijn gedurende het natte en droge seizoen.

Onze bevindingen suggereren dat de onderscheidende structurele en biochemische kenmerken van lianen en bomen een cruciale rol spelen in hun ecologische strategieën en interacties binnen het boscossysteem. Verder benadrukt de studie het potentieel van hyperspectrale reflectie als een proxy voor het monitoren van blad-

kenmerken. Deze inzichten dragen bij aan een beter begrip van de ecologische rollen van lianen en bomen en hun reacties op milieuveranderingen, wat essentieel is voor het voorspellen van de gevolgen van klimaatverandering voor tropische bosecosystemen.

# **ABSTRACT**

Liana, woody vines, are structural parasites, climbing trees to access the upper canopy layer. Their abundance and biomass is increasing in the Neotropics, which likely influences the functioning of these tropical ecosystems. Lianas have less structural tissue and limit the growth of trees, consequently the affected forests sequester less carbon. There are indications that their leaf reflectance is higher than that of trees altering the spectral signature of the tropical forests.

This study investigates the structural and biochemical leaf traits of lianas and trees in a secondary tropical forest in Panama. The investigated traits include leaf thickness, equivalent water thickness ( $C_w$ ), leaf mass area (LMA) and carbon and nitrogen content as well as their stable isotopes  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Additionally, it examines leaf reflectance between 350 and 2500 nm, focusing on differences between the two growth forms and how these traits vary with seasonal changes. Using a combination of leaf trait measurements and hyperspectral reflectance data, statistical tests and linear mixed-effects models were employed to analyze the data.

The results reveal significantly a lower LMA,  $C_w$  and  $\delta^{13}\text{C}$  content for lianas than trees. Seasonality does not have a significant effect on the leaf traits. The reflectance of liana leaves is significantly higher than for trees in two out of four water bands in the short-wave infrared region and the green region. Additionally, seasonal variations affect the reflectance properties of trees. They appear to have significantly different reflectance between seasons in the two remaining water bands and the near-infrared region. Lianas on the other hand are insignificantly affected by seasonality in the predetermined bands. The Kullback-Leiber divergence of the reflectance spectra between seasons is more than 4 larger for trees than lianas. These findings suggest that research on the reflectance of tree leaves should take seasonality into account. For lianas on the other hand, the reflectance seems rather unaffected by seasonality. Both the leaf traits and reflectance of lianas appears to be stable across the wet and dry season.

Our findings suggest that the distinct structural and biochemical characteristics of lianas and trees play a crucial role in their ecological strategies and interactions within the forest ecosystem. Furthermore, the study highlights the potential of hyperspectral reflectance as a proxy for monitoring leaf traits. These insights contribute to a better understanding of the ecological roles of lianas and trees and their

responses to environmental changes, which is essential for predicting the impacts of climate change on tropical forest ecosystems.

# **LIST OF ABBREVIATIONS**

## **Acronyms**

|              |                                          |
|--------------|------------------------------------------|
| <b>AGB</b>   | Aboveground biomass.                     |
| <b>ANOVA</b> | Analysis of variance.                    |
| <b>ASD</b>   | Analytical Spectral Devices.             |
| <b>BCI</b>   | Barro Colorado Island.                   |
| <b>BCNM</b>  | Barro Colorado Nature Monument.          |
| <b>ENSO</b>  | El Niño-southern Oscillation.            |
| <b>FS4</b>   | FieldSpec 4 Hi-Res.                      |
| <b>GHG</b>   | Greenhouse gas.                          |
| <b>GPP</b>   | Gross primary production.                |
| <b>ICC</b>   | Intraclass correlation coefficient.      |
| <b>IQR</b>   | Interquartile range.                     |
| <b>IR</b>    | Infrared radiation.                      |
| <b>KW</b>    | Kruskal-Wallis (non-parametric) test.    |
| <b>LOESS</b> | Locally estimated scatterplot smoothing. |
| <b>NIR</b>   | Near-infrared.                           |
| <b>NPP</b>   | Net primary production.                  |
| <b>NTFP</b>  | Non-timber forest products.              |
| <b>PAR</b>   | Photosynthetically active radiation.     |
| <b>PC</b>    | Principal component.                     |

|              |                                          |
|--------------|------------------------------------------|
| <b>PCA</b>   | Principal component analysis.            |
| <b>Pi</b>    | Inorganic phosphorus.                    |
| <b>PLSR</b>  | Partial least squares regression.        |
| <b>Po</b>    | Organic phosphorus.                      |
| <b>Q1</b>    | The first quartile.                      |
| <b>Q3</b>    | The third quartile.                      |
| <b>RMSEP</b> | Root mean square error of prediction.    |
| <b>STRI</b>  | Smithsonian Tropical Research Institute. |
| <b>SWIR</b>  | Shortwave infrared.                      |
| <b>VIS</b>   | Visible light.                           |
| <b>VPDB</b>  | Vienna Pee Dee Belemnite.                |
| <b>WUE</b>   | Water-use efficiency.                    |

## Variables

|                       |                                                     |
|-----------------------|-----------------------------------------------------|
| $\delta^{13}\text{C}$ | The content of the carbon-13 isotope [‰ vs. VPDB].  |
| $\delta^{15}\text{N}$ | The content of the nitrogen-15 isotope [‰ vs. AIR]. |
| <b>C</b>              | Carbon content [%].                                 |
| <b>C<sub>w</sub></b>  | Equivalent water thickness [g/cm <sup>2</sup> ].    |
| <b>LAI</b>            | Leaf area index [m <sup>2</sup> /m <sup>2</sup> ].  |
| <b>LMA</b>            | Leaf mass area [g/cm <sup>2</sup> ].                |
| <b>N</b>              | Nitrogen content [%].                               |
| <b>R<sup>2</sup></b>  | Coefficient of determination [-].                   |
| <b>R<sup>2</sup>C</b> | Conditional pseudo-R <sup>2</sup> [%].              |
| <b>R<sup>2</sup>M</b> | Marginal pseudo-R <sup>2</sup> [%].                 |
| <b>SLA</b>            | Specific leaf area [cm <sup>2</sup> /g].            |
| <b>VIP</b>            | Variable importance of projection [-].              |

# 1. INTRODUCTION

Tropical forest are often called "the lungs of the planet", as they sequester CO<sub>2</sub> and provide O<sub>2</sub>. 60% of all photosynthesis on Earth is happening in both these forests and savannahs, which makes preserving them a priority (Beer et al., 2010). Lianas are woody vines and are structural parasites, as they use trees to climb to the upper canopy layers. Their abundance is increasing across the Neotropics (Phillips et al., 2002, 2005), making it important to study the differences between this growth form and trees, as the species composition of tropical forests will likely evolve and potentially their functioning as well (Van Der Heijden et al., 2013; Schnitzer et al., 2000; Schnitzer and Carson, 2010). This shift potentially has important implications. Lianas sequester less carbon in their tissues than trees, as they need less structural tissue because they are structural parasites. On top of this, they increase mortality of their host trees by climbing them, which potentially causes damage, and by increasing competition for resources. Thereby they diminish the growth of the trees and thus the terrestrial carbon sink, exacerbating climate change (Van Der Heijden et al., 2013, 2015a,b; di Porcia E Brugnera et al., 2019).

Conversely, lianas are hypothesized to reflect more incoming radiation, potentially mitigating the climate change caused by their negative effect on the carbon balance, by reducing the amount of energy absorbed by Earth's system (Meunier et al., 2022; Sánchez-Azofeifa et al., 2009). There are, however, not a lot of studies on the spectrum from the visible to the shortwave infrared region (350 - 2500 nm). Often, specific sections of the spectrum are studied. For example, the region between 400 and 1100 nm has been the subject of multiple studies (Billings and Morris, 1951; Sánchez-Azofeifa et al., 2009). In the past, studies have often neglected the influence of seasonality on leaf spectral properties, which is one of the main topics of this thesis.

The goal of this research is to identify and quantify the differences and relations between multiple structural and biochemical leaf traits of trees and lianas, as well as the reflectance of the leaves, and to analyze how these traits change with the seasons. The four central research questions of this thesis are: (1) Are the leaf traits different between lianas and trees? (2) Is the reflection of liana leaves higher than that of tree leaves? (3) Are those leaf traits and the reflectance spectra subject to seasonal changes? (4) Can the reflectance spectra of leaves be linked to their

---

leaf traits? Since lianas have a growth advantage particularly in seasonal forests during the dry season (Schnitzer, 2005), finding differences that could explain this is relevant for our understanding of the dynamics of tropical forests in general.

The data was collected during the dry (January-February) and wet (August-September) seasons in Panama in the year 2023. The structural leaf traits, the leaf thickness, the equivalent water thickness ( $C_w$ ) and the leaf mass area (LMA), and biochemical leaf traits, the C and N content as well as their stable isotopes  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , were measured. The reflectance spectra of the leaves between 350 and 2500 nm were also measured. The data was then processed using statistical tests and partial least squares regression to link the hyperspectral data with the obtained leaf traits. Tropical forests are large and often inaccessible. If the spectral data could be linked with these leaf traits and upscaling is possible, new opportunities for remote-sensing based ecological research would emerge. Upscaling of these links is possible if the canopy structure, the leaf angle, the clumping of the leaves, the reflectance of the stem and branches etc. are taken into account. This would allow large areas of forest to be studied more quickly, and remote locations could potentially become observable without extensive human presence, thereby helping to preserve the forest.

## 2. LITERATURE REVIEW

### 2.1 (Neo)tropical forests

#### 2.1.1 General info

According to the climate classification of Trewartha and Horn (1980) a region is considered tropical if the mean temperature of the coldest month is higher than 18°C and the annual precipitation higher than the Patton's precipitation threshold (Patton, 1962). 20,44% of the world's continents (excluding Antarctica) are covered with a tropical climate (Fraedrich et al., 2001). These regions are indicated as tropical rainforest climate (Ar), tropical wet-and-dry (savanna) climate with a dry winter (Aw) or with a dry summer (As) in Figure 2.1. They are found around the equator on the American, African and Asian continents (Trewartha and Horn, 1980; Köppen, 1936; Belda et al., 2014). Mayaux et al. (1998) estimated the global closed tropical forest area to be between 1090 and 1220 million ha, 185 to 215 million hectares in Africa, 235 to 275 million hectares in Asia and 670 to 730 million hectares in America. Thus most of the global, tropical forest is situated in America, otherwise known as the Neotropics.

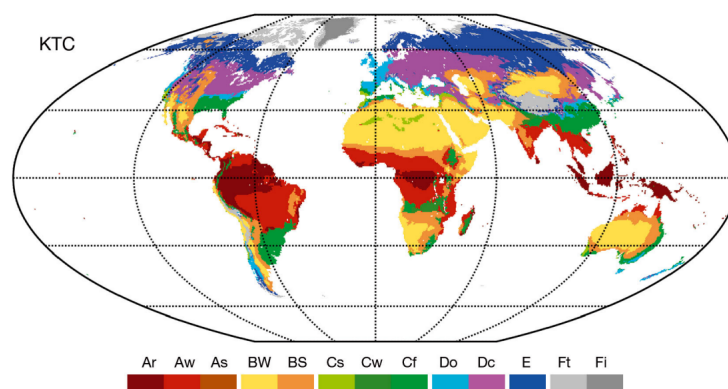


Figure 2.1: Köppen-Trewartha climate classification (adapted from Belda et al. (2014)). The climate types are: tropical rainforest (Ar), tropical wet-and-dry (savanna) dry-winter (Aw) or dry-summer (As), arid (BW), semi-arid (BS), subtropical dry-summer (Cs), subtropical dry-winter (Cw), subtropical humid (Cf), temperate oceanic (Do), temperate continental (Dc), boreal (E), tundra (Ft) and ice cap (Fi).

However, the global forest area is declining due to deforestation. It is estimated that the yearly decline of the total tropical forest area was, on average, 9.28 million ha per year between 2015 and 2020. This average is significantly lower than the period between 1990 and 2000, when it was 13.8 million hectares per year (FAO, 2020).

### 2.1.2 The forest's processes

#### Tropical forest in the global carbon cycle

The carbon cycle is a biogeochemical cycle, consisting of pools, i.e. reservoirs, in which the carbon can stay for a prolonged period of time, and fluxes, the streams of carbon traveling between the different pools. Figure 2.2 visually summarizes this cycle. Forests are part of the biotic pool and interact with the atmospheric and lithologic pools, the latter is the combination of the pedologic and geologic pools in the figure (Falkowski et al., 2000; Lal, 2008).

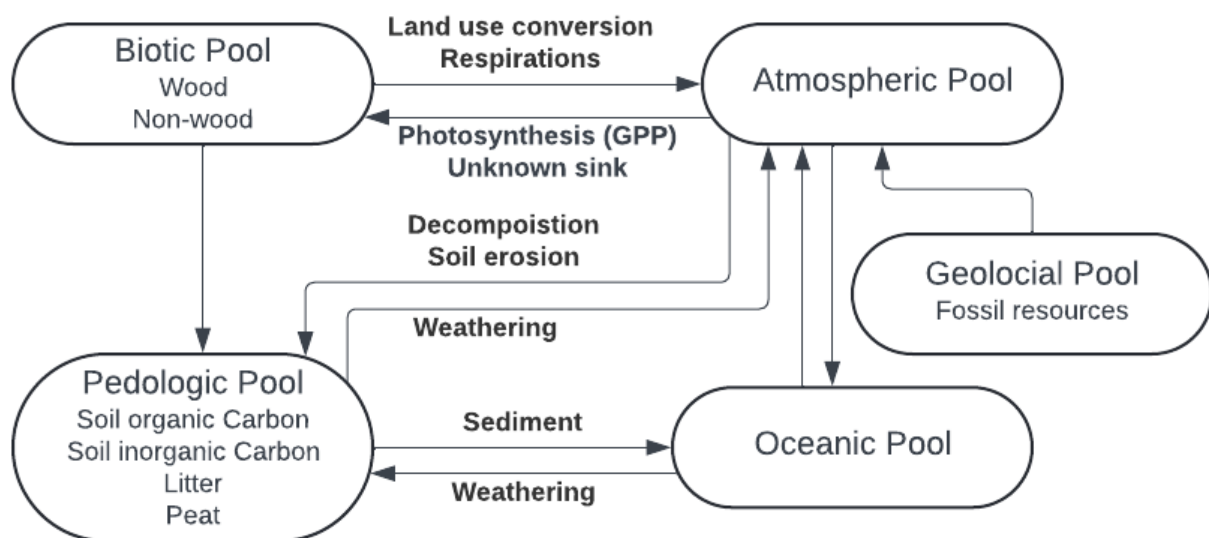


Figure 2.2: Global carbon cycle (adapted from Lal (2008)).

The largest carbon flux is the terrestrial gross primary production (GPP), between the atmospheric and biotic pool, the photosynthesis in tropical forests and savannas constitute 60% of this stream (Beer et al., 2010). This is balanced with an efflux from the forests, namely ecosystem respiration (Mitchard, 2018; Lal, 2008). Ecosystem respiration is divided into two main categories: autotrophic and heterotrophic respiration (Chambers et al., 2004; Lal, 2008). The vegetation (leaves, stems and roots) carries out autotrophic respiration, with the largest portion of this respiratory activity occurring in leaf tissues, as indicated by Cavaleri et al. (2008). Heterotrophic respiration occurs when litter and soil organic matter is decomposed

during microbial activity in the soil, this is the flux travelling between the carbon pools in the soil and atmosphere (Chambers et al., 2004).

Chave et al. (2001) studied the aboveground biomass (AGB) of the tropical forest in a permanent plot, which is separated into two geologically different areas, in French Guiana. They found that 79-81% of the AGB of the forest is represented by trees with a diameter of 30 cm or above (measured at 130 cm). The same trees only contribute to 19-21% of the basal area, meaning large trees contribute disproportionately to the total forest biomass. Using their calculations, they landed on an average AGB in the two areas of 237 and 254 Mg.ha<sup>-1</sup> exclusively for trees with a diameter larger than 30 cm. The total average AGB, including smaller trees, was 301 and 317 Mg.ha<sup>-1</sup>. The results of DeWalt and Chave (2004) are in the same order of magnitude, about 250 Mg.ha<sup>-1</sup> and a basal area of 30.2 m<sup>2</sup>.ha<sup>-1</sup>. They also looked at the structure of the Neotropical forest and found 75% of the individuals were trees, 19% lianas and 6% palms. Their contributions to the AGB are respectively 90.2%, 4.7% and 5%. In this case, this study might be more representative as it included 4 lowland Neotropical forests, one of which is the study site of this research.

### **The nutrient cycles in (tropical) forests**

Higher plants have 17 essential elements. They are divided in macronutrients, which are present in high concentrations: C, H, O, N, S, P, K, Ca and Mg, and micronutrients, which are present in low concentrations: Fe, Mn, Zn, Cu, B, Mo, Ni and Cl. For some higher plants, Na and Si are also shown to be essential (Kirkby, 2005). Nutrient supply affects the functioning of an ecosystem, making it an important variable when looking at these forests (Vitousek, 2004).

Healthy plants contain 10-50 mg N.(g dry matter)<sup>-1</sup> or 1-5 % (Karthika et al., 2018; Kirkby, 2005). They mainly take up nitrogen in 2 forms: ammonium ions (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>), for optimal growing conditions they need a mix of both (Kirkby, 2005). The 2 sources of nitrogen are the dead organic matter present as the layer of litter on the forest floor and the atmospheric dinitrogen (N<sub>2</sub>) that is fixed by the microbial community in the soil (Pajares and Bohannan, 2016).

Phosphorus is mainly present in rocks, plant and animal residues and the surfacing soil (El Attar et al., 2022). There are 2 main categories: inorganic phosphorus (Pi), representing about 35-70%, and organic phosphorus (Po), representing about 30-65% (Harrison, 1987). Pi is phosphorus that is either fixed in rock's structure and has reacted with Ca, Fe and/or Al forming discrete phosphates or has been adsorbed on the surface of clay minerals and Fe/Al oxides, forming various complexes (Shen et al., 2011; Zhang and Kovar, 2009). Pi can be released in low concentrations through weathering of these minerals (Shen et al., 2011). Po is present in

---

the residue of dead organisms and in the microbial biomass and can be released through mineralization by soil organisms and plant roots (El Attar et al., 2022; Shen et al., 2011). Unlike with nitrogen there is no natural input from outside the ecosystem and 90% of the total soil phosphorus is inaccessible for plant-uptake (Mengel and Kirkby, 1987).

The studies of Vitousek (2004); Vitousek et al. (1993) and Reich et al. (1997) concluded that in young forests the net primary production (NPP) is limited by nitrogen, but over time the pools build up and the limitation weakens. Mature forests are on the weathered soils and depleted of phosphorus over time (Vitousek et al., 1993). The Neotropics are mainly covered by oxisols and ultisols, which are highly weathered (Reed et al., 2011; U.S.D.A., 1999). Phosphorus becomes the main nutrient limiting the NPP and functioning of mature tropical forests (Vitousek, 1984; Herbert and Fownes, 1995; Reed et al., 2011; Cleveland et al., 2011). In more recent years the interest in other nutrients has picked up and potassium has become a key nutrient in some studies (Yavitt et al., 2011).

## **The water cycle in tropical forests**

The water balance has 2 inputs: precipitation and snowmelt, the latter is probably limited in the Neotropics. The precipitation in the Neotropics ranges from 878 to 3991 mm.year<sup>-1</sup> (Poorter et al., 2017) and this incoming water can be intercepted by vegetation and evaporated, evaporated from the soil, transpired, drained or become surface run-off (Kumagai et al., 2005). Evapotranspiration includes all evaporation and transpiration, on Barro Colorado Island (BCI, Panama) it yearly averages to 3.6 mm.day<sup>-1</sup>, which can be divided into 5.2 mm.day<sup>-1</sup> during the dry season and 2.8 mm.day<sup>-1</sup> during the rainy season (Larsen et al., 2021). Da Rocha et al. (2004) performed a study in the south of Brazil, they found an evapotranspiration of 3.51 mm.day<sup>-1</sup> and a yearly precipitation of at least 2200 mm. For both studies between 50% and 60% of the precipitation is returned back to the atmosphere. Recent research talks about a "forest sponge effect" (Ogden et al., 2013; Birch et al., 2021). The soil of tropical forests has an increased infiltration capacity and moisture retention during the wet season, storing more precipitation than pastures. This decreases the run-off at the same time and increases the baseflow, the water present in the system before a storm, in the dry season.

### **2.1.3 Ecosystem services**

In the previous section (2.1.2), some regulating and supporting ecosystem services have been described. These are not the only services forests provide. Tropical forests contain most of the Earth's terrestrial biodiversity and a large number of

## 2. Literature review

---

taxa have peak diversities in the tropics (Andresen et al., 2018; Corlett and Primack, 2011). The Neotropical forests specifically have a high species richness compared to other biotic realms (Antonelli et al., 2018), which is for instance important for the functioning of ecosystems, human health and well-being (Alho, 2008; Duffy, 2009; Sandifer et al., 2015).

Tropical forests also provide a whole range of non-wood resources: fruits, nuts, fibers and canes (e.g. rattan), essential oils, bamboo and resins. The rainforests of Peninsular Malaysia alone boast around 1283 species that serve human needs, excluding non-native species and those primarily sought for timber purposes. This constitutes approximately 16% of Malaysia's native species, indicating that one out of every six species holds value for humans beyond wood (Jacobs, 1982). An example is rattan, climbing palms from a subfamily of the palm family, the majority is used for their cane, but also their edible fruits are being used. Several studies have attempted to calculate the economic value of non-timber forest products (NTFP). Peters et al. (1989) studied a part of the Amazonian rainforest in Peru and looked solely at the production of fruits and latex. They used annual production rates, sampled or collected from literature, and average retail prices for the fruits locally and the rubber prices, which are controlled by the Peruvian government. They estimated a total value of 697.79 USD.ha<sup>-1</sup>.year<sup>-1</sup> for these NTFPs and for the commercial timber this was 1000.78 USD.ha<sup>-1</sup>.year<sup>-1</sup>. Grimes et al. (1994) studied the NTFP of the Jatun Sacha Biological Station in Ecuador. They estimated sustainable harvest amounts and performed a market surveys for 13 species that had a market value. The first 2 plots, located in a *tierra firme* forest with red clay, were valued at 146.93 and 136.06 USD.ha<sup>-1</sup>.year<sup>-1</sup> and the third plot, located in the floodplain forest with alluvial soil, was valued at 62.87 USD.ha<sup>-1</sup>.year<sup>-1</sup>.

In addition, another key aspect is that these tropical forests are a pool of genetic resources, which can be used in modern agriculture, medicine, industry and energy. The supplied genes lead to the production of many pharmaceuticals, which can lead to multiple billions in cross-counter sales (Myers, 1988). Another example for uses in agriculture comes from a primitive relative of modern maize found in a montane forest of south-central Mexico. This plant is perennial, unlike modern maize, and turned out to be resistant to 4 of the 8 major viruses and mycoplasmas, which caused a yearly loss of 1% of the global harvest worth 500 million USD. This creates possibilities to make modern maize more resistant. The plant is also adapted to cooler and damper areas which could potentially enlarge the range of cultivation by one-tenth (Iltis et al., 1979; Nault and Findley, 1981). It is important to note that all these studies were performed at least 30 years ago. These numbers indicate the importance of these NTFP, but they have probably increased in the last decades.

---

## 2.2 The Earth's Radiation Balance and Climate Forcing

### 2.2.1 The radiation balance

The radiation balance on Earth is maintained as the incoming solar radiation equals the outgoing radiation into space and is visualised in Figure 2.3. The planet receives on average an incoming solar shortwave radiation of  $342 \text{ W.m}^{-2}$ . The atmosphere, clouds and aerosols reflect  $77 \text{ W.m}^{-2}$  (22.5%) and the greenhouse gasses (GHG) in the atmosphere absorb  $67 \text{ W.m}^{-2}$  (19.6%). 57.9% of the radiation ends up reaching the surface and depending on the albedo of this surface, this is partially reflected and absorbed by the surface. Averaged over the whole planet  $30 \text{ W.m}^{-2}$  (8.8%) is reflected and  $168 \text{ W.m}^{-2}$  (49.1%) is absorbed, the latter warming the Earth's surface. Since the Earth's surface temperature is above 0 K, it sends out long-wave, infrared radiation (IR). However, when this radiation is emitted, it is partially absorbed by the atmosphere. The heated atmosphere then also emits radiation both back to Earth (back radiation) and into space. The part directly emitted to space (in the atmospheric window, 8-12  $\mu\text{m}$ ) and emitted by the atmosphere into space is equal to radiation reaching the surface. Without this back radiation, the average Earth's surface temperature would be  $-18^\circ\text{C}$  (255.15 K) instead of the  $15^\circ\text{C}$  (288.15 K) it is now. This is what is called the greenhouse effect (Berger and Tricot, 1992; Kiehl and Trenberth, 1997). The absorption by the atmosphere is due to GHGs present, they absorb infrared radiation in the range 5  $\mu\text{m}$  to 25  $\mu\text{m}$  due to the vibrational modes of their molecular structure (Tuckett, 2015). The most prominent GHGs are Water vapour ( $\text{H}_2\text{O}$ ),  $\text{CO}_2$ , methane ( $\text{CH}_4$ ), nitrous oxide ( $\text{N}_2\text{O}$ ) and halocarbons (IPCC, 1990, 2023).

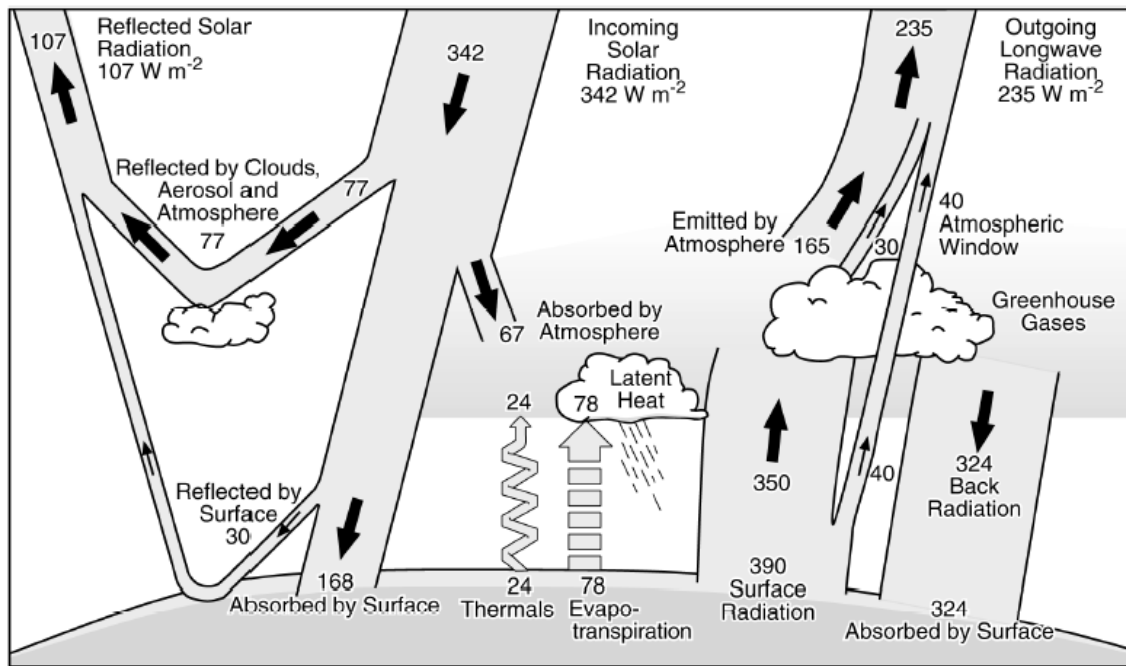


Figure 2.3: The Earth's energy balance (adapted from Kiehl and Trenberth (1997)).

### 2.2.2 Radiative forcing

Atmospheric  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  concentrations have rapidly increased in the last century due to human activities (IPCC, 1990, 2023). From ice cores extracted in Antarctica and Greenland, a  $\text{CO}_2$  concentration between 270 and 280 ppmv was determined for the period between 1300 and 1800 (Friedli et al., 1986; Neftel et al., 1982). The IPCC documented a concentration of 409.9 ppmv in 2019, this is an increase of about 47%. Between the years 1000 and 1750, the concentration of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  were respectively 700 ppb and 270 ppb. However, by 2019, the concentrations have reached 1866 ppb and 335 ppb, resulting in a 156% and 24% increase, respectively. (IPCC, 1990, 2007, 2023).

The largest sources of  $\text{CO}_2$  in the atmosphere are the emission of fossil fuels and changes in land-use. Deforestation, a form of land-use change, is one of the major drivers of the global gross  $\text{CO}_2$  sources (Friedlingstein et al., 2022). The initial increase of the  $\text{CO}_2$  concentration was due to deforestation and other land-use change activities, the  $\text{CO}_2$  emissions increased and simultaneously the forest area was declining (IPCC, 2021). Both the increase of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  are linked to the intensification of food production. For (biogenic)  $\text{CH}_4$ , the main sources are wet rice fields, cattle, animal waste, landfills and biomass burning. For (biogenic)  $\text{N}_2\text{O}$ , they are land-use change, fertilizer production and use and manure application (Van Amstel and Swart, 1994).  $\text{N}_2\text{O}$  is released by microorganisms in the nitrogen cycle during both the denitrification and nitrification pathway. It is the major driver behind  $\text{N}_2\text{O}$  emissions (Barton and Atwater, 2002; Kampschreur et al., 2009; Adouani et al., 2015; Andalib et al., 2018).

The GHGs keep the temperature above 0°C (273.15 K) and are responsible for the liquid water and a livable planet. They are necessary for life on earth, however, due to the increase of anthropogenic GHGs this effect has been enhanced. The atmosphere captures more of the outgoing radiation causing rising temperatures. This enhanced effect is called (positive) radiative forcing. There is also a cooling effect due to the increased presence of anthropogenic aerosols which reflect the electromagnetic waves, but this effect peaked in the late 20<sup>th</sup> century and the temperature has continued to rise (IPCC, 2023). It is important to note that not all of the GHGs have the same effect for the same concentration.

### 2.2.3 Tropical forests and the radiation balance

#### Reflective properties of forest canopies

As previously mentioned, the albedo of the Earth's surface influences how much radiation is absorbed and reflected. Tropical forests cover a vast area of the planet and thus, have a significant impact on the radiation balance (Mayaux et al., 1998). When light touches a leaf, there are 3 options: absorption, reflection and transmission. Figure 2.4 visualises a typical reflectance pattern of a leaf for wavelengths ranging from 400 to 2 500 nm.

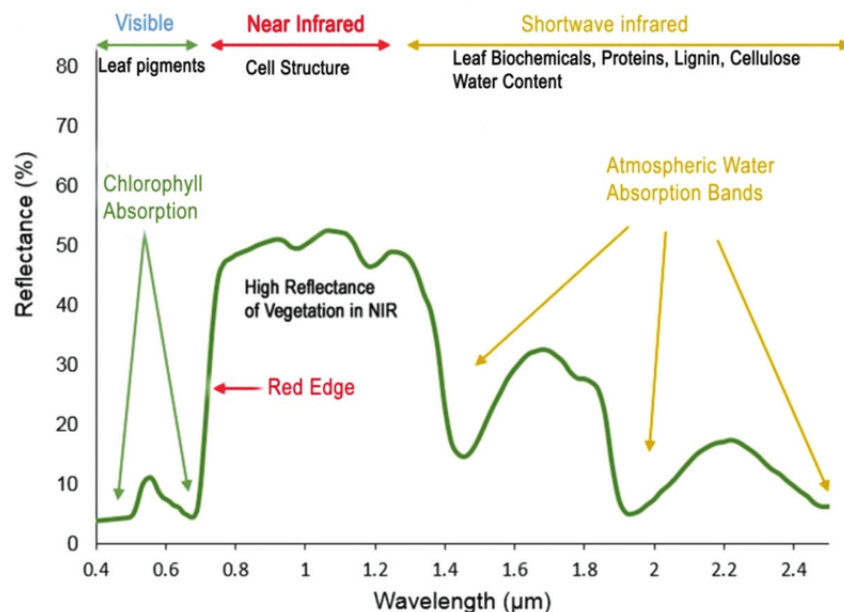


Figure 2.4: Leaf reflectance pattern (adapted from Roman and Ursu (2016)).

The visible light (VIS; 400-700 nm) more or less coincides with the photosynthetically active radiation (PAR), meaning that plants use these wavelengths for their photosynthesis (McCree and Keener, 1974; McCree, 1981; Vogelmann and Gorton,

2014). The plant's pigments, chlorophyll (a and b), anthocyanin and carotenoids absorb the light energy and convert it into chemical energy (Rabideau et al., 1946; Knipling, 1970; Zur et al., 2000). Absorption is not only dependent on pigment concentration but also on the pigment's composition and wavelength-specific absorption (Vogelmann and Gorton, 2014). In the VIS range, the leaves absorb most in the blue and red wavelengths and reflect most in the green ones (the peak at 533 nm), causing the leaves to appear green to the human eyes (Knipling, 1970; Roman and Ursu, 2016). Beans, spinach, Swiss chard and tobacco, four dicot species with relatively thin leaves, on average absorb 82% of PAR, reflect 10% and transmit 8% (Moss and Loomis, 1952).

In the near-infrared range (NIR; 700-1350 nm) the distribution changes drastically absorption is low and reflectance and transmittance become high (Merzlyak et al., 2002). Woolley (1971) looked at the spectrum of soybeans and the sum of the reflectance and transmittance was about 96% in the 800-1100 nm range. The absorption is limited to the biochemicals making up the dry matter of the leaves (Jacquemoud and Ustin, 2019). The scattering of light in NIR depends on characteristics of tissue anatomy, primarily cell shape and the volume and shape of the intercellular air spaces (Vogelmann and Gorton, 2014; Roman and Ursu, 2016).

In the shortwave infrared (SWIR; 1350-2500 nm) the water in fresh leaves leads to absorption at 1200 nm, 1450 nm, 1920 nm, and 2500 nm (Jacquemoud and Ustin, 2019; Carter, 1991). Water has primary effects, which are due to the absorption of radiation at specific wavelengths, as well as secondary effects. The latter can't be explained by water's radiative properties and are for instance linked to the water content, which influences wavelength-independent processes, or due to absorption by other substances present in the leaf. However, these secondary effects have a lot less influence than the primary (Carter, 1991).

### **Impacts of radiative forcing on the Neotropical forest**

During photosynthesis plants take up CO<sub>2</sub> from the air and since the CO<sub>2</sub> concentration is increasing, a plant can take up more CO<sub>2</sub> from the same volume of air, an effect called "CO<sub>2</sub> fertilization". This could lead to an increase in photosynthesis or GPP if the leaf area index (LAI) remains the same (Cernusak et al., 2013; Drake et al., 1997). This also goes hand in hand with an increased water-use efficiency (WUE) as the stomata will need to be open less time for the same amount of CO<sub>2</sub> (Cernusak et al., 2013). However, the increased CO<sub>2</sub> concentration in the atmosphere also leads to an increased temperature, which negatively impacts the potential net photosynthesis. The specificity of RuBisCO, the enzyme responsible for fixing CO<sub>2</sub>, decreases at higher temperatures and it starts to fixate a higher amount of O<sub>2</sub> and subsequently release CO<sub>2</sub> (Farquhar et al., 1980; Long, 1991). On the other hand there is relatively less O<sub>2</sub> available in this case, so this effect is suppressed at some capacity. It is speculated that the temperature threshold,

---

beyond which the net photosynthesis declines, is a lot closer to current average air temperatures in the tropics and other negative effects might occur sooner (Doughty and Goulden, 2008; Doughty, 2011). For instance, if the leaf temperature is higher than 45°C, RuBisCO may become denatured (Berry and Bjorkman, 1980). Even if the temperature stays below this threshold, nutrient availability might become the limiting factor and reduce the GPP increase (McMurtrie et al., 2008; Cernusak et al., 2013).

Hulme and Viner (1998) modelled a future climate change scenario for the tropics and the results indicate that the mean seasonal rainfall will decrease in the Neotropics and the dry season will lengthen. This means that overall there will be less rainfall and longer periods of drought, thus more extremes. More droughts create larger water deficits which subsequently leads to increased tree mortality which then results in a decrease of the forest biomass (Phillips et al., 2009; Enquist and Enquist, 2011). (Nepstad et al., 2007; Brando et al., 2008; Phillips et al., 2009).

In addition, forest disturbance activities are known to be influenced by climate (change), yet our understanding of the precise mechanisms remains limited. Common disturbances are drought, pathogens, insects, fire and wind (Seidl et al., 2017). They affect the structure, composition and functioning of the ecosystem, resulting in changes of the resource availability and physical environment (Pickett and White, 2013). Most knowledge on this topic comes from research on temperate or boreal forests, but from these studies it has become clear that changing these patterns will have profound impacts on the forest ecosystems in the next decades (Lindner et al., 2010). In the Neotropics the activities of pathogens, fires and droughts are affected, the activity in most cases being enhanced (Seidl et al., 2017). However, Seidl et al. (2017) mentioned that broadleaved and mixed forest types suffer less than coniferous forests from increased disturbances.

Based on paleo-ecological data Malhi and Phillips (2004) learned that the Neotropical forests were constantly shifting in composition and structure during the Pleistocene (10 000 to 2 Myr BP) and the relatively stable Holocene (past 10 000 years). They are clearly dynamic ecosystems and their sensitivity to climate change makes it inevitable that they will continue to change.

### 2.3 Lianas

#### 2.3.1 Differences with trees

Lianas, often defined as woody vines, are a polyphyletic group, i.e. the character trait grouping these species is not uniquely derived from a common ancestor (Farris, 1974; Schnitzer and Bongers, 2002). They share the same growth strategy, as they ascend towards the canopy using other plants' architecture (Schnitzer and Bongers, 2002).

#### Growth strategy/structural tissues

As opposed to epiphytes and hemiepiphytes, lianas are structural parasites that remain rooted in the ground for their entire life (Schnitzer and Bongers, 2002). Lianas do not need to support their own weight to stand up. Thus, they need to invest less mechanical support and bending resistance (Schenck, 1892; Schimper, 1898; Schnell, 1970; Putz, 1983). This allows them to rapidly expand upwards when they find a tree to climb (Putz, 1984b). On the other hand, trees are self-supporting requiring a proportional growth in basal area with each height increment to accommodate the added length (Greenhill, 1881; McMahon, 1973). Furthermore, the xylem in trees - in contrast to lianas - can only maintain its conducting properties for a couple of years and afterward, it turns into nonconducting heartwood and provides extra structural support (Zimmerman et al., 1971).

In an evergreen tropical rainforest in the Rio Negro Basin (Venezuela), lianas represent up to 19% of the LAI. However, their diameters are relatively small and increase at an extremely slow rate, they account for only about 4.5% of the AGB (Putz, 1990, 1983; Jordan and Uhl, 1978). This all results in a high specific leaf area (SLA), leaf area per unit of dry mass, (Collins et al., 2016). However, even though the stems are small, they can transport enough water and minerals for the plant's growth (Putz, 1983). The xylem vessels in lianas are specialized, they have larger diameters allowing higher flow rates (Putz, 1983; Ayensu and Stern, 1964). They have other anomalous secondary growth features such as included or intruded phloem and more parenchyma in their vascular system (Ayensu and Stern, 1964). Parenchyma cells are often simple and unspecified and coincidentally they have the highest degree of developmental plasticity. They can be transformed into all other cell types, which can play an important role in wound repair (Crang et al., 2018). In contrast to trees, lianas lack nonconducting heartwood. Combined with the slow growth rate of their diameter, it is suggested that the xylem maintains its conducting properties for decades (Putz, 1983).

On average lianas have a lower wood density than trees (Campanello et al., 2016) and the higher the wood density, the higher the contribution to the total biomass

---

in (tropical) forests (Nam et al., 2018). The total leaf weight expressed as the basal area ratio ( $\text{kg dry weight.m}^{-2}$ ) is much higher for lianas than for trees (Putz, 1983). These findings both suggest lianas allocate more resources towards their leaves, which are a form of short-term carbon storage, than trees.

### **Optical and structural leaf properties**

In the preceding section, it is discussed how lianas allocate a greater portion of their resources to their leaves, resulting in a higher SLA. This allocation has prompted several studies to propose that lianas may have evolved specialized leaves optimized for optimal light capture (Avalos et al., 1999; Sánchez-Azofeifa and Castro-Esau, 2006; Kalacska et al., 2007).

Sánchez-Azofeifa and Castro-Esau (2006) conducted research in a seasonally dry forest in Panama, revealing that lianas exhibited higher reflectance at 550 nm compared to trees, along with lower chlorophyll concentration. Subsequently, Sánchez-Azofeifa et al. (2009) expanded their study to include an aseasonal rainforest, where they found that lianas consistently displayed higher SLA and water content than trees across both sites. However, they observed lower chlorophyll and carotenoid concentrations, as well as higher reflectance at 550 nm, specifically in the seasonally dry forest.

Kalacska et al. (2007) focused exclusively on the reflective spectra of both growth forms in the same seasonally dry forest studied by Sánchez-Azofeifa et al. (2009), utilizing models to differentiate between them. They identified the top 10 important wavebands for distinguishing between lianas and trees: three in the VIS range (405 nm, 535 nm, 688 nm), one in NIR (987 nm), and five in SWIR (2252 nm, 1389 nm, 1376 nm, 1661 nm, 1350 nm), with 62% of the 100 most important wavebands falling in the VIS region. Figure 2.5 compares the spectra obtained. Additionally, Kalacska et al. (2007) examined canopy-level differences using data collected with remote sensing, identifying the top 10 most important wavebands, all of which were above 2000 nm in the SWIR region. Among the top 80 wavebands, 50% were in the VIS, 12% in NIR, and 38% in SWIR.

Meunier et al. (2022) corroborated the findings of Sánchez-Azofeifa et al. (2009), reporting that lianas had significantly lower chlorophyll content ( $11.1 \mu\text{g.cm}^{-2}$  on average) and slightly lower carotenoid content (about  $4.7 \mu\text{g.cm}^{-2}$ ). However, when examining six different leaf-level studies, they noted a lack of consensus regarding the difference in reflectance between lianas and trees. While most studies agreed that lianas were more reflective in the VIS range, opinions diverged in the NIR and SWIR regions.

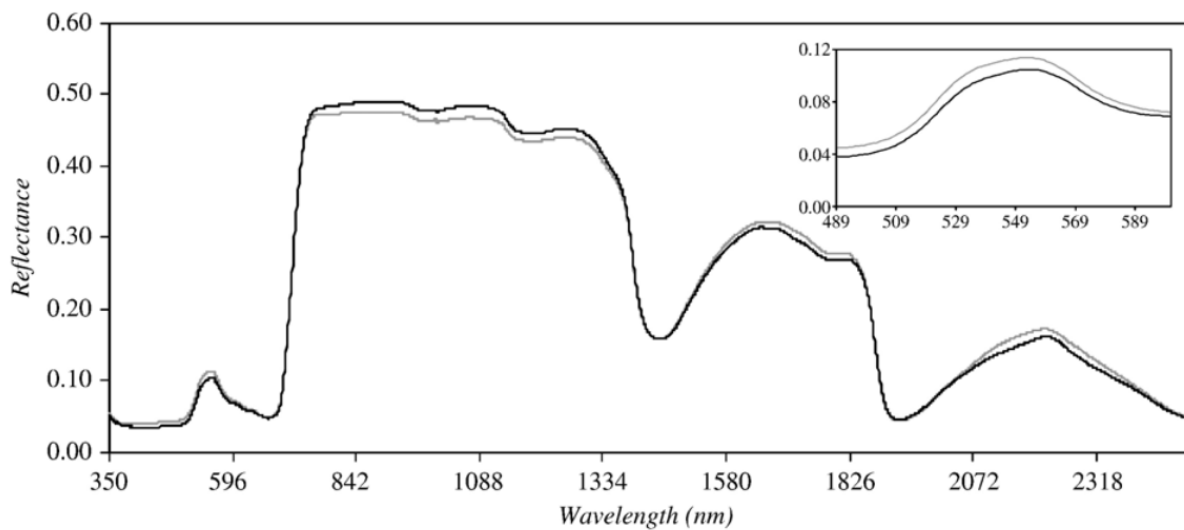


Figure 2.5: Reflective spectra of liana and tree leaves, depicted respectively in grey and black (adapted from Kalacska et al. (2007)).

The interaction between leaves and light doesn't only depend on biochemical properties, there are also structural traits that are of importance. It has long been proven that the leaf angle influences the light interception of leaves (Nobel and Long, 1985; Falster and Westoby, 2003; Duursma et al., 2012). In the tropics, the maximum light capture of horizontal leaf angles is around midday and, at the same moment, vertical leaf angles experience a minimal light capture during the day (Falster and Westoby, 2003; Ventre-Lespiauq et al., 2018). Plants with horizontal leaf angles have a greater whole-day light interception than the vertical ones (Falster and Westoby, 2003). Clumping of leaves also affects the light interception (de Castro and Fetcher, 1999). If every other factor is equal, the clumping causes increased self-shading (Falster and Westoby, 2003). Lianas tend to have flatter/more horizontal leaf angles than trees, which enhances their light capture efficiency. However, the leaves are also clumped more, which works counteractive (Meunier et al., 2022).

### 2.3.2 Impact of lianas on forest functioning

#### Carbon cycle

In the past 2 to 3 decades it has become clear that lianas negatively influence the carbon cycle, meaning less carbon is stored in forests when more lianas are present (Van Der Heijden et al., 2013, 2015a,b; di Porcia E Brugnara et al., 2019). Meunier et al. (2021) quantified this decrease using a modelling approach: in a liana removal plot the total long-term carbon storage after 3 and 10 years is respectively 1.2 and 1.8 kg C.m<sup>-2</sup> higher compared to a control plot. Van der Heijden and Phillips (2009)

---

specifically studied treefall gaps and how lianas affect the evolution in these. The estimation is that lianas reduce the forest net carbon uptake in the gaps with nearly 10%.

As lianas are climbing trees, the trees can become deformed or their stem or branches can break. (Putz, 1991; Putz et al., 1995). They also tend to form a dense layer of foliage covering the tree and limiting the light it receives, creating a heavier competition for light (Putz et al., 1995; Avalos et al., 1999, 2007). The impact of all this seems likely as host trees appear to have less leaf biomass on a one-to-one basis with their liana infestation (Ogawa, 1965; Kira and Ogawa, 1971). The reasons will be explained later in more detail, but the liana abundance is increasing in the Neotropics and this exacerbates these effects (Phillips et al., 2002; Schnitzer and Bongers, 2011; Van Der Heijden et al., 2013). Lianas thus cause a reduction of tree growth and an increased tree mortality, but also a shift in tree species composition, which then all results in a decrease of the carbon uptake Van Der Heijden et al. (2013, 2015b). The focus will now be on how they change the tree species composition of the forest, on this topic there are currently discussions. According to Putz (1984a); Clark and Clark (1990); Schnitzer et al. (2000); Van Der Heijden and Phillips (2008); Van der Heijden and Phillips (2009); Ingwell et al. (2010); Schnitzer and Carson (2010), lianas are more often climbing slow-growing, dense-wooded and shade-tolerant tree species, which means that these species are more prone to a liana infestation than faster-growing and light-wooded species. Combined with their increasing abundance this affects the species composition, favoring the light-wooded species. These dense-wooded species store the vast majority of the forest carbon and are suffering the highest infestation rate with the coupled reductions in growth, survival and recruitment. The light-wooded species have on average a 15% lower wood density and their growth rates are about 3 times higher. Lianas could thus alter the species composition in the Neotropics by altering the competition amongst the species (Van Der Heijden et al., 2013; Schnitzer et al., 2000; Schnitzer and Carson, 2010). If these effects persist, it can potentially lead to a liana-driven reduction in carbon stored in tropical forest trees of 97 Pg C worldwide (Van Der Heijden et al., 2013). Another estimation is a loss of 76% of the net AGB accumulation, calculated 3 years after removal of the lianas (Van Der Heijden et al., 2015a,b). After an additional 3 years the estimated, liana-induced carbon accumulation by trees is 46.9% in the dry and 48.5% in the wet season, showing that this might be a temporary loss (Van Der Heijden et al., 2019). However, there are thus other hypotheses, Muller-Landau and Visser (2019) studied the influence of lianas on tree communities and related the tree species' shade-tolerance to liana prevalence and its overall tolerance of lianas. Shade-intolerant trees have a lower liana tolerance, which, combined with more liana shedding, leads to a lower prevalence (Visser et al., 2018a,b). The low tolerance increases mortality of the host tree, which then decreases the prevalence of lianas. Thus the trees with the highest tolerance against lianas are more competitive and consequentially more abundant

(Muller-Landau and Visser, 2019). Muller-Landau and Visser (2019) also points out that there are more trait variations of both trees and lianas which could determine the liana tolerance. This thus gives a different explanation for the impact of lianas on tree community composition than Van Der Heijden et al. (2013); Schnitzer et al. (2000); Schnitzer and Carson (2010)

Long-term carbon storage in trees is decreasing due to the impact of liana on their growth and mortality, but at the same time the abundance of the lianas is increasing and this biomass should be accounted for to see if it can compensate for these losses. Multiple studies have been carried out and the consensus is that this compensatory effect is not large enough. Van der Heijden and Phillips (2009) quantified this effect and the lianas only compensate for 30% of the reduction in carbon uptake by tree growth they cause, Laurance et al. (1997) even goes as low as 8%. Not only do the lianas take up less carbon due to the lack of structural tissues, they also have higher turnover rates causing the residence time of the carbon in lianas to be about 3 times lower than in trees, meaning that the carbon that is stored is emitted back into the atmosphere a lot faster (Phillips et al., 2005).

### **Nutrient cycle**

The study of Sánchez-Azofeifa et al. (2009), stated that leaf nitrogen and phosphorus concentrations were not notably different between liana and tree leaves. More recently however, Kazda (2015) studied the difference in the nutrient content in lianas and their host trees. They found that the mass-based nutrient (nitrogen and phosphorus) content was higher in liana leaves compared to tree leaves. Multiple studies by the same research team compared lianas with their respective host tree and liana leaves consistently have a lower leaf mass area (LMA) and a higher mass-based nitrogen concentration. This because they focus on rapidly growing leaves, which causes those to be thin rather than thick (Kazda and Salzer, 2000; Kazda and Mehlreter, 2001; Salzer et al., 2006; Kazda et al., 2009). The results are similar to those of Cai and Bongers (2007) and Gallagher and Leishman (2012). The relation between LMA and area-based nitrogen concentration is about twice as steep in the climbers than in trees Salzer et al. (2006); Santiago and Wright (2007). This, combined with the smaller area-based nitrogen concentration, makes Salzer et al. (2006) suggest that climbers are better adjusted to light conditions than their host trees. In a different study in a tropical rainforest in Madagascar Kazda et al. (2009) found that lianas invest 5.5 and 2.7 times less nitrogen per volume space in leaves compared to trees in a shade and high-light environment, respectively. For carbon, the numbers are respectively 7.7 and 3.6. The data makes it clear that lianas invest less carbon and nitrogen in the same growth space than trees and prefer high-light environments.

The mass-based phosphorus concentrations are also higher in lianas than trees

---

according to Kazda (2015). Cai and Bongers (2007) researched the nitrogen and phosphorus content in mature and senescent leaves from lianas and trees. The overall mean nitrogen and phosphorus resorption efficiency are respectively 48.9% and 58.5%. Noticeable was that the phosphorus resorption efficiencies of lianas were lower, creating litter with a higher concentration.

Lianas grow horizontally until they find an adequate, vertical structure which they can climb. This means that lianas can even grow up to 100 m away from their original position and root along the way. Therefore, they can relocate nutrients through horizontal transport (Penalosa, 1984). Certainly, since the leaf litter of lianas is nutrient-rich and easily decomposed (Laurance et al., 2001; Schnitzer et al., 2005; Tang et al., 2012). This litter is hypothesized to be an important factor in maintaining the productivity of the highly dynamic rainforests (Kazda, 2015; Tang et al., 2012). There are also studies hypothesizing that lianas have deep root system, which would give them access to more resources, this is discussed in the next section.

## **Water cycle**

The earlier and more well-known hypothesis of Schnitzer et al. (2005) regarding the increase of lianas relative to trees, is that they have a strong belowground competition for both nutrients and water. One of the key aspects is that lianas may have a deeper root system, causing them to have access to deeper water reserves. Testing this hypothesis by excavating the roots of trees and lianas on a large scale, has proven to be difficult. However, Smith-Martin et al. (2019) measured the roots of lianas and trees in a dry-season irrigation experiment with five-year seedlings and found lianas did not have deeper roots than trees, but longer roots per stem diameter than tree. Different experiments have been undertaken such as cutting down the lianas and measuring the sap flow in the remaining trees (Schnitzer, 2005; Toledo-Aceves and Swaine, 2008; Álvarez-Cansino et al., 2015). In these cases, the sap flow increased, but this doesn't constitute a single causal relation. Cutting down these lianas also removes the light competition in the canopy, thus assigning this increase to just a larger or deeper root system is incorrect (De Deurwaerder et al., 2018). Other experiments used the single stable water isotope approach. Here the isotope partitioning of the water inside the plant is linked to that in the different soil layers. Chen et al. (2015) used this approach, using 3 different water depths and deuterium as isotope. They found that lianas and trees both use deeper water reserves during the dry season, but lianas are using more than their co-occurring trees. Additionally, they found that the seasonal variation in leaf-level photosynthesis varies less, which could support this hypothesis further as the deeper water is a more stable source. However, the study of Andrade et al. (2005), using almost the same technique, provided contradictory evidence. They found that lianas mostly use water from the upper soil layers.

More recently the general quality of the method and interpretation of these methods has been questioned as many suggest a dual stable isotope experiment is more reliable (Renée Brooks et al., 2010; Stahl et al., 2013; Evaristo et al., 2016). Since then De Deurwaerder et al. (2018) have quantitatively studied the below-ground competition between canopy trees and canopy lianas in the lowland *terra firme* rainforest of the Paracou Experimental Station (French Guiana) for the first time using the proposed dual stable isotope approach. This research took place in the dry season, when water limitation is most prevalent. They found that trees use water from deeper soil layers. The trees in this experiment mainly depended on wet season replenishment and the majority of this water originates from wet season rainfall that has infiltrated to deeper soil layers. Lianas on the contrary used the precipitation in the superficial soil layers. The study on its own isn't enough to disprove the prevailing hypothesis but further examination of deeper soil samples or root excavation could help to come to a conclusion. Since the lianas and trees access different sources of water this would also mean that there is only limited competition going on. However, the nutrient concentration is highest in the top soil layers, which could give lianas the sought advantage over trees. These findings should also be tested further.

There is thus no consensus on whether or not lianas access deeper water reserves. However, there are other advantages that lianas have which increase their water-use efficiency. The opening and closing of the stomata determines the water loss by transpiration. If the stomata are open the plant is able to capture CO<sub>2</sub> for its photosynthesis, but simultaneously water is lost due to transpiration (Ketellapper, 1963). Balancing these 2 processes is thus of high importance. Since lianas are often in places with a lot of sunlight and a high vapor pressure deficit, they need to regulate this balance carefully and they might do so more rapidly than trees (Campanello et al., 2016). Lianas also have the ability to adjust their internal water potential gradient, this allows them to take up water under drier conditions (De Guzman et al., 2017; Maréchaux et al., 2017). This does not mean that this is an advantage for lianas during longer drought periods (De Deurwaerder et al., 2018). To conclude, lianas have specialized mechanisms to increase their WUE, but there is no consensus about the general depth of the root system, which is not ideal.

### 2.3.3 Increasing abundance

As previously mentioned the abundance of lianas is clearly increasing in Neotropical forests Phillips et al. (2002, 2005) were the first to publish these findings, and since many studies found supporting evidence (Wright et al., 2004b; Schnitzer, 2005; Ingwell et al., 2010; Yorke et al., 2013; Laurance et al., 2014). This increase is clearly present in seasonal forests, but less outspoken or absent in aseasonal rainforests (Schnitzer, 2005; Smith et al., 2017). Multiple studies calculated the liana stem density (ha<sup>-1</sup>) increase for different seasonal, old-growth tropical forests. Phillips et al.

---

(2002) found an average increase of 4.03 % over 5 years in 4 Amazonian regions (North Peru, South Peru, Bolivia and Ecuador), Laurance et al. (2014) found 1% yearly increase north of Manaus (Brasil) and Yorke et al. (2013) found one of 14% over 8 years in northeastern Costa Rica. For liana basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ), the values were 4.58%, 4.32% and 17.5% respectively. The leading hypothesis for the mechanisms behind this increase was that they have a deeper root system and a more efficient vascular system giving them a competitive advantage during the dry season (Schnitzer, 2005). As explained in the section 2.3.2 about the water cycle, there is no consensus on this topic and other hypotheses have also been formed. Decreasing rainfall and increasing seasonality and temperature are key components to the increasing abundance (Schnitzer, 2005; DeWalt et al., 2010; Swaine and Grace, 2007). However other components are emerging and abundance seems positively correlated to disturbance, tree mortality and forest turnover, meaning the faster the dynamics in the forest, the more the liana abundance increases (Schnitzer et al., 2000, 2004; Schnitzer and Carson, 2001, 2010; Schnitzer and Bongers, 2011; Laurance et al., 2014). Lianas seem more efficient at colonizing new tree gaps than trees, using more recruitment methods (Schnitzer et al., 2000; Schnitzer and Bongers, 2011). Combined with their growth strategy allowing them to grow more rapidly in height than trees, up to 7 times more during the dry season and 2 times during the wet season (Schnitzer, 2005), this gives them a competitive advantage to fill these gaps, which are high-resource environments (Schnitzer and Bongers, 2011; Schnitzer and van der Heijden, 2019). Lianas also increase tree mortality (Ingwell et al., 2010; Van Der Heijden et al., 2013, 2015b) and thus forest turnover creating a positive feedback loop (Schnitzer and Bongers, 2011). Higher  $\text{CO}_2$  concentrations could potentially be an other reason for the increased liana abundance (Schnitzer and Bongers, 2011; Phillips et al., 2002). Granados and Körner (2002) set up a seedling experiment in a greenhouse and lianas did respond to elevated  $\text{CO}_2$  concentrations. Marvin et al. (2015) performed a similar experiment along a secondary forest edge in the Neotropics and found no evidence to support this hypothesis. Lianas are responding faster to ambient higher  $\text{CO}_2$  concentrations in the temperate forests (Hättenschwiler and Körner, 2003; Belote et al., 2004). This could be due to their relatively high leaf area to total plant mass (Cai et al., 2009; Zhu and Cao, 2009, 2010). However, there is not yet a similar study with ambient  $\text{CO}_2$  concentrations in the tropics. The hypothesis is that for the same unit leaf area a liana will generally grow faster than a tree. This then works as positive feedback as the plant grows more photosynthetic tissue (Schnitzer and Bongers, 2011). Zhu and Cao (2010) hypothesized that liana leaf characteristics are the reason, they have a higher SLA, photosynthetic rates, nitrogen and phosphorus use efficiencies and lower leaf construction cost and life span. As mentioned in section 2.2.3 the stomata can be open a shorter time and capture the same amount of  $\text{CO}_2$  at elevated concentrations. As lianas are seemingly better adapted to growing under drought stress, they are able to profit more than trees (Schnitzer, 2005; Cai et al.,

## 2. Literature review

---

2009; Zhu and Cao, 2009).

More recently Umaña et al. (2020) found that the increase in relative abundance of lianas has levelled off. This could potentially lead to the same effect for adult lianas in the future, but this needs to be monitored.

---

### 3. MATERIALS AND METHODS

#### 3.1 Description of the studied site

The fieldwork for this research was carried out on Gigante Peninsula which is part of the Barro Colorado Nature Monument (BCNM; 9.15°N, 79.85°W) in Panama, under the management of the Smithsonian Tropical Research Institute (STRI). The peninsula is covered by a seasonally dry, secondary tropical moist forest about 60 years old (Van Der Heijden et al., 2015a) and 8-9% of the area is covered with drought deciduous trees (Bohlman, 2010). The soils in the BCNM are mostly oxisols and inceptisols, which are highly weathered (Marvin et al., 2016).

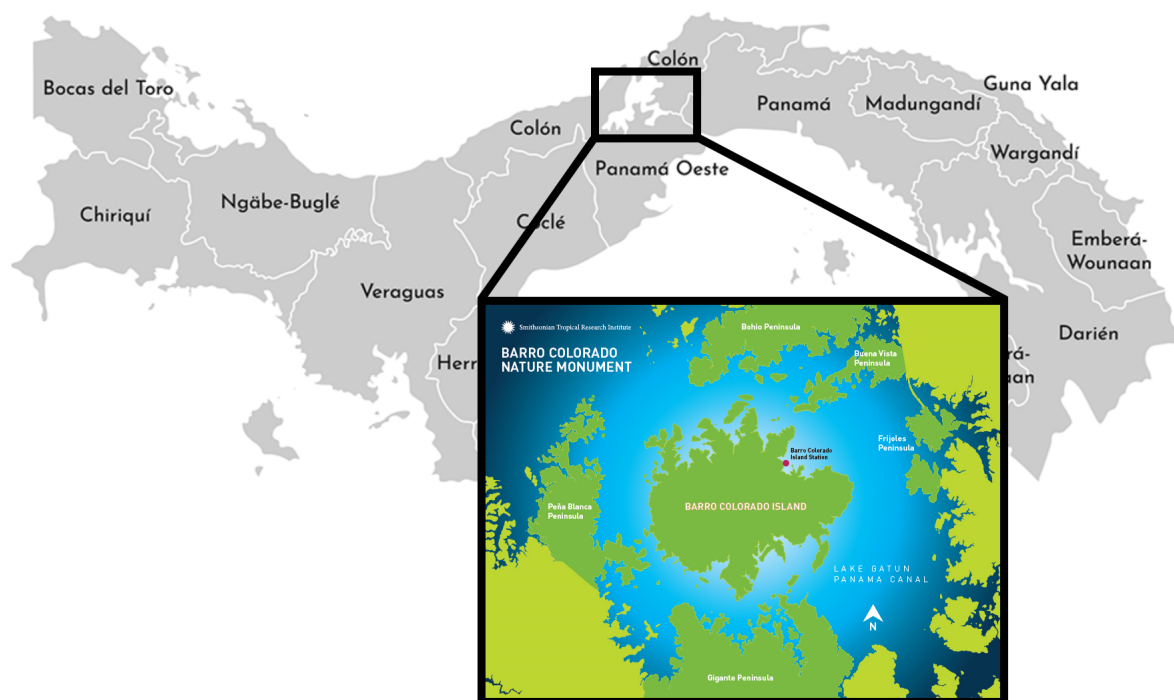


Figure 3.1: Map of studied site (adapted from STRI (2024)).

The site has a distinct wet (May-December) and dry (January-April) season (Alfaro, 2002; Phillips et al., 2004; Cornthwaite, 1919). Paton (2024) summarized the yearly precipitation at Barro Colorado Island (BCI) for the last 100 years. The minimum, maximum and average yearly precipitation are, respectively, 1699 mm (in 1997), 4487 mm (in 1981) and 2465 mm. In 2023 the total precipitation was 1704 mm and

---

the minimum and maximum temperatures were, respectively, 23.0°C and 32.0°C. Starting in mid-October of 2023 the indicators in the central-eastern tropical Pacific were consistent with El Niño, the warm phase of El Niño-Southern Oscillation (ENSO) (W.M.O., 2023). During El Niño years, there is a sharp decrease of the annual precipitation as visible in 2023 (Estoque et al., 1985).

## **3.2 Data collection**

The fieldwork took place during the wet season of 2023 (August-September) in continuation of the fieldwork previously done during the dry season of the same year (January-February) by ir. Line Van Der Sichel, ir. James Counye and ir. Kasper Coppieters. There is an ongoing liana removal experiment on Gigante Peninsula. It consists of 16 (60 x 60 m) plots, which were established in 2008 (Van Der Heijden et al., 2015a). In March 2011, half of the plots were randomly selected and the lianas were removed, the other 8 were left unchanged and act as the control plots. All the removal plots are kept liana-free up to this day. The focus was on the species of both growth forms with the largest basal area in the 16 plots from the liana removal experiment (Van Der Heijden et al., 2015a). Leaf samples were gathered from both trees and lianas, predominantly within the sunlit layer of the canopy, with a smaller portion originating from the second layer, the layer just below. The samples were collected on Gigante Peninsula outside of the 16 plots in order to maintain their scientific integrity, as the collection process could potentially impact the sampled individual. The collection process involved utilizing the "Notch Big Shot" throw weight launcher (Figure 3.2), in conjunction with a throw weight. A throwing line was attached to the weight and propelled towards a suitable branch. Upon achieving proper placement, the weight was lowered to ground level and exchanged for a sturdier rope. This rope was then manoeuvred over the branch using the throw line, and once both ends reached ground level, it was tightened and manually pulled to fracture the branch (Youngentob et al., 2016). Successful execution of this method resulted in the branch falling to the ground with at least 4 mature, undamaged leaves. For each individual, a unique number, the time of sampling, the coordinates, a description of the location, as well as the position in the canopy and growth form were recorded. Table A.1 in Appendix A gives a summary of all sampled species during the two field campaigns. In total 219 individuals were sampled across both seasons, 124 trees (42 species) and 95 lianas (43 species). 37 trees and 32 lianas in the dry season and 87 trees and 63 lianas in the wet season.

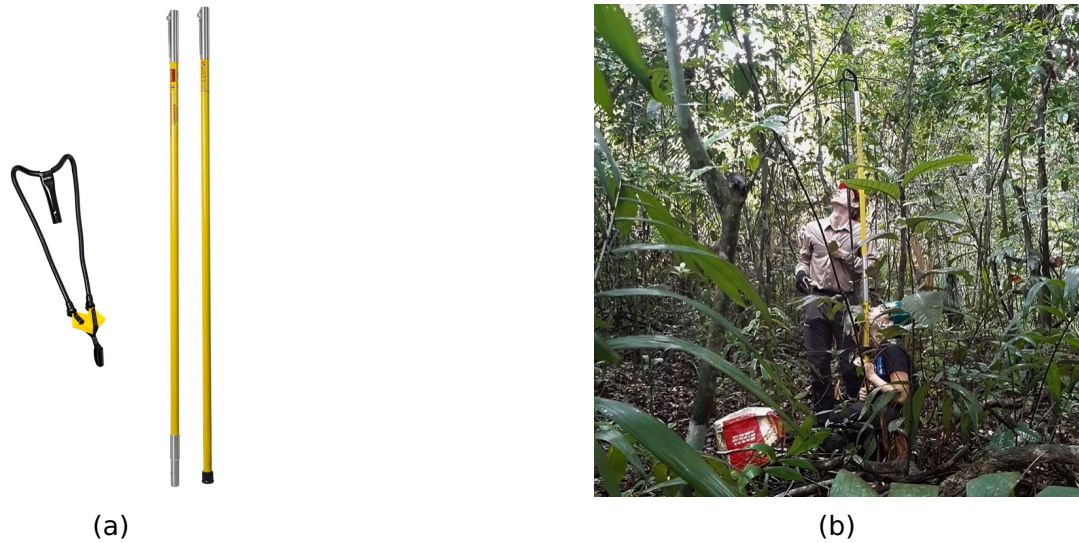


Figure 3.2: A "Notch Big Shot" throw weight launcher (a) (adapted from Notch (nd)) and (b) used in the field.

#### 3.2.1 Leaf reflectance measurements

After collection (20 min - 1 h), the sample's reflectance was measured for wavelengths between 350 and 2500 nm with the ASD FieldSpec 4 (Analytical Spectral Devices (ASD) FieldSpec 4 Hi-Res; Malvern Panalytical, Longmont, CO, USA) portable spectroradiometer (FS4) equipped with an ASD Leaf Clip attached to a Plant Probe (Figure 3.3). This setup ensured minimal ambient light interference with the measurement. Before measuring spectra, the ASD was first turned on for 30 minutes, allowing the internal sensors to reach their optimal temperature. Next, a mylar film (a wavelength calibration puck) was scanned to ensure the FS4 was working correctly. The Leaf Clip is equipped with both a white and black cap. About every 2 minutes the white cap was used to take a white reference, as the result is set as 100% reflection, to ensure the calibration was optimal. The black cap was used while measuring the reflectance of a leaf as it is assumed to absorb all wavelengths the leaf transmits. Between scans, there was a small wait period to ensure the Leaf Clip was properly placed. The ASD was set to average over 10 scans per sample and 20 scans per white reference. Only mature leaves with minimal damage were selected for scanning, and prominent veins were avoided during the scanning. Per sampled individual, four leaves were selected and four samples were taken on every leaf, resulting in 16 samples per individual with each a unique scan number. If the leaves were too small to make multiple measurements, additional leaves were scanned to obtain 16 samples.



(a)



(b)

Figure 3.3: (a) ASD FieldSpec 4 portable spectroradiometer (adapted from Analytik (nd) and (b) ASD Leaf Clip (adapted from Malvern Panalytical (2019)).

### 3.2.2 Leaf structural and biochemical traits

Each leaf was labeled, its reflectance spectrum was scanned with the ASD FS4 and it was photographed in the field for future reference and identification purposes. The thickness of each leaf was measured in two places, using a thickness measuring micrometer with an accuracy of  $0.001\ \mu\text{m}$ , again avoiding prominent veins. Other leaf traits were measured in the lab. To minimize the moisture loss between the sampling and the further processing, the sampled branch and the sampled leaves were put in a black plastic bag.  $\text{CO}_2$  was added by exhaling in the bag, since stomata start closing at high  $\text{CO}_2$  concentrations (Zeiger et al., 1987). Upon arrival at the laboratory on BCI (1.5 to 8 hours after sampling), the samples were photographed using a fixed camera to calculate the leaf area using ImageJ (Figure 3.4). Separate pictures were taken from the scanned leaves, and from additional leaves that were included to increase the sample size and make sure the weight of all the leaves was sufficient to get accurate measurements of the difference in dry and wet weight for each individual. The leaves were weighted to obtain the wet weight and then placed in a paper envelope and collectively dried in an oven at  $60\ ^\circ\text{C}$  for at least 48 hours. Afterwards, the weight was measured again to obtain the leaf dry content (LMA; dry weight/leaf area;  $\text{g.cm}^{-2}$ ) and the leaf equivalent water thickness ( $C_w$ ; water weight/leaf area;  $\text{g.cm}^{-2}$ ). The residual fresh leaves and branches were used to identify the species by a local botanist and field technician with years of experience, Boris Bernal. The dried samples were placed in tight ziplock bags to avoid water uptake from the air. These samples were transported back to Belgium, accompanied by silica gel. All samples were then ground into a thin powder using a high-speed rotor mill (Retsch Ultra Centrifugal Mill ZM 200, at 14 000 rpm and 0.25 mm sieve size with trapezoid holes). This powder was then weighed, 1.5 mg for tree leaves and 2 mg for liana leaves, both with a deviation of maximum 10%. The samples were weighed in a tin measuring cup, which was consecutively rolled into a small ball. From these samples the carbon (C) and nitrogen (N) content as well

### 3. Materials and methods

as their stable isotopes, carbon-13 ( $\delta^{13}\text{C}$ ) and nitrogen-15 ( $\delta^{15}\text{N}$ ), were determined with an elemental analyser - isotope ratio mass spectrometer (EA-IRMS), EA IsoLink interfaced through a ConFloIV to a delta Q of Thermo Scientific, Bremen. Measured  $\delta^{13}\text{C}$  values were normalised on the Vienna Pee Dee Belemnite (VPDB) scale using USGS 61 (Caffeine #1  $-35.05 \pm 0.04$  ‰ v.s. VPDB) and B2159 (Sorghum (EM)  $-13.78 \pm 0.19$  ‰ v.s. VPDB), and IA-R001-2019 (Wheat  $-26.43 \pm 0.08$  ‰ v.s. VPDB) was used as quality control. Measured  $\delta^{15}\text{N}$  values were normalised on the AIR scale using Acetanilide #3 ( $40.57 \pm 0.04$  ‰ v.s. AIR) and B2159 (Sorghum (EM)  $-13.78 \pm 0.19$  ‰ v.s. AIR), and IA-R001-2019 (Wheat  $-26.43 \pm 0.08$  ‰ v.s. AIR) was used as quality control.



Figure 3.4: Picture taken to calculate leaf area with ImageJ (a) before and (b) after processing.

### 3.3 Data pre-processing

The leaf reflectance spectra measured in the field were saved as txt files and collectively loaded into R Studio (2023.12.1 Build 402 (Posit, 2024) with R 4.3.3. version (R Core Team, 2021)). All spectra were linked with information on species, growthform, season etc. using the unique individual number and the name of the spectrum. Each individual had about 16 spectra of 4 different leaves, in total 4166 spectra were collected. These spectra came from 215 individuals of which 124 trees and 91 lianas, the leaves of 4 lianas were too small to measure the reflectance spectra. The spectra were all visualised in a plot grouping the subsamples of each leaf. From these graphs three possible problems were recognized, which are visualised in red in Figure 3.5. There were noisy or leafless spectra (A) in which cases the leaf-clip was either improperly covering the leaf, letting in spectral interference from the environment, or the spectrum was taken on accident. A second kind of faulty spectra was a zero spectrum (B), meaning a spectrum was saved where the black cap was used and no leaf was present. Both these kinds of spectra were removed, totaling 4 noisy spectra and 2 zero spectra. Finally, there were floating spectra (C), they were essentially hovering above the rest of the subsamples of the same leaf

with a similar distance over the entire spectrum. These last ones were outliers and were bias-corrected.

To identify the outliers, the mean reflectance ( $R_{\text{mean}}$ ) of each subsample over the

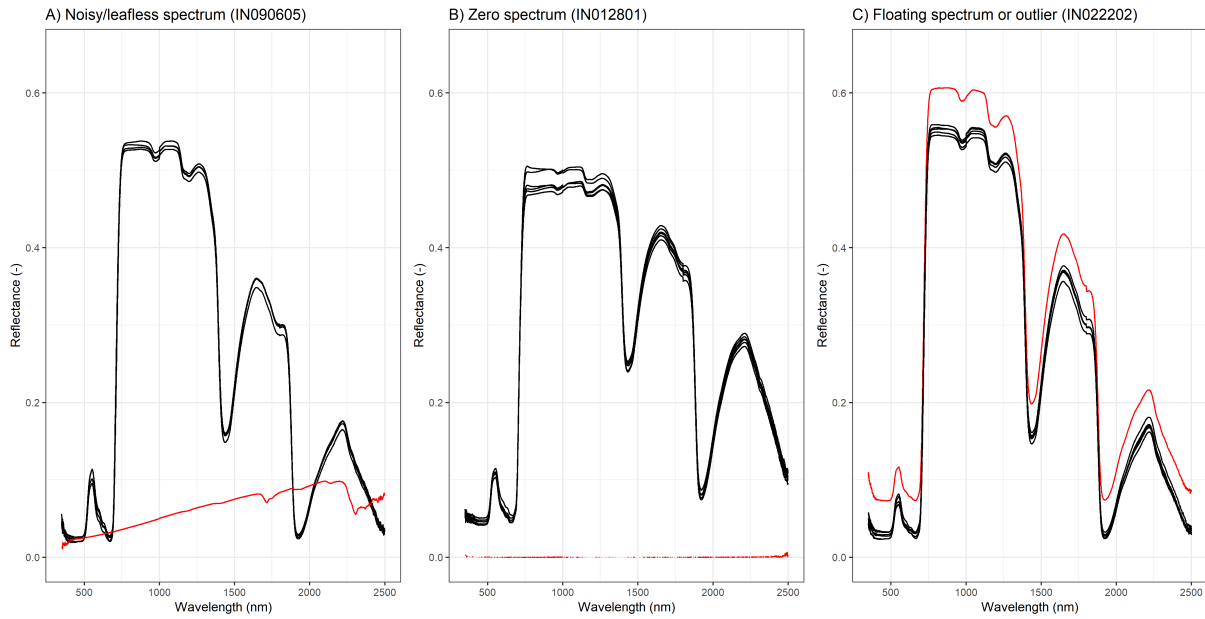


Figure 3.5: Examples of faulty spectra.

entire spectrum was calculated as well as the mean reflectance of the individual, the interquartile range (IQR), the first (Q1) and third quartile (Q3). Then a range was determined:  $[Q1(\text{Individual}) - 1.5 \times IQR; Q3(\text{Individual}) + 1.5 \times IQR]$ . If the mean of the subsample fell outside of this range, it was deemed an outlier and the following set of calculations was applied.

$$\text{Bias} = R_{\text{mean}}(\text{individual excl. outlier}) - R_{\text{mean}}(\text{outlier}) \quad (3.1)$$

$$\text{Reflectance}(\text{corrected outlier, } WV) = \text{reflectance}(\text{outlier, } WV) - \text{bias} \quad (3.2)$$

The results of this bias correction is visualised in Figure 3.6. For lianas, there were 58 outliers and for trees 111, meaning about 4.1% of the 4 160 spectra (excl. the 6 noisy and zero spectra) were identified as an outlier and subsequently bias-corrected.

The cleaned spectral dataset was then merged with the datasets with the information on the nutrient content ( $N$ ,  $C$ ,  $\delta^{15}N$ ,  $\delta^{13}C$ ), the leaf thickness and the structural characteristics ( $LMA$ ,  $C_w$ ). The nutrient content and structural characteristics were measured on the sampled individual level and coupled to all spectra of that individual. The leaf thickness was measured on a leaf level, coupling the average thickness of the 2 measurements to the corresponding leaf number.

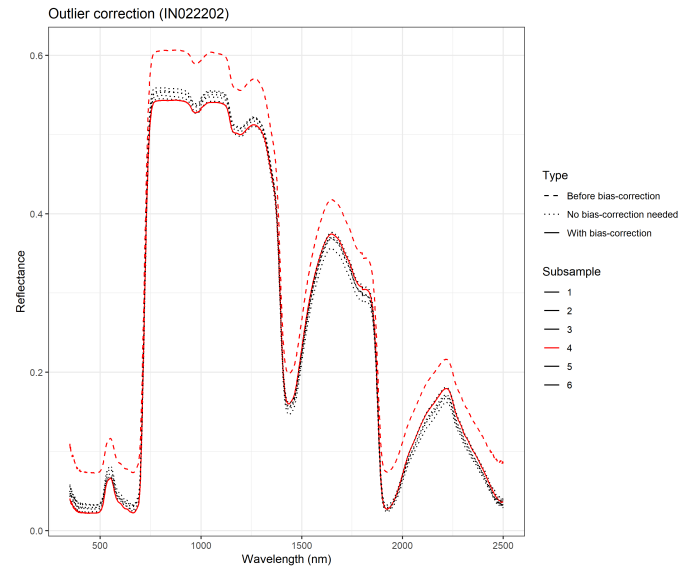


Figure 3.6: Bias-correction on an outlier, before correction: red dashed line, after correction: red solid line, non-outliers: black dotted lines.

## 3.4 Data analysis

### 3.4.1 Comparing leaf traits and reflectance bands

Different bands were extracted from the reflectance spectra, which according to literature seemed to contain most information (the chosen intervals are mentioned in Table 3.1). The average reflectance over these bands was calculated for each subsample. The distributions of the structural and biochemical leaf traits (C,  $\delta^{13}\text{C}$ , N,  $\delta^{15}\text{N}$ , LMA,  $C_w$  and the leaf thickness) as well as the reflectance in the specific bands were visualized using violin plots in combination with the "geom\_signif" function of the "ggsignif" package (Ahlmann-Eltze, 2022), which used the unpaired two-sample Wilcoxon test to evaluate the difference between the growth forms or seasons for each variable. To assess the statistical difference between the growth forms and the seasonality in each growth form a Kruskal-Wallis (non-parametric) test (KW) and the analysis of variance (ANOVA) test of package "stats" (Bolar, 2019) was used (Kruskal and Wallis, 1952). The relative changes between growth forms and seasons were determined, using trees or the wet season as the references respectively. The sunlit leaves were also extracted and assessed to remove effects from the canopy layer.

Table 3.1: Spectral bands

| Band   | Interval wavelength (nm) |
|--------|--------------------------|
| Blue   | 425 - 475                |
| Green  | 525 - 575                |
| Red    | 645 - 695                |
| NIR    | 750 - 950                |
| Water1 | 1425 - 1475              |
| Water2 | 1915 - 1965              |
| Water3 | 955 - 1005               |
| Water4 | 1215 - 1265              |

Subsequently the correlations of the different variables was analysed. The `corrplot` package (Wei et al., 2021) was used to calculate the correlation between different leaf traits. The correlation between the structural and biochemical leaf traits and the average reflectance in each band was calculated. This was done for both growth forms, all trees and lianas separately and then for each season and growth form. The difference between the dry and wet season correlation was visualised using a heatmap. The r-squared values ( $R^2$ ) of these correlation coefficients were computed as well. These values are the squares of the correlation coefficients and provide an indication of the strength of the correlation.

### 3.4.2 Linear mixed-effects models

The collected data is not independent, as multiple samples of the same species were sampled. Linear mixed-effects models allow us to assess fixed and random effects, a fixed effect is a parameter that does not vary in contrast to a random effect, which is a random variable parameter. In this case the response variable is the average reflectance in a certain spectrum band. The growth form, season and layer are the fixed effects and the species, individual and leaf are the random effects, which are nested in each other. Two linear mixed-effects models were applied to the whole dataset: Model 1 and 2 using "lmer" from package "lme4" (Bates et al., 2024). The difference was the introduction of variable slopes for the random effect for each growth form in Model 2. An ANOVA test was then performed and if the random slopes added a significant difference, the random slopes were used. The square root transformation was applied to improve normality.

Model 1 :

$$\sqrt{Band} \sim Growth\ form * Season + Layer + (1|Species / Individual / Leaf)$$

### 3. Materials and methods

---

Model 2 :

$$\sqrt{Band} \sim Growth\ form * Season + Layer \\ + (1 + Growth\ form|Species / Individual / Leaf)$$

The variance proportions of the model components were subsequently assessed with the following equations (3.3-3.5) using the packages "performance" (Lüdecke et al., 2024) and "partR2" (Stoffel et al., 2024).

$$\% \text{ Residual variance} = 100\% - R^2C \times 100\% \quad (3.3)$$

$$\% \text{ Random variance} = (R^2C - R^2M) \times 100\% \quad (3.4)$$

$$\% \text{ Fixed variance} = R^2M \times 100\% \quad (3.5)$$

The marginal pseudo- $R^2$  ( $R^2M$ ) is the percentage of variance explained by the fixed effects, the conditional pseudo- $R^2$  ( $R^2C$ ) is the percentage of variance explained by both fixed and random effects. The residual variance is not explained by either. The random variance was then subdivided between the different variables (species, individuals and leaves) with the "VarCorr" function.

However, the results of these models are not statistically interpretable before the model assumptions are checked. Gelman and Hill (2006) listed the four necessary assumptions to make statistically relevant conclusions.

1. A *linear* relation between the predictors, fixed and random, and the response variable. This assumption can be assessed visually by plotting the residuals against the predicted values as well as the locally estimated scatterplot smoothing (LOESS). If the points are randomly dispersed around the horizontal axis and the LOESS goes horizontally across the x-axis, this assumption is fulfilled.
2. There must be *no autocorrelation*, independence of the residuals. This assumption can be assessed with the Durbin-Watson test which is part of the "car" package (Fox et al., 2023) (Durbin and Watson, 1950). The Durbin-Watson statistic generally ranges from 0 to 4, a value of 2 suggests no autocorrelation, less than 2 suggests positive autocorrelation and above 2 suggests negative correlation. Additionally the residuals are plotted against the relevant predictors in violin plots to search for possible patterns.
3. The residuals should be *homoskedastic*, this can be assessed with the Levene test (Levene, 1960).
4. The residuals should be *normally* distributed. This can be visually assessed with quantile-quantile plots (Galton, 1886) and statistically with the Shapiro-Wilk normality test (Shapiro and Wilk, 1965; Shapiro et al., 1968).

---

However the last two assumptions are less important than the first two.

### **3.4.3 Partial least squares regression (PLSR)**

Variables in a dataset are often correlated, which complicates model analysis. Partial Least Squares Regression (PLSR) addresses this issue by combining the variables into components. Each variable is assigned a weight, and the components are formed by multiplying these weights with the variables and summing the results. This technique reduces dimensionality and minimizes correlation among variables. In PLSR, the weights are chosen to maximize the covariance between the dependent (response) and independent (predictor) variables first, and then to maximize the variance explained in the data. This dual focus allows PLSR to effectively capture the relationships between predictors and responses. PLSR is similar to Principal Component Analysis (PCA) in that both techniques create components from the original variables. However, while PCA determines weights to maximize the variance within the data, PLSR optimizes the weights to account for both the variance in the predictors and their covariance with the response variables. Consequently, PLSR assigns higher weights to the variables that best explain the dependent variable. In summary, PLSR offers a significant advantage by considering the relationship between predictors and responses, making it a powerful tool for predictive modeling (Abdi, 2003; Wold, 1966).

Here the protocol of Burnett et al. (2021) was applied to assess the relationship between the leaf reflectance at different wavelengths and specific structural and biochemical leaf traits: C,  $\delta^{13}\text{C}$ , N,  $\delta^{15}\text{N}$ , LMA,  $C_w$  and the leaf thickness. In order to predict these leaf traits from leaf-level hyperspectral data. Burnett et al. (2021) recommended removing the smallest and largest wavelengths since they tend to interfere, so the spectrum was limited from 400 to 2400 nm. Otherwise there are no 'hard' distribution assumptions PLSR relies on. First the data is split in a calibration and validation dataset, the data was grouped per individual so all spectra of the same individual are in the same dataset. Subsequently, the optimal amount of components was determined using PLSR with a maximum of 16 components and the model with the correct amount of components was fitted. The performance of this model is then evaluated using leave-one-out cross validation and the RMSE and  $R^2$  are reported. Afterwards, each wavelength is linked with its coefficient and variable influence of projection (VIP). A VIP higher than 0.8 indicates that the wavelength is of importance for the model prediction. Finally, a model uncertainty analysis is performed using a Jackknifing approach. This method removes one observation, retrains the model with the leftover samples and then uses the removed sample to evaluate the model's performance. This results in a plot with the mean, the minimum and the maximum coefficient and the 95% confidence interval indicated.

When the differences between growth forms and between seasons within growth

forms was assessed, when a wavelength's VIP was important in one growth form or season and not in the other, it was indicated by a solid line in the graphs.

#### 3.4.4 Discrimination hyperspectral data

To assess whether the spectral data was able to distinguish between seasons and growth forms, the Kullback-Leibler divergence ( $D_{KL}$ ) was calculated between both groups using equation 3.6, which was used over the full spectrum (350 - 2500 nm) (Kullback and Leibler, 1951; Visser et al., 2021).

$$D_{KL}(1|2) = \int_{Start\ WV}^{End\ WV} \log \left( \frac{\sigma_1(\lambda)}{\sigma_2(\lambda)} + \frac{\sigma_2(\lambda)^2 + (\mu_1(\lambda) - \mu_2(\lambda))^2}{2\sigma_1(\lambda)_2^2} - \frac{1}{2} \right) d\lambda \quad (3.6)$$

With  $\sigma_1(\lambda)$  and  $\sigma_2(\lambda)$  as the standard deviations of the first and second group for wavelength  $\lambda$  and  $\mu_1(\lambda)$  and  $\mu_2(\lambda)$  as the respective means.



## 4. RESULTS

### 4.1 Comparing leaf traits and reflectance bands

The results of the non parametric Kruskal-Wallis (KW) test and ANOVA test indicate the same significant differences. Lianas and trees exhibit significant differences in  $\delta^{13}\text{C}$  content,  $C_w$  and LMA (Table 4.1). For all these variables the mean value for the trees is higher than that of lianas as indicated by negative relative changes. The violin plots in Figure B.1 and B.2 compare the growth forms in both seasons and in the dry season the  $\delta^{13}\text{C}$  content is not significantly different anymore. The seasonal differences of the leaf traits within the growth forms are also studied and show no significant seasonal changes. When only the sunlit leaves are assessed, the leaf thickness of trees is also significantly higher than that of lianas. This is only present in the dry season (ANOVA: p-value = 0.00; KW: p-value = 0.03) and when the seasons are combined (ANOVA and KW: p-value = 0.00).

When both seasons and layers are taken into account, trends across the seasons are the same. However, if the growth forms are compared within seasons, there are some differences. The carbon, nitrogen and  $\delta^{15}\text{N}$  content are (insignificantly) higher in lianas in the dry season, but in the wet season, this is the opposite (Table 4.2).

Table 4.1: The average value  $\pm$  the standard deviation for each leaf trait for both growth forms (88 lianas and 107 trees) are given. The column ' $\Delta$  %' indicates whether there is a relative increase or decrease of the trait's value for a liana leaf compared to a tree leaf. The significant p-values between growth forms, according to the ANOVA test (ANOVA) as well as the Kruskal-Wallis test (KW), are underlined.

| Variable              | Unit                  | Tree              | Liana             | $\Delta$ % | ANOVA       | KW          | $\chi^2$ |
|-----------------------|-----------------------|-------------------|-------------------|------------|-------------|-------------|----------|
| C                     | [%]                   | 43.21 $\pm$ 3.13  | 42.95 $\pm$ 3.58  | -0.60      | 0.49        | 0.81        | 0.06     |
| $\delta^{13}\text{C}$ | [‰]                   | -29.82 $\pm$ 1.47 | -30.36 $\pm$ 1.19 | -1.81      | <u>0.01</u> | <u>0.00</u> | 9.23     |
| N                     | [%]                   | 1.93 $\pm$ 0.67   | 1.79 $\pm$ 0.48   | -7.31      | 0.10        | 0.26        | 1.26     |
| $\delta^{15}\text{N}$ | [‰]                   | 0.37 $\pm$ 1.47   | 0.51 $\pm$ 1.42   | 37.83      | 0.58        | 0.60        | 0.27     |
| $C_w$                 | [g.cm <sup>-2</sup> ] | 0.018 $\pm$ 0.01  | 0.013 $\pm$ 0.00  | -24.18     | <u>0.00</u> | <u>0.00</u> | 28.8     |
| LMA                   | [g.cm <sup>-2</sup> ] | 0.011 $\pm$ 0.00  | 0.009 $\pm$ 0.00  | -16.18     | <u>0.00</u> | <u>0.00</u> | 12.6     |
| Thickness             | [mm]                  | 0.25 $\pm$ 0.07   | 0.23 $\pm$ 0.05   | -6.98      | 0.06        | 0.25        | 1.34     |

Table 4.2: The average leaf traits for leaves of the sunlit layer for different growth forms and seasons. Columns SL and ST represent the relative seasonal change in lianas and trees, respectively, when transitioning from the wet to the dry season. Columns D and W indicate the relative change from a tree leaf to a liana leaf during the dry and wet seasons, respectively. The changes that are significant according to the ANOVA and Krustal-Wallis tests are underlined.

| Variable              | Unit                  | Liana: |       | Tree: |       | % SL  |       | % ST         |              | % D |  | % W |  |
|-----------------------|-----------------------|--------|-------|-------|-------|-------|-------|--------------|--------------|-----|--|-----|--|
|                       |                       | Dry    | Wet   | Dry   | Wet   |       |       |              |              |     |  |     |  |
| C                     | [‰]                   | 43.2   | 42.8  | 42.6  | 43.2  | 1.04  | -1.37 | 1.49         | -0.93        |     |  |     |  |
| $\delta^{13}\text{C}$ | [‰v.s. VPDB]          | -30.3  | -30.4 | -29.9 | -29.2 | -0.25 | 2.26  | 1.44         | <u>3.99</u>  |     |  |     |  |
| N                     | [‰]                   | 1.79   | 1.79  | 1.72  | 1.88  | -0.36 | -8.78 | 4.11         | -4.69        |     |  |     |  |
| $\delta^{15}\text{N}$ | [‰v.s. AIR]           | 0.74   | 0.38  | 0.11  | 0.44  | 93.7  | -75.4 | 592          | -12.04       |     |  |     |  |
| $C_w$                 | [g.cm <sup>-2</sup> ] | 0.01   | 0.01  | 0.02  | 0.02  | -9.81 | -5.96 | <u>-31.9</u> | <u>-29.0</u> |     |  |     |  |
| LMA                   | [g.cm <sup>-2</sup> ] | 0.01   | 0.01  | 0.01  | 0.01  | -1.08 | 10.8  | <u>-29.0</u> | <u>-20.5</u> |     |  |     |  |
| Thickness             | [mm]                  | 0.21   | 0.24  | 0.28  | 0.26  | -11.8 | 7.47  | <u>-25.4</u> | -9.11        |     |  |     |  |

There is a statistical difference between the leaf reflectance of the growth forms in the Green, Water1 and Water2 bands across both seasons (Figure 4.1). The mean reflectance in these bands is 1 to 2 % higher for lianas than trees (Table 4.3). If the data is split up between the seasons. There are no significant differences in the reflectance of any of the bands in the dry season (Figure B.3). The reflectance of lianas is (insignificantly) higher than trees in Green and Water1 band and (insignificantly) lower in the remaining bands. In the wet season, the reflectance of the Water1 and Water2 bands is significantly higher for lianas, in the other bands the reflectance is insignificantly higher for lianas (Figure B.4). When only the sunlit layer is taken into account, there are no added changes, however, the significance of the difference in the Water1 and Water2 bands increases.

## 4. Results

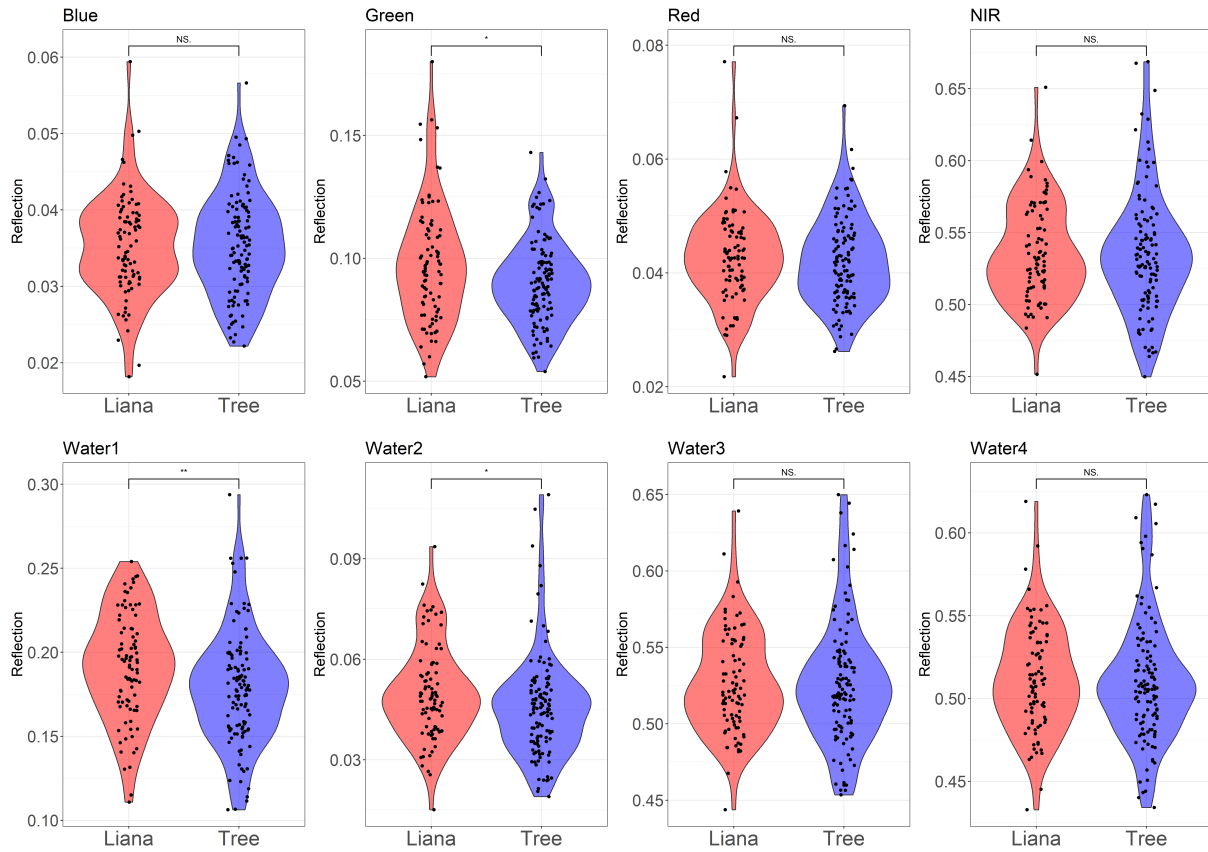


Figure 4.1: Violin plots for each band comparing the two growth forms. An ANOVA test was implemented to assess possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance). The y-axis varies per band.

Table 4.3: The mean reflectance and standard deviation (%) for each band and growth form. Bands that are significantly different between lianas and trees are underlined.

|              | Tree                             | Liana                            |               | Tree                             | Liana                            |
|--------------|----------------------------------|----------------------------------|---------------|----------------------------------|----------------------------------|
| Band         | Mean $\pm$ sd                    | Mean $\pm$ sd                    | Band          | Mean $\pm$ sd                    | Mean $\pm$ sd                    |
| Blue         | 0.04 $\pm$ 0.01                  | 0.04 $\pm$ 0.01                  | <u>Water1</u> | <u>0.17 <math>\pm</math>0.03</u> | <u>0.19 <math>\pm</math>0.03</u> |
| <u>Green</u> | <u>0.09 <math>\pm</math>0.02</u> | <u>0.10 <math>\pm</math>0.02</u> | <u>Water2</u> | <u>0.04 <math>\pm</math>0.02</u> | <u>0.05 <math>\pm</math>0.01</u> |
| Red          | 0.04 $\pm$ 0.01                  | 0.04 $\pm$ 0.01                  | Water3        | 0.53 $\pm$ 0.04                  | 0.53 $\pm$ 0.03                  |
| NIR          | 0.54 $\pm$ 0.05                  | 0.53 $\pm$ 0.03                  | Water4        | 0.51 $\pm$ 0.04                  | 0.51 $\pm$ 0.03                  |

The reflectance of lianas is not significantly influenced by seasonality. However, for trees, the reflectance is significantly different between the seasons, as the NIR, Water3 and Water4 bands have increased reflectance in the wet season compared to the dry season (Figure 4.2; Table B.1).

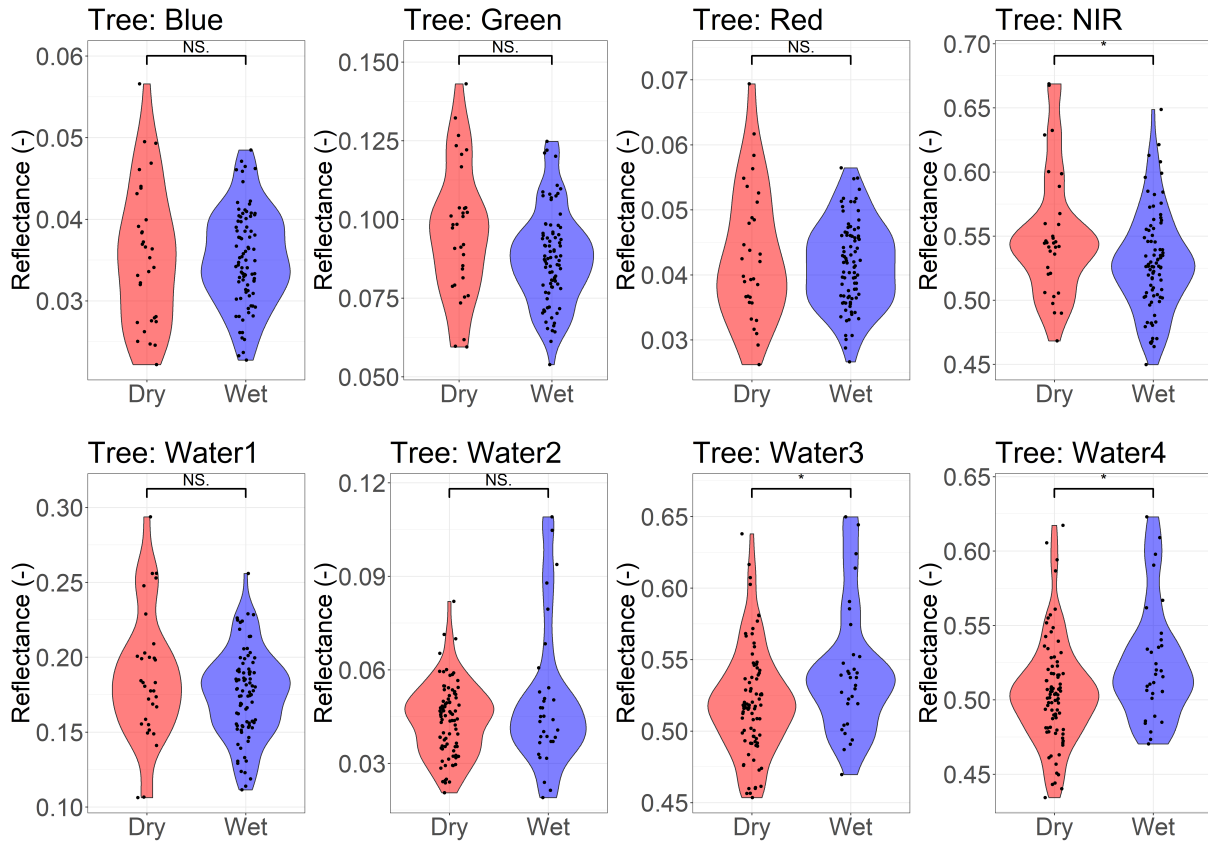
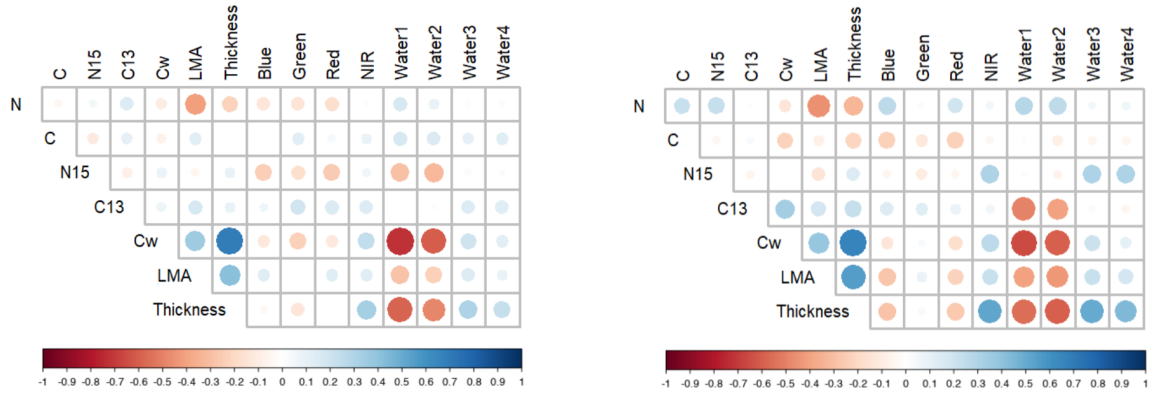


Figure 4.2: Violin plots for each band comparing them between the two seasons for trees. An ANOVA test was implemented to assess possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance). The y-axis varies per band.

Lianas seem to have less correlation between leaf traits and between the leaf traits and the reflectance in the bands, as the dots are both smaller and lighter in color (Figure 4.3). The mean and median correlation of lianas are, respectively, 0.17 and 0.13 and for trees, they are 0.22 and 0.19, only the relevant combinations are included.  $\delta^{13}\text{C}$  appears to be uncorrelated to the Water1 and Water2 bands in lianas, but in trees a negative correlation is present. For lianas  $\delta^{15}\text{N}$  seems to be negatively correlated with the Blue, Green, Red, Water1 and Water2 bands, but for trees, it is positively correlated with the NIR, Water3 and Water4 bands. When the correlation is calculated for each season separately, it results in higher correlations in most cases. The mean and median correlation of lianas increases to, respectively, 0.21 and 0.16 in the dry season and 0.21 and 0.15 in the wet season. For trees, it increases to 0.29 and 0.25 in the dry season and in the wet season the mean decreases to 0.21, but the median increases to 0.21.

## 4. Results



(a) The correlation in lianas.

(b) The correlation in trees.

Figure 4.3: The correlation (in)between leaf traits and reflectance in certain bands. A dark blue color is a positive correlation value, white is a correlation value of 0 and red is a negative correlation value. From top to bottom, the variables are: N, C,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ,  $C_w$ , LMA, Thickness, and from left to right: C,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ,  $C_w$ , LMA, Thickness, Blue, Green, Red, NIR, Water1, Water2, Water3 and Water4.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are noted as N15 and C13 in these figures.

All  $R^2$  values between the combinations of leaf traits across seasons are below 0.50. The  $R^2$  value between  $C_w$  and leaf thickness is the highest for both growth forms. They are, respectively, 0.48 and 0.45 for lianas and trees. The correlation between some leaf traits appears to be reversed for the growth forms, but in these cases the  $R^2$  values are low. For 14 of the 21 combinations, lianas have a lower correlation between the variables than trees. When the seasons are split up, the  $R^2$  values of the correlations between the different leaf traits for each season separately are still generally low. The  $R^2$  of the combination  $C_w$  and leaf thickness in lianas is 0.56 and 0.50 in the wet and dry season, respectively, and is the only one above 0.50. For trees, there are no  $R^2$  values above 0.50 for any season.

The correlation between the leaf traits and the reflectance in the different bands was also studied for both growth forms across seasons. The five highest correlations are the same for both growth forms: between  $C_w$  or leaf thickness and the Water1 or Water2 band and between thickness with the Water3 band, only the third and fourth place are swapped. Here only the  $R^2$  for the combination of  $C_w$  and the Water1 band in lianas is above 0.50 at 0.52. The biggest difference between the growth forms is the correlation between  $\delta^{13}\text{C}$  and the Water1 band, for trees the correlation is about -0.50 whereas for lianas it is -0.01. For 34 of the 56 combinations, the correlation is lower for lianas than for trees.

The  $R^2$  of the correlations between the leaf traits and the reflectance in the specific bands within the same growth form for each season separately is again generally

low. For lianas, only the  $R^2$  of the correlation between  $C_w$  and Water1 is above 0.50 (dry 0.63; wet 0.50). For trees there are two combinations of leaf thickness with Water1 and Water2, which are respectively 0.54 and 0.56 in the dry season, but in the wet season, they are respectively 0.21 and 0.27.

Between leaf traits, the seasonal difference seems relatively small with some notable exceptions ( $|\text{Difference correlation}| > 0.25$ ). For lianas, those are: N -  $\delta^{13}\text{C}$  (0.51) and N - leaf thickness (0.31),  $C_w$  - LMA (-0.30),  $C_w$  and LMA - leaf thickness (-0.25;-0.48). For trees, only the difference in correlation between LMA and  $C_w$  (0.32), is higher than 0.25. Both growth forms display seasonality in the correlation between the leaf traits and the reflectance in the specific bands. The correlation in trees between the reflectance and C and  $\delta^{13}\text{C}$  seems affected by seasonality (mostly higher in the dry season), but not for lianas. The opposite is the case for N and  $\delta^{15}\text{N}$ , there appears to be seasonality in lianas, but not in trees. The seasonality in the correlation between  $C_w$  and LMA and the reflectance is opposite between growth forms, for lianas negative and for trees positive. The correlation between thickness and reflectance is minimally affected by seasonality in lianas but is in trees with a higher correlation in the dry season (Figure 4.4).

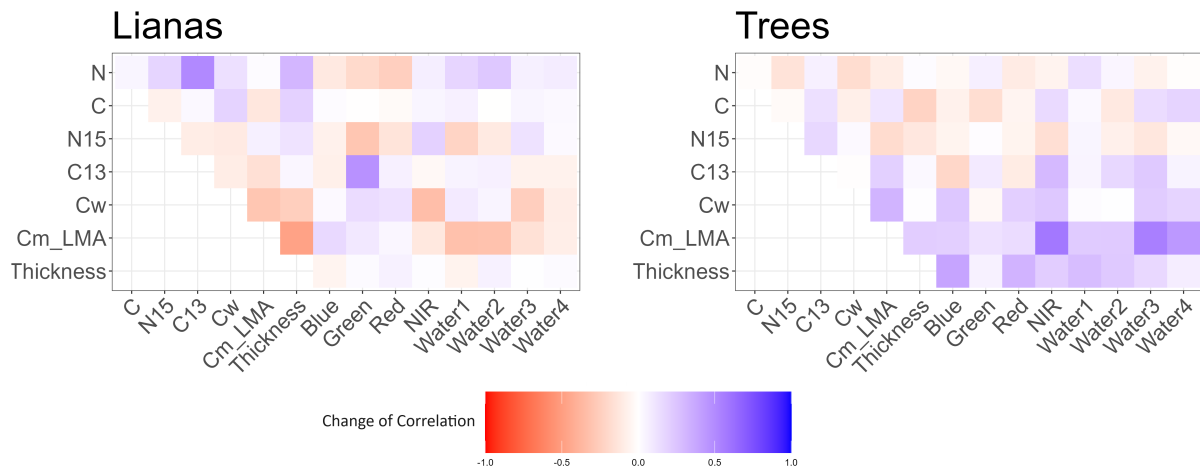


Figure 4.4: A heat map of the difference in absolute correlation between the dry and wet season (dry-wet). The differences are between -1 and 1, the color gradient goes from red (-1) to white (0) to blue (1). A positive value (blue) means there is more correlation in the dry season and a negative value (red) means the opposite. From top to bottom the variables are: N, C,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ,  $C_w$ , LMA, Thickness, and from left to right: C,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ,  $C_w$ , LMA, Thickness, Blue, Green, Red, NIR, Water1, Water2, Water3 and Water4.

## 4.2 Linear mixed-effects models

The linear mixed-effects models try to estimate the reflectance in the specific spectral bands based on the growth form, season and layer (fixed effects) as well as the

## 4. Results

species, individual and leaf (random effects). In the first model the slopes of the random effects are fixed and in the second they are variable for the growth form. The addition of the variable slopes for the random effects only results in significant differences in the Green and Red bands as the ANOVA test results in p-values of 0.047 and 0.009, respectively.

The residual plots of all bands (Figure B.5) do not present a clear pattern and the LOESS represented by the red lines in the plots follow the x-axis with small deviations at the end of the Red and Green bands. The Durbin-Watson statistic is close to 2 and the plots of the residuals against the predictors do not appear to have patterns, which suggests there is no autocorrelation present. In the Q-Q plots (Figure B.6) some tailing is present and the Shapiro-Wilk test states that the residuals are not normally distributed. The Levene test indicates that the residuals in the Blue, Green Red and Water4 bands are homoskedastic. The NIR, Water1, Water2 and Water3 bands appear to be heteroskedastic (Table B.2). However as previously mentioned the last two assumptions are less important. For the Blue and NIR bands there are no significant fixed effects, for all other bands the seasonal effect is significant and for the Water2 band the interaction between the growth form and the season is significant as well (Table B.3). Most of the explained variance comes from the random effects, as the average marginal pseudo- $R^2$  is 7.95% (0.7%-8.2%) and the average conditional pseudo- $R^2$  is 85.1% (65.3%-94.8%). The residual variance is on average 14.9% (5.2%-34.7%) and the highest in the Blue and Red bands, respectively 34.7% and 28.5% (Table 4.4).

Table 4.4: The pseudo- $R^2$  statistics of the linear mixed-effects models for each band. The marginal pseudo- $R^2$  ( $R^2M$ ) represents the amount of variance explained by the fixed effects. The conditional pseudo- $R^2$  ( $R^2C$ ) represents the amount of variance explained by the fixed and random effects. The residual variance is unexplained variance present in the model.

|              | Blue | Green | Red  | NIR  | Water1 | Water2 | Water3 | Water4 |
|--------------|------|-------|------|------|--------|--------|--------|--------|
| $R^2M$ (%)   | 0.7  | 8.2   | 2.7  | 2.3  | 6.9    | 4.5    | 3.0    | 3.5    |
| $R^2C$ (%)   | 65.3 | 87.1  | 71.5 | 90.7 | 94.8   | 86.7   | 91.9   | 93.0   |
| Residual (%) | 34.7 | 12.9  | 28.5 | 9.3  | 5.2    | 13.3   | 8.1    | 7.0    |

The variance is further divided between the different components, the fixed effects (growth form, season and layer) explain on average 3.5% with all except in the Green (8.2%) band below 5%. For most bands, except Green and Red, the difference in the reflectance is due to the different species. However, in the Water3 band, the difference on the individual level comes close with only 1.2% less explained variance. In the Green band, the difference between individuals is the largest component (25.8%) and in the Red band, the variation in the individuals due to the

different growth forms is the largest explained variance component (22.1%) (Figure 4.5; Table B.4).

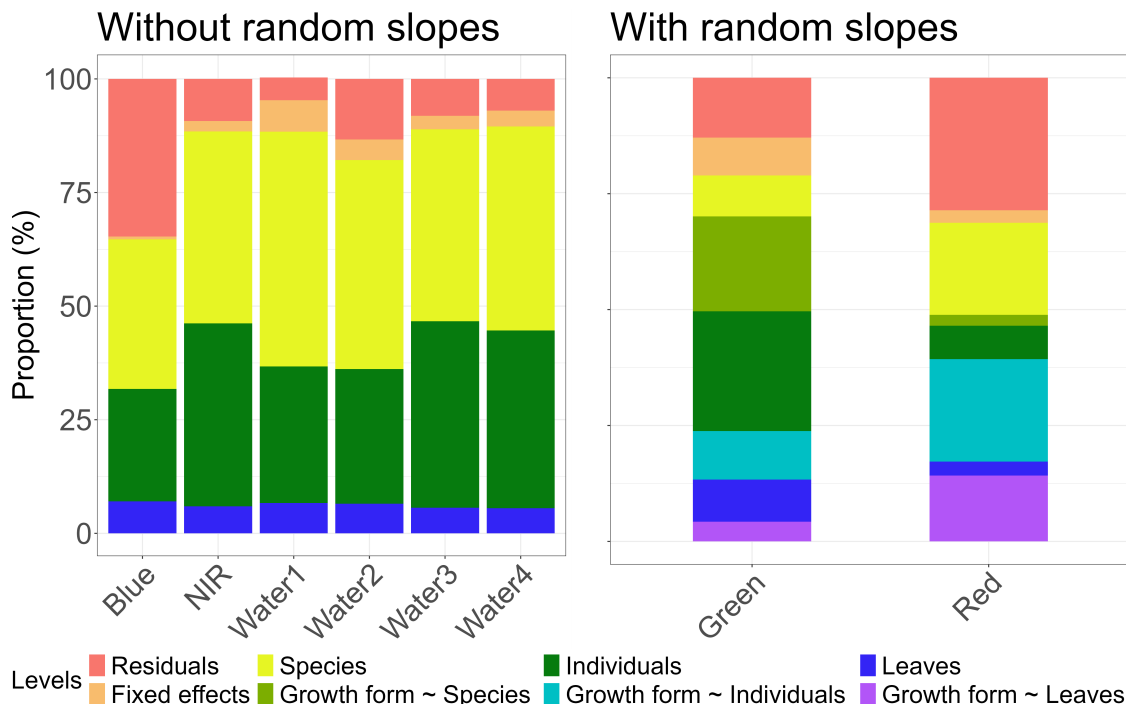


Figure 4.5: The explained variance proportions in response to each different predictor and the unexplained variance proportion of the specified spectral bands. The variance in the response, the reflectance in a certain band, is explained by fixed effects (growth form, season, layer and the interaction between growth form and season) and random effects (species, individual and leaves) or is unexplained (residuals). The models in the right panel use a fixed slope and in the left panel they use a random slope.

### 4.3 Partial least squares regression (PLSR)

The models performance is expressed in  $R^2$ , the root mean square error of prediction (RMSEP) and its percentage (RMSEP%). The average  $R^2$  for all variables for trees and lianas are 0.60 and 0.58, respectively. However, once the seasons are split up, the average  $R^2$  for trees in the dry and in the wet season, respectively, increases to 0.79 (+32.0%) and 0.62 (+4.30%). The average  $R^2$  for lianas in the dry and wet season increases to 0.82 (+39.1%) and 0.66 (+13.6%), respectively. There are two cases in which the  $R^2$  of the combined seasons is higher than when separated, LMA for trees in the wet season and N for lianas in the wet season. The relation between the reflectance in specific wavelengths is more outspoken within the seasons. The performance of the PLSR is generally better in the dry season for most leaf traits with some exceptions.

The RMSEP is quite low overall, in order to correctly interpret the value %RMSEP is more important as it represents the relative error. When both seasons are com-

## 4. Results

---

binned, most values are between 8% and 15% except  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for lianas, which are respectively 18.07% and 16.13%. After the seasons are split the %RMSEP goes down in 18 of the 28 cases with decreases between 0.42% and 6.27%, for the other 10 it increases between 0.09% and 1.91%. Overall the performance is adequate in most cases, but there is room for improvement (Table B.5).

The wavelengths important to estimate  $C_w$  appear to be quite stable between both growth forms as there are only a small number with differing importance and the differences present are relatively small. Lianas tend to have a higher number of important wavelengths for the estimation of  $\delta^{13}\text{C}$ , mostly in the VIS and NIR regions. The opposite trend is present for N as trees have a higher number of important wavelengths over the whole spectrum. The patterns of LMA and leaf thickness show that in the VIS and SWIR region, lianas have additional important wavelengths, whereas in the NIR region trees have additional wavelengths. For  $\delta^{15}\text{N}$  the NIR region has increased importance for trees and the SWIR region for lianas. For C, there seems to be no distinguishable pattern (Figure 4.6).

Next, the VIPs are compared for lianas between the different seasons. For N and  $\delta^{15}\text{N}$  the wet season has increased importance over the whole spectrum. For C there doesn't appear to be a pattern. However, for the other variables ( $C_w$ , LMA, Thickness, and  $\delta^{13}\text{C}$ ), the importance of the NIR region increased in the dry season, while the importance of the SWIR region increased in the wet season (Figure B.7). For trees, the dry season has increased importance for the  $\delta^{15}\text{N}$  over the whole spectrum. The VIS region appears to gain importance in the wet season for multiple variables. In the cases of  $C_w$ , LMA, N and  $\delta^{13}\text{C}$  the NIR region's importance increases in the dry season. In the SWIR region, the wavelengths between 1 900 and 2 000 appear to become more important in the dry season for  $C_w$ , LMA, leaf thickness and  $\delta^{13}\text{C}$  (Figure B.8).

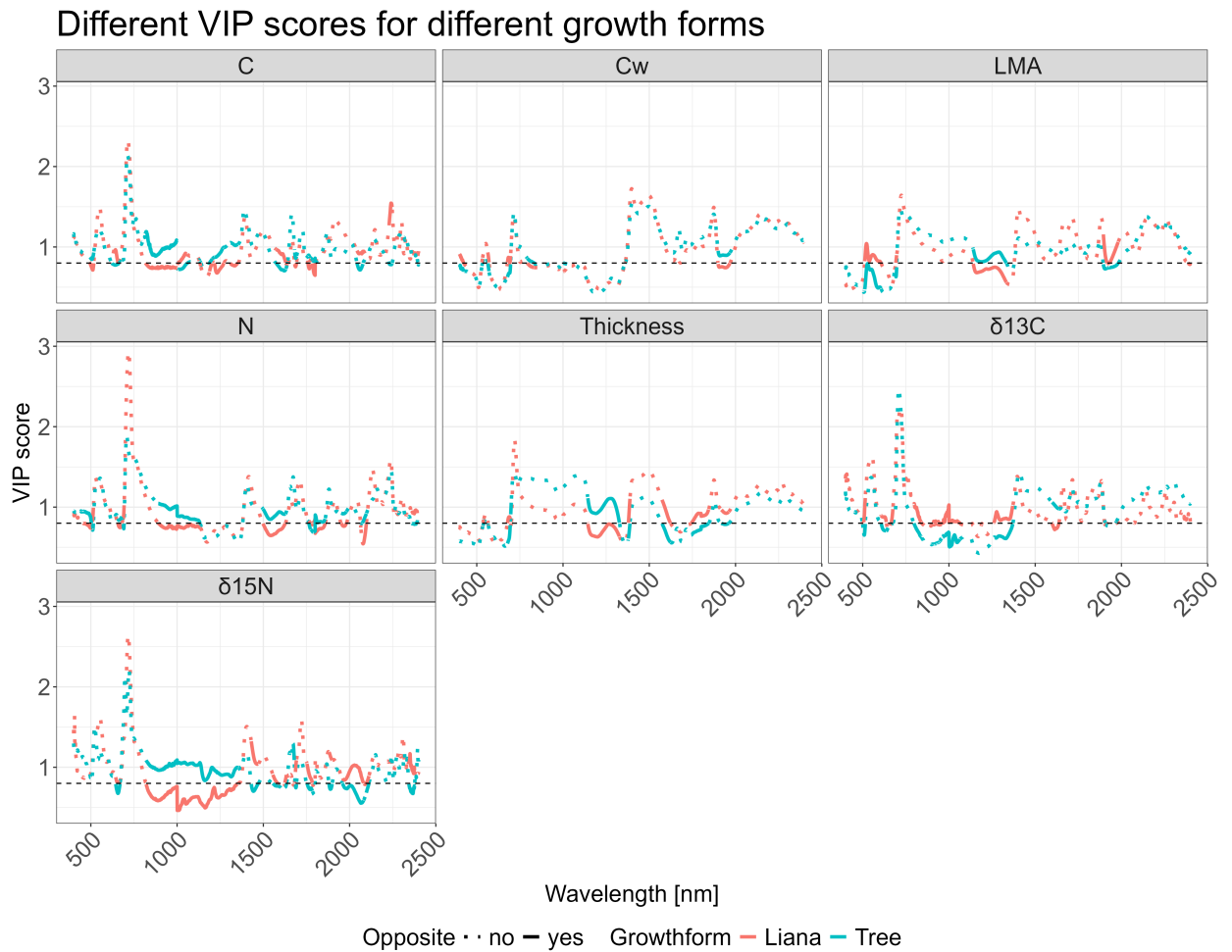


Figure 4.6: The VIP scores for all wavelengths. When they are important ( $> 0.80$ ; above the black dashed line) for one growth form and unimportant ( $< 0.80$ ; below the black line) for the other growth form, the lines are solid and otherwise the lines are dotted. The solid line indicates a difference between the two growth forms. From left to right and top to bottom the variables are C,  $C_w$ , LMA, N, Thickness,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$

## 4.4 Discrimination hyperspectral data

The Kullback-Leibler distance (164.64) indicates that the reflective spectra differ between the growth forms. However, this distance increases when the data is split up into different seasons, the difference between growth forms is thus greater within each season separately. The greatest distance is present when investigating the seasonality of the reflective spectra of tree leaves. The distance for liana leaves is more than 4 times smaller, which indicates that the seasonality of the reflective spectra in lianas is a lot smaller than in trees (Table 4.5).

#### 4. Results

Table 4.5: The Kullback-Leibler distance over the full spectrum (350 - 2 500 nm) between object 1 and 2. A value of 0 would mean identical distributions.

| Object 1           | Object 2           | $D_{KL}$ |
|--------------------|--------------------|----------|
| Liana              | Tree               | 164.64   |
| Tree - Dry season  | Liana - Dry season | 365.56   |
| Tree - Wet season  | Liana - Wet season | 242.38   |
| Tree - Dry season  | Tree - Wet season  | 392.83   |
| Liana - Dry season | Liana - Wet season | 93.09    |

The Kullback-Leibler divergence between lianas and trees (blue bars) seems uniformly distributed between 2.5 and 5. When split up between the seasons, certain wavelengths become more important. In all cases, the wavelengths larger than 1800 nm (SWIR) explain most of the divergence. The divergence in the dry season (orange bars) is also peaking in the NIR region. Whereas in the wet season (green bars) there is an extra peak in the VIS region. Both also have peaks between 1400 and 1500 nm (SWIR). The remaining seasonal divergence in trees (purple bars) is generally between 5 and 10 for all wavelengths except for the blue region. For lianas (red bars), the VIS region and the beginning of the NIR region are more important (Figure 4.7). From the predetermined bands, the NIR, Water2, Green, and Water1 bands have the highest divergence, listed with decreasing importance (Figure 4.8).

## Kullback-Leibler divergence distribution

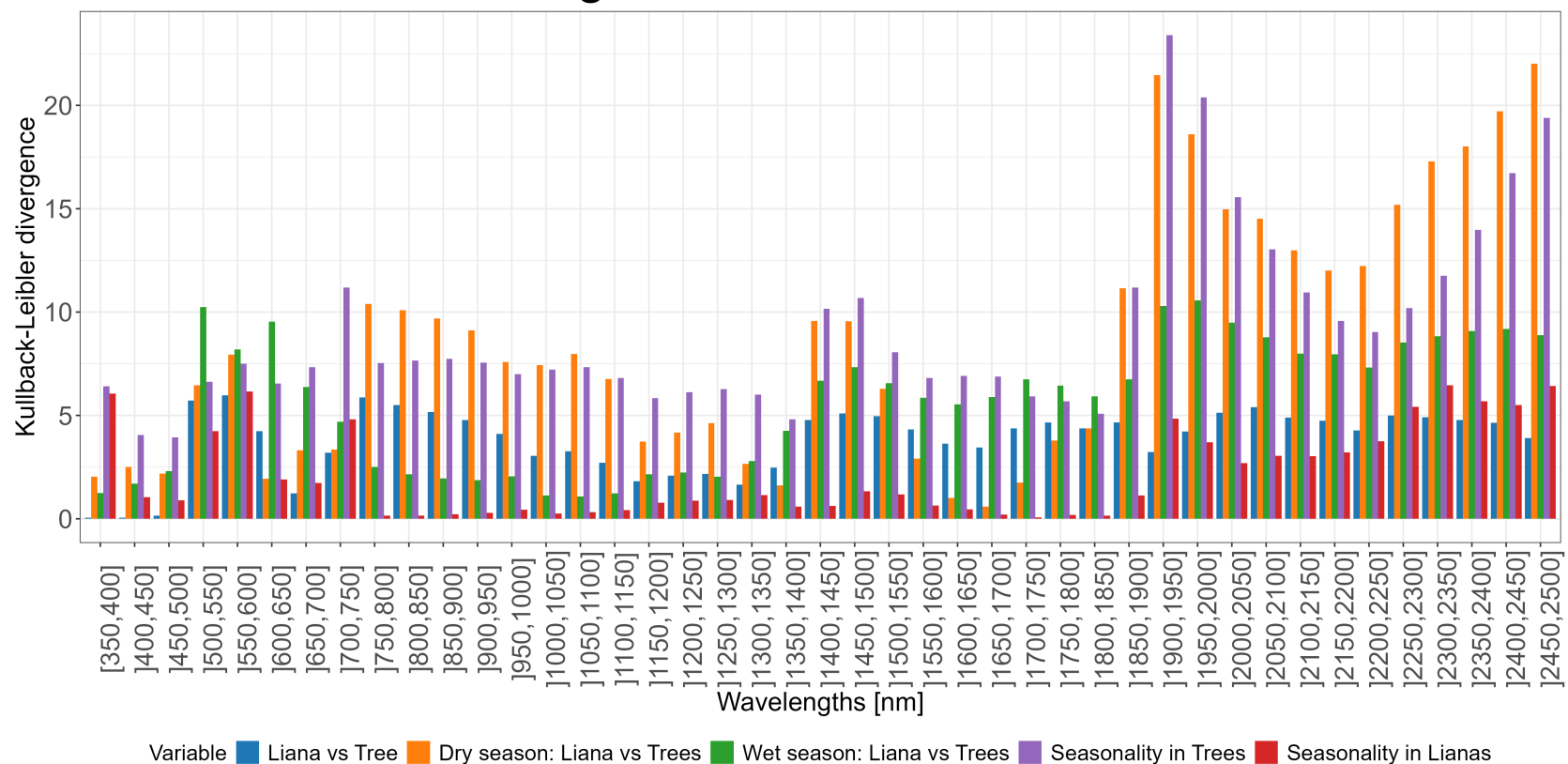


Figure 4.7: The sum of the Kullback-Leibler divergence between the different reflectance spectra for each 50 consecutive wavelengths. Except for the first bar which contains 51 wavelengths (350 - 400 nm). The bars indicate the statistical divergence of the reflectance spectra between the two groups. The higher the bar, the better the groups can be distinguished.

#### 4. Results

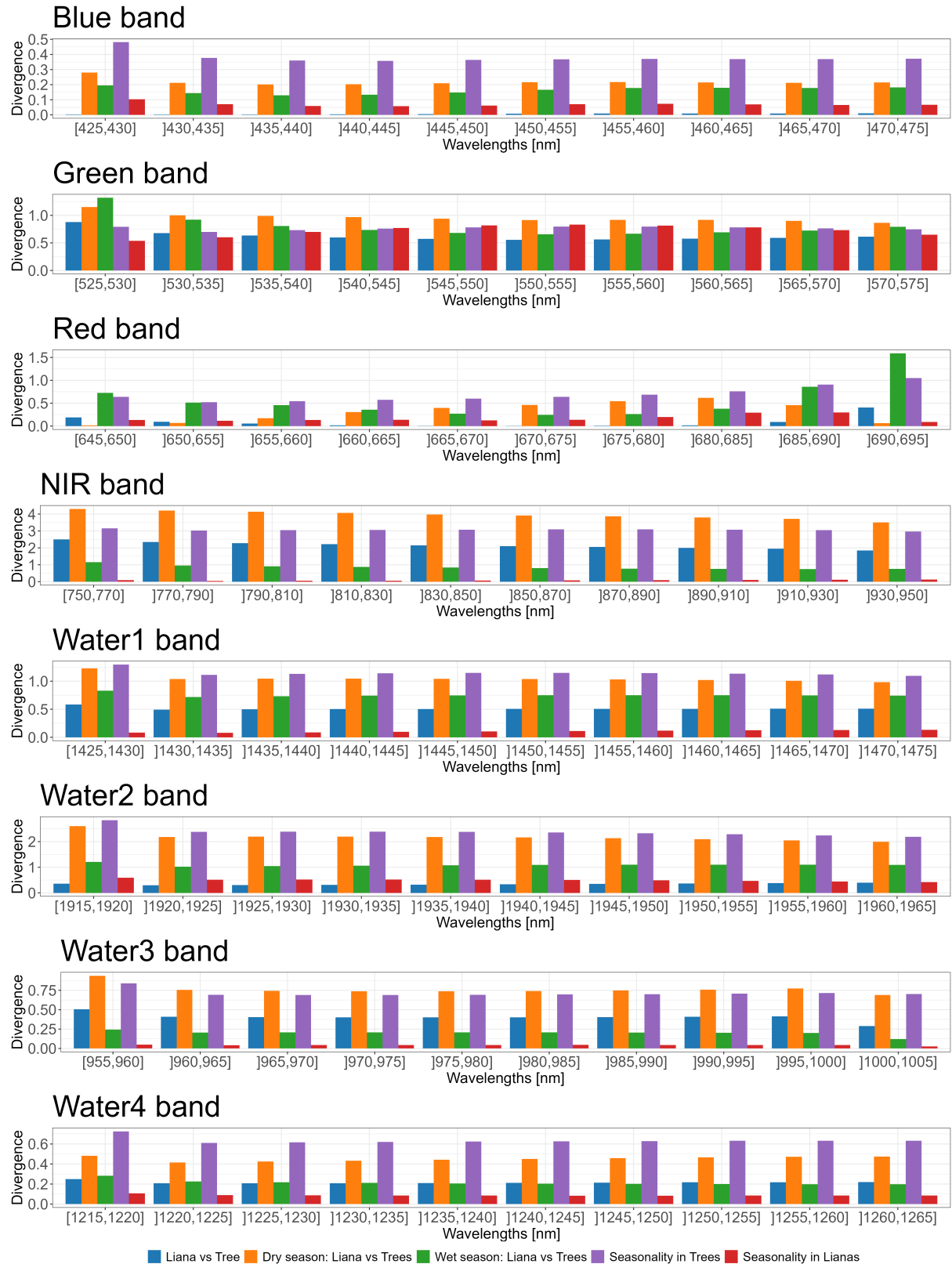


Figure 4.8: The sum of the Kullback-Leibler distance between the different reflectance spectra for each interval. The first interval contains one more wavelength than the other ones. The bars indicate the statistical divergence of the reflectance spectra between the two groups. The higher the bar, the better the groups can be distinguished. The y-axis varies between the different bands.



## 5. DISCUSSION

### 5.1 Differences between growth forms

#### 5.1.1 Differences in leaf structural and biochemical traits.

Significant differences are found for  $\delta^{13}\text{C}$ ,  $C_w$  and LMA between both growth forms across seasons. However, while in the wet season they are all still present, the difference of  $\delta^{13}\text{C}$  becomes insignificant in the dry season.  $\delta^{13}\text{C}$  has been linked to the intrinsic WUE of a plant, which is the ratio of the net assimilation to the stomatal conductance (Seibt et al., 2008). When  $\delta^{13}\text{C}$  is higher (less negative), the WUE is typically also higher (Lambers et al., 2008). The results indicate that lianas have a lower  $\delta^{13}\text{C}$  and thus a lower WUE, which is in contrast with the findings of Cai et al. (2009) and Domingues et al. (2007), who found higher  $\delta^{13}\text{C}$  content for lianas. Asner and Martin (2012) and Mello et al. (2020) did not find a significant difference between the growth forms. Section 2.3.2 on the water cycle in the Literature review mentioned that lianas might be able to regulate the stomatal closure and aperture more rapidly than trees (Campanello et al., 2016). This appears to not be the case according to the results of this thesis. However, Seibt et al. (2008) have indicated that  $\delta^{13}\text{C}$  alone is not a reliable indicator as it is influenced by other factors, such as gas exchange parameters. In order to determine if the WUE differs between growth forms, leaf gas exchange should be measured. As mentioned the  $\delta^{13}\text{C}$  is insignificantly lower for lianas than trees (0.15 ‰) in the dry season, generally this season should have the largest difference since during this time the lianas appear to have a growth advantage, which is hypothesized to be related to more access to water or a higher WUE (Sánchez-Azofeifa et al., 2009; Schnitzer, 2005).

The LMA for liana leaves is lower than trees (-16.2%), so there is less dry matter for an equal leaf surface area, which is consistent with the results of Seibt et al. (2008); Cai et al. (2009); Asner and Martin (2012) and Gallagher and Leishman (2012). A low LMA is associated with the quick-return end of the leaf economic spectrum, which has leaves with a higher photosynthetic capacity, shorter lifespan, thinner leaves and a higher N concentration (Wright et al., 2004a). However, the N concentration in lianas (1.79%) is (insignificantly) lower than in the tree leaves (1.93%). Except in the dry season when only the sunlit leaves are taken into account, then the N content is (insignificantly) higher in lianas (1.79%) than trees (1.72%). The results are only partially in accordance with past research, which indicated a higher

---

N content in lianas (Kazda and Salzer, 2000; Sánchez-Azofeifa et al., 2009; Mello et al., 2020). The research of Sánchez-Azofeifa et al. (2009) was also based in Panama (Parque Nacional San Lorenzo, southwest of BCI) and carried out in the wet season. They found concentrations of 2.0% and 1.83% for lianas and trees, respectively. In general, healthy leaves contain 1 to 5 % N (Karthika et al., 2018; Kirkby, 2005), so both growth forms are on the lower end of the range. The site is described to contain modest concentrations of KCl-extractable  $\text{NO}_3$  and  $\text{NH}_4$  (Yavitt et al., 2011). There is no definitive explanation for the lower N concentration, but it might indicate that lianas are not limited to the quick-return end of the leaf economic spectrum. During the grinding process, the petioles were also ground. This may have affected the ratio of the nutrients as the petioles contain more than 5 times the concentration of  $\text{NO}_3\text{-N}$  of the leaf blade (Minotti et al., 1989). There were more trees with compound leaves, which would result in a proportionally higher amount of petioles. However, since the other studies do not mention excluding the petioles it is assumed they also included them (Kazda and Salzer, 2000; Sánchez-Azofeifa et al., 2009; Mello et al., 2020). Liana leaves are thinner (-6.98%) than tree leaves and significantly thinner in case they are part of the sunlit layer of the canopy (-14.4%).

$C_w$  was also significantly different between both growth forms, lianas ( $0.013 \text{ g.cm}^{-2}$ ) contain less water relative to their leaf area than trees ( $0.018 \text{ g.cm}^{-2}$ ), which is consistent with the findings of Sánchez-Azofeifa et al. (2009). The results of this thesis do not completely align with the previously mentioned hypotheses of the competitive growth advantage of lianas. Their intrinsic WUE and nitrogen content appear to be lower. However, the intrinsic WUE does not talk about the water uptake of a plant or the depth of its root system. Thus, in case the lianas have a higher water uptake and simultaneously transpire a lot, the net water uptake could still be higher. The reason for lower the nitrogen content of lianas, especially in combination with the lower LMA, remains unclear, as it goes against past research.

### **5.1.2 Differences in reflectance**

The reflectance of the leaves is significantly higher for lianas in the Green, Water1 and Water2 bands, the average increase of reflectance is, respectively, 0.72%, 1.3% and 0.42%. However, in the dry season there appears to be no significant difference and in the wet season, the significance in the green band disappears. The difference in the Green band is consistent with the findings of Kalacska et al. (2007) and Castro-Esau et al. (2004). Kalacska et al. (2007) noted that the wavelength 535 nm was one of the most important ones to distinguish between both growth forms. The water1 and water2 bands do not contain the top 10 wavelengths specified, but 5 of the 10 are in the SWIR region. The water content of the leaf influences the reflectance between 1300 and 3 000 nm (Grant, 1987), as the four absorption bands for water are located at 1200 nm, 1450 nm, 1920 nm and 2 500 nm

(Jacquemoud and Ustin, 2019; Carter, 1991). The significantly lower  $C_w$  for lianas thus explains the increased reflectance as less water is available to absorb in these specific bands. The Water1 and Water2 bands, respectively, include the 1450 nm and the 1920 nm wavelengths. These are also one of the more negative correlations present in the dataset with the higher  $R^2$  values. The reason why there are no significant differences in the dry season cannot be explained by this water content as it is still significantly different. However, it might be influenced by the smaller sample size (dry season: 34 trees, 31 lianas; wet season: 84 trees and 61 lianas), since in the violin plots of Figure B.3 there seem to be some visual differences in the distributions.

The Kullback-Leibler divergence between both growth forms is 164.64 across seasons, 242.38 in the wet season and 365.56 in the dry season. This suggests the spectral signatures of both growth forms are distinguishable. In comparison, the divergence Visser et al. (2021) found between the two growth forms was between 500 and 1000, which is twice as high. However, the Kullback-Leibler divergence is dependent on the sample size and the research of Visser et al. (2021) used 411 tropical tree species and 47 tropical liana species. The wavelengths larger than 1900 nm appear to contain most of the divergence, suggesting that the SWIR region is where the spectral differences between lianas and trees are more clear. This is only partially consistent with the findings of Kalacska et al. (2007) as they found most of the top 100 most different wavelengths were in the VIS region (62%) and the SWIR region (34%) was only second.

The outcome of the linear mixed-effects models, however, indicates that the difference between growth forms is insignificant. The addition of the canopy layer did not add to the significant difference, which suggests that it is not necessary to sample the highest, sunlit leaves to compare the reflectance spectra. This is not in accordance with the research of Deepak et al. (2019), who researched the effect of canopy layers on the spectral signature in silver birch. The chlorophyll concentration in leaves also decreases with the height so absorption should be higher in lower layers (Ellsworth and Reich, 1993). This research did not focus on the effects of canopy layers and there are only a few individuals from which both layers were sampled. The models also show that the species- and individual-layer effects outweigh the effects of the growth form, season and layer which might be the cause of this (Figure 4.5).

The results of this thesis do agree with the general findings that lianas reflect more radiation than trees particularly in the SWIR region. The results of the ANOVA and Kruskal-Wallis tests and the Kullback-Leibler divergence contradict each other, however, the latter looks at the whole spectral range and indicates a more outspoken difference during the dry season. Thus after up-scaling of the methods, using re-

---

mote sensing would appear to be most effective during the dry season. This seems ideal as the weather conditions are better for drone surveys and there is less precipitation left on the leaves, which would interfere with the spectral data.

## 5.2 Seasonality in both growth forms

The Kruskal-Wallis test indicated that the leaf traits of both lianas and trees do not appear to be subjected to seasonal changes. The correlation between these variables was subject to some seasonal changes, however, since the  $R^2$  values were low this does not indicate relevant changes. Domingues et al. (2014) studied leaf-level photosynthesis limitation in the dry season and found leaves are not significantly limited in their photosynthesis, which is in line with the obtained results. Cai et al. (2009) studied the difference of variables due to the interaction of season and growth form. They found significant differences for  $\delta^{13}\text{C}$ , but not for N and LMA. So lianas and trees only responded differently to seasonal variation for  $\delta^{13}\text{C}$ . For lianas the reflectance of the specific bands also seems relatively unchanged by the seasons. The Kullback-Leibler divergence between the seasons in lianas is low at 93.09. The most important differences are located in the VIS and SWIR regions. In trees, the reflectance in the Water3 and Water4 bands was significantly higher in the wet season (+2%). The  $C_w$  (insignificantly) increases 0.1%, which doesn't explain the increased reflectance. The reflectance in the NIR band is significantly lower in the wet season (-2%). This decrease remains unexplained as well. The Kullback-Leibler divergence in trees (392.83) was four times higher than for lianas and most of it was located in the SWIR region, it was generally higher over the whole spectrum. This suggests seasonal changes in the leaf reflectance of trees as well.

In the linear mixed-effects models, seasonality significantly impacts the reflectance in all bands except the Blue and NIR bands. For the Water2 band, the interaction of the growth form and season is significant as well. This partially goes against the previously mentioned results. On the other hand, the variation explained by the season, growth form and layer is less than 10%, which indicates that most of the variation is due to the different species and individuals rather than the season.

If the research does not include hyperspectral plant data, the influence of the season is minimal and consequently, the results of different seasons, of the same location, could be compared. When the subject is on the optical properties of leaves, one should take seasonal differences into account when comparing data.

### 5.3 Reflective spectra as proxy indicators for leaf structural and biochemical traits (PLSR)

When the models include the data of both seasons, the performance is generally worse than when the seasons are split up. This indicates that seasonality is present in the link between the hyperspectral data of the plant and the different leaf traits. Figure 4.4 also indicates some seasonality in the link with the different correlations in the different seasons. So these models are the focus of the further discussion. The seasonal PLSR models generally perform quite well for  $C_w$  ( $R^2$ : 0.72-0.82; %RMSEP: 8.55-11.25) and thickness ( $R^2$ : 0.74-0.93; %RMSEP: 7.3-10.06), which is logical as the correlations between these variables and the reflectance in the bands are relatively high in comparison with the other leaf traits. Furthermore, the  $C_w$  directly impacts the absorption in the SWIR region and, generally, the thicker the leaf, the more absorption. Meerdink et al. (2016); Nunes et al. (2017) and Chen et al. (2022) examined the link of the water content of leaves, expressed as a percentage, and found similar model performances with the value for  $R^2$  between 0.83 and 0.89 and %RMSEP between 5.7% and 10.2%. For  $C_w$ , the most important wavelengths are rather similar between the two growth forms as well as both seasons for each growth form. The growth forms do have different important wavelengths for thickness, the NIR region (trees) and the SWIR region (lianas). These regions are also the drivers behind the seasonal changes in lianas. LMA also is estimated well by the models ( $R^2$ : 0.81-0.87; %RMSEP: 9.68-11.08%) except for trees in the wet season ( $R^2$ : 0.56; %RMSEP: 12.68%). Chen et al. (2022); Serbin et al. (2019); Nunes et al. (2017) and Yang et al. (2016) found a high performance with an  $R^2$  ranging from 0.81 to 0.93 and an %RMSEP ranging from 16.9% to 18.3%. Meerdink et al. (2016) on the other hand found an  $R^2$  of 0.56 and an %RMSEP of 18.3%. The VIS and SWIR regions are the cause of variance between the growth forms. For lianas, these regions are subject to seasonal effects and for trees the NIR region as well. For C and  $\delta^{13}\text{C}$ , the PLSR models are adequate at estimating in the dry season ( $R^2$ : 0.71-0.83; %RMSEP: 9.86-12.9%), however, in the wet season they are performing poorly ( $R^2$ : 0.48-0.55; %RMSEP: 12.47-15.4%). There thus seems to be a seasonal effect present for both growth forms that the model is not able to explain well. However, in Figure 4.4, the correlation seems rather unaffected by the seasons for lianas. This is at least in part consistent with previous findings, which demonstrated poor performance of models to predict C and  $\delta^{13}\text{C}$  from the reflectance spectra of a leaf with  $R^2$  overall under 0.70 for both. The wavelengths for both leaf traits appear not influenced by the season and minimally by the growth form in the NIR region. The N content of leaves appears to be estimated adequately ( $R^2$ : 0.78-0.86; %RMSEP: 9.06-10.77%) except for lianas in the wet season ( $R^2$ : 0.61; %RMSEP: 13.57%). Other studies found either  $R^2$  values between 0.55 and 0.63 (Nunes et al., 2017; Meerdink et al., 2016; Yang et al., 2016) or  $R^2$  values between 0.86 and 0.96 (Chen et al., 2022; Richardson and Reeves Iii, 2005). Thus the re-

---

sults of this study fall within the ranges previously found. The NIR region is variable between growth forms as well as between seasons in trees as it gains importance in trees and in the dry season. For its isotope  $\delta^{15}\text{N}$  on the other hand, the model performance is rather low ( $R^2$ : 0.45-0.67; %RMSEP: 13.21-15.63%). Past studies found variable performances for this isotope: Nunes et al. (2017) found poor model performance ( $R^2$ : 0.16; RMSEP%: 28.7%), where as Kleinebecker et al. (2009) and Chen et al. (2022) found a rather high  $R^2$  values between 0.85 and 0.99. However, the %RMSEP of the model of Chen et al. (2022) was 27.2%, which is rather high and indicates a lower performance.

For lianas, the importance of the NIR region increases in the dry season for  $C_w$ , LMA, Thickness, and  $\delta^{13}\text{C}$  and the SWIR region in the wet season. For  $C_w$ , LMA, Thickness, N, C and  $\delta^{13}\text{C}$  in trees, the importance of both the NIR and SWIR region increases in the dry season and the VIS region becomes more important during the wet season.

The reflective spectra appear to be a good proxy indicator for structural leaf traits ( $C_w$ , leaf thickness, LMA). On the other hand for biochemical leaf traits (C,  $\delta^{13}\text{C}$ , N,  $\delta^{15}\text{N}$ ), the performance seems to be case-specific for both season, growth form and location. The performance of the PLSR models does have room for improvement overall. Transforming the data to a more normal distribution might be an opportunity to accomplish this as the results are often better (Burnett et al., 2021). The NIR and SWIR regions appear to be more variable in importance between the different seasons.

## 5.4 Further research opportunities

To more effectively compare the leaf traits of lianas and trees, it would be interesting to carry out an in depth comparison of the lianas and their host trees, like the study of Sánchez-Azofeifa et al. (2009) for instance. The data collected for this thesis does encompass links between individuals, which makes linking the lianas with their host trees possible with the current data. Since the seasonal differences in this study are based on independent sampling, it would be interesting to follow certain individuals through time with an approach similar to Medina-Vega et al. (2021, 2022). They studied specific branches of lianas and trees for over a year and sampled them at least 13 times. This thesis did not take into account that not each species is sampled in both seasons, deciduous species for instance do not have leaves in both seasons. Theoretically, it is possible that the absence or presence of some species cause a lot of the differences between seasons.

Sampling more individuals of the same species to gain more of an idea of how the leaf traits change within the species also seems a promising research subject, as the linear mixed-effects models clearly show that the species effects or in general the most important ones to explain the variance of the leaf reflectance. In order to

## 5. Discussion

---

compare the WUE between growth forms using the  $\delta^{13}\text{C}$  content, rather than excavation of the root system, measuring the leaf gas exchanges of carbon and water seems necessary.



## 6. CONCLUSION

This study provides a comprehensive comparison of the structural and biochemical leaf traits between lianas and trees in a Neotropical forest, focusing on their reflectance spectra and how these traits change with the seasons. The research highlights several key findings:

The study found distinct differences between lianas and trees for the  $\delta^{13}\text{C}$  content, the equivalent water thickness and the LMA. The correlation of leaf traits was also different, but due to the low  $R^2$  no definitive conclusions could be drawn. However, the differences of the correlations of both growth forms suggest that both growth forms respond differently to environmental factors, which could impact their roles in forest dynamics. The results align with the general findings that liana leaves have a higher reflectance. The differences are mostly located in the SWIR region and appear to be linked with structural leaf traits. This answers the first two central research questions, some leaf traits differ between growth forms and the reflectance of liana leaves is generally higher than that of tree leaves.

The analysis revealed that seasonality significantly affects the reflectance spectra of trees, but not of the lianas and that the biochemical and structural leaf traits of both growth forms are not significantly different. Although some traits showed similar correlations in both seasons, others varied, indicating that both growth forms have adapted their physiological processes to seasonal changes to an extent. This seasonal effect complicates the use of spectral data for predicting leaf traits, as the performance of predictive models varied between dry and wet seasons for biochemical leaf traits. Returning to the third research question, seasonal changes affect the reflectance of leaves, but only in trees, and the leaf traits of neither group are affected.

Partial Least Squares Regression and linear mixed-effects models were used to analyze the data. While the reflective spectra served as good proxies for structural leaf traits such as leaf thickness and LMA, the models were less reliable for biochemical traits like carbon, nitrogen and their isotopes. This suggests that hyperspectral data can be used to assess structural leaf traits, which answers the final research question. Upscaling of these links is possible if the canopy structure, the leaf angle, the clumping of the leaves, the reflectance of the stem and branches etc. are taken into account. If successful, remote sensing can expedite forest research by

---

providing quick assessments of structural traits, but biochemical traits still require more direct measurement methods.

In conclusion, this research underscores the importance of considering both structural and biochemical traits, as well as their seasonal variations, in studies of forest dynamics. The findings contribute to a better understanding of how lianas and trees interact with their environment, which is crucial for predicting the future composition and functioning of Neotropical forests under changing climatic conditions.

Acknowledgement of the use of generative artificial intelligence, ChatGTP, to proof-read and improve the structure of the text (OpenAI, 2024). Using commands like: 'Reword', 'Check' etc.

# **BIBLIOGRAPHY**

- Abdi, H. (2003). Partial least square regression (pls regression). *Encyclopedia for research methods for the social sciences*, 6(4):792–795.
- Adouani, N., Limousy, L., Lendormi, T., and Sire, O. (2015). N<sub>2</sub>O and NO emissions during wastewater denitrification step: Influence of temperature on the biological process. *Comptes Rendus Chimie*, 18(1):15–22.
- Ahlmann-Eltze, C. (2022). ggsignif: Significance brackets for 'ggplot2'. R package version 0.6.4, URL: <https://cran.r-project.org/web/packages/ggsignif/index.html>, accessed May 11, 2024.
- Alfaro, E. (2002). Some characteristics of the annual precipitation cycle in central america and their relationships with its surrounding tropical oceans. *Tópicos Meteorológicos y Oceanográficos*, 9(2):88–103.
- Alho, C. J. R. (2008). The value of biodiversity. *Brazilian Journal of Biology*, 68:1115–1118.
- Álvarez-Cansino, L., Schnitzer, S. A., Reid, J. P., and Powers, J. S. (2015). Liana competition with tropical trees varies seasonally but not with tree species identity. *Ecology*, 96(1):39–45.
- Analytik (n.d.). Asd fieldspec 4 series. URL: <https://analytik.co.uk/product/portable-remote-sensing-spectroradiometry-fieldspec/>, accessed March 31, 2024.
- Andalib, M., Taher, E., Donohue, J., Ledwell, S., Andersen, M. H., and Sangrey, K. (2018). Correlation between nitrous oxide (N<sub>2</sub>O) emission and carbon to nitrogen (C/N) ratio in denitrification process: a mitigation strategy to decrease greenhouse gas emission and cost of operation. *Water Science and Technology*, 77(2):426–438.
- Andrade, J. L., Meinzer, F. C., Goldstein, G., and Schnitzer, S. A. (2005). Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees*, 19:282–289.
- Andresen, E., Arroyo-Rodríguez, V., and Escobar, F. (2018). *Tropical Biodiversity: The Importance of Biotic Interactions for Its Origin, Maintenance, Function, and Conservation*, pages 1–13. Springer International Publishing, Cham.

- 
- Antonelli, A., Ariza, M., Albert, J., Andermann, T., Azevedo, J., Bacon, C., Faurby, S., Guedes, T., Hoorn, C., Lohmann, L. G., et al. (2018). Conceptual and empirical advances in neotropical biodiversity research. *PeerJ*, 6:e5644.
- Asner, G. P. and Martin, R. E. (2012). Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition. *Ecology Letters*, 15(9):1001–1007.
- Avalos, G., Mulkey, S. S., and Kitajima, K. (1999). Leaf optical properties of trees and lianas in the outer canopy of a tropical dry forest. *Biotropica*, pages 517–520.
- Avalos, G., Mulkey, S. S., Kitajima, K., and Wright, S. J. (2007). Colonization strategies of two liana species in a tropical dry forest canopy. *Biotropica*, 39(3):393–399.
- Ayensu, E. S. and Stern, W. L. (1964). Systematic anatomy and ontogeny of the stem in passifloraceae. *Systematic plant studies*.
- Barton, P. K. and Atwater, J. W. (2002). Nitrous oxide emissions and the anthropogenic nitrogen in wastewater and solid waste. *Journal of environmental engineering*, 128(2):137–150.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., Krivitsky, P. N., Tanaka, E., and Jagan, M. (2024). lme4: Linear mixed-effects models using 'eigen' and s4. R package version 1.1-35.3, URL: <https://cran.r-project.org/web/packages/lme4/index.html>, accessed May 11, 2024.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., et al. (2010). Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, 329(5993):834–838.
- Belda, M., Holtanová, E., Halenka, T., and Kalvová, J. (2014). Climate classification revisited: from köppen to trewartha. *Climate research*, 59(1):1–13.
- Belote, R. T., Weltzin, J. F., and Norby, R. J. (2004). Response of an understory plant community to elevated [co<sub>2</sub>] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist*, 161(3):827–835.
- Berger, A. and Tricot, C. (1992). The greenhouse effect. *Surveys in geophysics*, 13(6):523–549.
- Berry, J. and Bjorkman, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of plant physiology*, 31(1):491–543.
- Billings, W. and Morris, R. J. (1951). Reflection of visible and infrared radiation from leaves of different ecological groups. *American Journal of Botany*, pages 327–331.

- Birch, A. L., Stallard, R. F., and Barnard, H. R. (2021). Precipitation characteristics and land cover control wet season runoff source and rainfall partitioning in three humid tropical catchments in central panama. *Water Resources Research*, 57(2):e2020WR028058.
- Bohlman, S. A. (2010). Landscape patterns and environmental controls of deciduousness in forests of central panama. *Global Ecology and Biogeography*, 19(3):376–385.
- Bolar, K. (2019). Stat: Interactive document for working with basic statistical analysis. R package version 0.1.0, URL: <https://cran.r-project.org/web/packages/STAT/index.html>, accessed May 11, 2024.
- Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., and Cargomo, P. (2008). Drought effects on litterfall, wood production and belowground carbon cycling in an amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1498):1839–1848.
- Burnett, A. C., Anderson, J., Davidson, K. J., Ely, K. S., Lamour, J., Li, Q., Morrison, B. D., Yang, D., Rogers, A., and Serbin, S. P. (2021). A best-practice guide to predicting plant traits from leaf-level hyperspectral data using partial least squares regression. *Journal of Experimental Botany*, 72(18):6175–6189.
- Cai, Z.-q. and Bongers, F. (2007). Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in xishuangbanna, south-west china. *Journal of Tropical Ecology*, 23(1):115–118.
- Cai, Z.-Q., Schnitzer, S. A., and Bongers, F. (2009). Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia*, 161:25–33.
- Campanello, P. I., Manzané, E., Villagra, M., Zhang, Y.-J., Panizza, A. M., di Francescantonio, D., Rodriguez, S. A., Chen, Y.-J., Santiago, L. S., and Goldstein, G. (2016). Carbon allocation and water relations of lianas versus trees. *Tropical tree physiology: Adaptations and responses in a changing environment*, pages 103–124.
- Carter, G. A. (1991). Primary and secondary effects of water content on the spectral reflectance of leaves. *American journal of botany*, 78(7):916–924.
- Castro-Esau, K. L., Sánchez-Azofeifa, G., and Caelli, T. (2004). Discrimination of lianas and trees with leaf-level hyperspectral data. *Remote Sensing of Environment*, 90(3):353–372.
- Cavaleri, M. A., Oberbauer, S. F., and Ryan, M. G. (2008). Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell & Environment*, 31(4):473–483.

- 
- Cernusak, L. A., Winter, K., Dalling, J. W., Holtum, J. A., Jaramillo, C., Körner, C., Leakey, A. D., Norby, R. J., Poulter, B., Turner, B. L., et al. (2013). Tropical forest responses to increasing atmospheric CO<sub>2</sub>: current knowledge and opportunities for future research. *Functional plant biology*, 40(6):531–551.
- Chambers, J. Q., Tribuzy, E. S., Toledo, L. C., Crispim, B. F., Higuchi, N., Santos, J. d., Araújo, A. C., Kruijt, B., Nobre, A. D., and Trumbore, S. E. (2004). Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications*, 14(sp4):72–88.
- Chave, J., Riéra, B., and Dubois, M.-A. (2001). Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology*, 17(1):79–96.
- Chen, L., Zhang, Y., Nunes, M. H., Stoddart, J., Khoury, S., Chan, A. H., and Coomes, D. A. (2022). Predicting leaf traits of temperate broadleaf deciduous trees from hyperspectral reflectance: can a general model be applied across a growing season? *Remote Sensing of Environment*, 269:112767.
- Chen, Y.-J., Cao, K.-F., Schnitzer, S. A., Fan, Z.-X., Zhang, J.-L., and Bongers, F. (2015). Water-use advantage for lianas over trees in tropical seasonal forests. *New Phytologist*, 205(1):128–136.
- Clark, D. B. and Clark, D. A. (1990). Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology*, 6(3):321–331.
- Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M. M., Chuyong, G., Dobrowski, S. Z., Grierson, P., Harms, K. E., Houlton, B. Z., et al. (2011). Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters*, 14(9):939–947.
- Collins, C. G., Wright, S. J., and Wurzbarger, N. (2016). Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. *Oecologia*, 180:1037–1047.
- Corlett, R. T. and Primack, R. B. (2011). *Tropical rain forests: an ecological and biogeographical comparison*. John Wiley & Sons.
- Cornthwaite, H. G. (1919). Panama rainfall. *Monthly Weather Review*, 47(5):298–302.
- Crang, R., Lyons-Sobaski, S., and Wise, R. (2018). *Parenchyma, Collenchyma, and Sclerenchyma*, pages 181–213. Springer International Publishing, Cham.
- Da Rocha, H. R., Goulden, M. L., Miller, S. D., Menton, M. C., Pinto, L. D., de Freitas, H. C., and e Silva Figueira, A. M. (2004). Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological applications*, 14(sp4):22–32.

- de Castro, F. and Fetcher, N. (1999). The effect of leaf clustering in the interception of light in vegetal canopies: theoretical considerations. *Ecological Modelling*, 116(2-3):125–134.
- De Deurwaerder, H., Hervé-Fernández, P., Stahl, C., Burban, B., Petronelli, P., Hoffman, B., Bonal, D., Boeckx, P., and Verbeeck, H. (2018). Liana and tree below-ground water competition—evidence for water resource partitioning during the dry season. *Tree physiology*, 38(7):1071–1083.
- De Guzman, M. E., Santiago, L. S., Schnitzer, S. A., and Álvarez-Cansino, L. (2017). Trade-offs between water transport capacity and drought resistance in neotropical canopy liana and tree species. *Tree Physiology*, 37(10):1404–1414.
- Deepak, M., Keski-Saari, S., Fauch, L., Granlund, L., Oksanen, E., and Keinänen, M. (2019). Leaf canopy layers affect spectral reflectance in silver birch. *Remote Sensing*, 11(24):2884.
- DeWalt, S. J. and Chave, J. (2004). Structure and biomass of four lowland neotropical forests. *Biotropica*, 36(1):7–19.
- DeWalt, S. J., Schnitzer, S. A., Chave, J., Bongers, F., Burnham, R. J., Cai, Z., Chuyong, G., Clark, D. B., Ewango, C. E., Gerwing, J. J., et al. (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, 42(3):309–317.
- di Porcia E Brugnera, M., Meunier, F., Longo, M., Krishna Moorthy, S. M., De Deurwaerder, H., Schnitzer, S. A., Bonal, D., Faybishenko, B., and Verbeeck, H. (2019). Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests. *Global change biology*, 25(11):3767–3780.
- Domingues, T. F., Martinelli, L. A., and Ehleringer, J. R. (2007). Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern amazonia, brazil. *Plant Ecology*, 193:101–112.
- Domingues, T. F., Martinelli, L. A., and Ehleringer, J. R. (2014). Seasonal patterns of leaf-level photosynthetic gas exchange in an eastern amazonian rain forest. *Plant Ecology & Diversity*, 7(1-2):189–203.
- Doughty, C. E. (2011). An in situ leaf and branch warming experiment in the amazon. *Biotropica*, 43(6):658–665.
- Doughty, C. E. and Goulden, M. L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences*, 113(G1).
- Drake, B. G., González-Meler, M. A., and Long, S. P. (1997). More efficient plants: a consequence of rising atmospheric co<sub>2</sub>? *Annual review of plant biology*, 48(1):609–639.

- 
- Duffy, J. E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, 7(8):437–444.
- Durbin, J. and Watson, G. S. (1950). Testing for serial correlation in least squares regression: I. *Biometrika*, 37(3/4):409–428.
- Duursma, R. A., Falster, D. S., Valladares, F., Sterck, F. J., Pearcy, R. W., Lusk, C. H., Sendall, K. M., Nordenstahl, M., Houter, N. C., Atwell, B. J., et al. (2012). Light interception efficiency explained by two simple variables: a test using a diversity of small-to medium-sized woody plants. *New Phytologist*, 193(2):397–408.
- El Attar, I., Hnini, M., Taha, K., and Aurag, J. (2022). Phosphorus availability and its sustainable use. *Journal of Soil Science and Plant Nutrition*, 22(4):5036–5048.
- Ellsworth, D. and Reich, P. (1993). Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*, 96:169–178.
- Enquist, B. J. and Enquist, C. A. (2011). Long-term change within a neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology*, 17(3):1408–1424.
- Estoque, M., Luque, J., Chandeck-Monteza, M., and Garcia, J. (1985). Effects of el nino on panama rainfall. *Geofisica Internacional*, 24(3):355–381.
- Evaristo, J., McDonnell, J. J., Scholl, M. A., Bruijnzeel, L. A., and Chun, K. P. (2016). Insights into plant water uptake from xylem-water isotope measurements in two tropical catchments with contrasting moisture conditions. *Hydrological Processes*, 30(18):3210–3227.
- Falkowski, P., Scholes, R., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Högberg, P., Linder, S., et al. (2000). The global carbon cycle: a test of our knowledge of earth as a system. *science*, 290(5490):291–296.
- Falster, D. S. and Westoby, M. (2003). Leaf size and angle vary widely across species: what consequences for light interception? *New phytologist*, 158(3):509–525.
- FAO (2020). *Global Forest Resources Assessment 2020: Main report*. Food and Agriculture Organization of the United Nations.
- Farquhar, G. D., von Caemmerer, S. v., and Berry, J. A. (1980). A biochemical model of photosynthetic co<sub>2</sub> assimilation in leaves of c<sub>3</sub> species. *planta*, 149:78–90.
- Farris, J. S. (1974). Formal definitions of paraphyly and polyphyly. *Systematic Zoology*, 23(4):548–554.
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., Heiberger, R., Krivitsky, P., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Nilsson, H., Ogle, D.,

## BIBLIOGRAPHY

---

- Ripley, B., Short, T., Venables, W., Walker, S., Winsemius, D., Zeileis, A., and R-Core (2023). *car: Companion to applied regression*. R package version 3.1-2, URL: <https://cran.r-project.org/web/packages/car/index.html>, accessed May 11, 2024.
- Fraedrich, K., Gerstengarbe, F.-W., and Werner, P. (2001). Climate shifts during the last century. *Climatic Change*, 50(4):405–417.
- Friedli, H., Löttscher, H., Oeschger, H., Siegenthaler, U., and Stauffer, B. (1986). Ice core record of the 13c/12c ratio of atmospheric co2 in the past two centuries. *Nature*, 324(6094):237–238.
- Friedlingstein, P., O'sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I. T., Olsen, A., Peters, G. P., et al. (2022). Global carbon budget 2022. *Earth System Science Data Discussions*, 2022:1–159.
- Gallagher, R. V. and Leishman, M. R. (2012). Contrasting patterns of trait-based community assembly in lianas and trees from temperate australia. *Oikos*, 121(12):2026–2035.
- Galton, F. (1886). Regression towards mediocrity in hereditary stature. *The Journal of the Anthropological Institute of Great Britain and Ireland*, 15:246–263.
- Gelman, A. and Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge university press.
- Granados, J. and Körner, C. (2002). In deep shade, elevated co2 increases the vigor of tropical climbing plants. *Global Change Biology*, 8(11):1109–1117.
- Grant, L. (1987). Diffuse and specular characteristics of leaf reflectance. *Remote Sensing of Environment*, 22(2):309–322.
- Greenhill, G. (1881). Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and the greatest height to which a tree of given proportions can grow. In *Proceedings of the Cambridge Philosophical Society*, volume 4, page 65.
- Grimes, A., Loomis, S., Jahnige, P., Burnham, M., Onthank, K., Alarcón, R., Cuenca, W. P., Martinez, C. C., Neill, D., Balick, M., et al. (1994). Valuing the rain forest: the economic value of nontimber forest products in ecuador. *Ambio*, pages 405–410.
- Harrison, A. F. (1987). *Soil organic phosphorous: a review of world literature*. CAB international.
- Hättenschwiler, S. and Körner, C. (2003). Does elevated co2 facilitate naturalization of the non-indigenous prunus laurocerasus in swiss temperate forests? *Functional Ecology*, 17(6):778–785.

- 
- Herbert, D. A. and Fownes, J. H. (1995). Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry*, 29:223–235.
- Hulme, M. and Viner, D. (1998). A climate change scenario for the tropics. *Climatic Change*, 39(2):145–176.
- Iltis, H. H., Doebley, J. F., Guzmán M, R., and Pazy, B. (1979). *Zea diploperennis* (gramineae): a new teosinte from mexico. *Science*, 203(4376):186–188.
- Ingwell, L. L., Joseph Wright, S., Becklund, K. K., Hubbell, S. P., and Schnitzer, S. A. (2010). The impact of lianas on 10 years of tree growth and mortality on barro colorado island, panama. *Journal of Ecology*, 98(4):879–887.
- IPCC (1990). *FAR Climate Change: Scientific Assessment of Climate Change*. The Press Syndicate of the University of Cambridge, Cambridge.
- IPCC (2007). *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]*. IPCC, Geneva, Switzerland.
- IPCC (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]*. Cambridge University Press.
- IPCC (2023). *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]*. IPCC, Geneva, Switzerland.
- Jacobs, M. (1982). The study of minor forest products. *Flora Malesiana Bulletin*, 35(1):3768–3782.
- Jacquemoud, S. and Ustin, S. (2019). *Leaf Optical Properties in Different Wavelength Domains*, page 124–169. Cambridge University Press.
- Jordan, C. and Uhl, C. (1978). Biomass of a "tierra firme" forest of the amazon basin.
- Kalacska, M., Bohlman, S., Sanchez-Azofeifa, G. A., Castro-Esau, K., and Caelli, T. (2007). Hyperspectral discrimination of tropical dry forest lianas and trees: Comparative data reduction approaches at the leaf and canopy levels. *Remote Sensing of Environment*, 109(4):406–415.
- Kampschreur, M. J., Temmink, H., Kleerebezem, R., Jetten, M. S., and van Loosdrecht, M. C. (2009). Nitrous oxide emission during wastewater treatment. *Water research*, 43(17):4093–4103.

- Karthika, K., Rashmi, I., and Parvathi, M. (2018). Biological functions, uptake and transport of essential nutrients in relation to plant growth. *Plant nutrients and abiotic stress tolerance*, pages 1–49.
- Kazda, M. (2015). Liana–nutrient relations. *Ecology of lianas*, pages 309–322.
- Kazda, M. and Mehltreter, K. (2001). Contrasting leaf nutrition and leaf mass per unit area in lianas and trees from the subtropical island martin garcia, argentina. *Dissertationes Botanicae*, 346:131–139.
- Kazda, M., Miladera, J., and Salzer, J. (2009). Optimisation of spatial allocation patterns in lianas compared to trees used for support. *Trees*, 23:295–304.
- Kazda, M. and Salzer, J. (2000). Leaves of lianas and self-supporting plants differ in mass per unit area and in nitrogen content. *Plant Biology*, 2(3):268–271.
- Ketellapper, H. (1963). Stomatal physiology. *Annual review of plant physiology*, 14(1):249–270.
- Kiehl, J. T. and Trenberth, K. E. (1997). Earth’s annual global mean energy budget. *Bulletin of the American meteorological society*, 78(2):197–208.
- Kira, T. and Ogawa, H. (1971). Assessment of primary production in tropical and equatorial forests. *Productivity of forest ecosystems*.
- Kirkby, E. (2005). Essential elements. *Encyclopedia of soils in the environment*, pages 478–485.
- Kleinebecker, T., Schmidt, S. R., Fritz, C., Smolders, A. J., and Hölzel, N. (2009). Prediction of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in plant tissues with near-infrared reflectance spectroscopy. *New Phytologist*, 184(3):732–739.
- Knipling, E. B. (1970). Physical and physiological basis for the reflectance of visible and near-infrared radiation from vegetation. *Remote sensing of environment*, 1(3):155–159.
- Koppen, W. (1936). Das geographische system de klimate. *Handbuch der klimatologie*.
- Kruskal, W. H. and Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American statistical Association*, 47(260):583–621.
- Kullback, S. and Leibler, R. A. (1951). On information and sufficiency. *The annals of mathematical statistics*, 22(1):79–86.
- Kumagai, T., Saitoh, T. M., Sato, Y., Takahashi, H., Manfroi, O. J., Morooka, T., Kuraji, K., Suzuki, M., Yasunari, T., and Komatsu, H. (2005). Annual water balance and seasonality of evapotranspiration in a bornean tropical rainforest. *Agricultural and Forest Meteorology*, 128(1):81–92.

- 
- Lal, R. (2008). Sequestration of atmospheric co<sub>2</sub> in global carbon pools. *Energy & Environmental Science*, 1(1):86–100.
- Lambers, H., Chapin, F. S., Pons, T. L., et al. (2008). *Plant physiological ecology*, volume 2, chapter 2. Springer.
- Larsen, M. C., Stallard, R. F., and Paton, S. (2021). Lutz creek watershed, barro colorado island, republic of panama. *Hydrological Processes*, 35(4):e14157.
- Laurance, W. F., Andrade, A. S., Magrach, A., Camargo, J. L., Valsko, J. J., Campbell, M., Fearnside, P. M., Edwards, W., Lovejoy, T. E., and Laurance, S. G. (2014). Long-term changes in liana abundance and forest dynamics in undisturbed amazonian forests. *Ecology*, 95(6):1604–1611.
- Laurance, W. F., Laurance, S. G., Ferreira, L. V., Rankin-de Merona, J. M., Gascon, C., and Lovejoy, T. E. (1997). Biomass collapse in amazonian forest fragments. *Science*, 278(5340):1117–1118.
- Laurance, W. F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P. M., D’Angelo, S., Jerozolinski, A., Pohl, L., and Lovejoy, T. E. (2001). Rain forest fragmentation and the structure of amazonian liana communities. *Ecology*, 82(1):105–116.
- Levene, H. (1960). Robust tests for equality of variances. *Contributions to probability and statistics*, pages 278–292.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., et al. (2010). Climate change impacts, adaptive capacity, and vulnerability of european forest ecosystems. *Forest ecology and management*, 259(4):698–709.
- Long, S. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric co<sub>2</sub> concentrations: has its importance been underestimated? *Plant, Cell & Environment*, 14(8):729–739.
- Lüdecke, D., Makowski, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., Wiernik, B. M., Thériault, R., Arel-Bundock, V., Jullum, M., gjo11, and Bacher, E. (2024). performance: Assessment of regression models performance. R package version 0.11.0, URL: <https://cran.r-project.org/web/packages/performance/index.html>, accessed May 11, 2024.
- Malhi, Y. and Phillips, O. L. (2004). Tropical forests and global atmospheric change: a synthesis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359(1443):549–555.
- Malvern Panalytical (2019). A newly designed leaf clip with smoother single-handed operation for the asd range. URL: <https://www.malvernpanalytical.com/fr/learn/knowledge-center/insights/a-newly-designed-leaf-clip-with-smoother-single-handed-operation-for-the-asd-range>, accessed March 31, 2024.

- Maréchaux, I., Bartlett, M. K., Iribar, A., Sack, L., and Chave, J. (2017). Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an amazonian forest. *Biology letters*, 13(1):20160819.
- Marvin, D. C., Asner, G. P., and Schnitzer, S. A. (2016). Liana canopy cover mapped throughout a tropical forest with high-fidelity imaging spectroscopy. *Remote Sensing of Environment*, 176:98–106.
- Marvin, D. C., Winter, K., Burnham, R. J., and Schnitzer, S. A. (2015). No evidence that elevated  $\text{CO}_2$  gives tropical lianas an advantage over tropical trees. *Global Change Biology*, 21(5):2055–2069.
- Mayaux, P., Achard, F., and Malingreau, J.-P. (1998). Global tropical forest area measurements derived from coarse resolution satellite imagery: a comparison with other approaches. *Environmental Conservation*, 25(1):37–52.
- McCree, K. and Keener, M. (1974). Effect of atmospheric turbidity on the photosynthetic rates of leaves. *Agricultural Meteorology*, 13(3):349–357.
- McCree, K. J. (1981). Photosynthetically active radiation. In *Physiological plant ecology I: responses to the physical environment*, pages 41–55. Springer.
- McMahon, T. (1973). Size and shape in biology: elastic criteria impose limits on biological proportions, and consequently on metabolic rates. *Science*, 179(4079):1201–1204.
- McMurtrie, R. E., Norby, R. J., Medlyn, B. E., Dewar, R. C., Pepper, D. A., Reich, P. B., and Barton, C. V. (2008). Why is plant-growth response to elevated  $\text{CO}_2$  amplified when water is limiting, but reduced when nitrogen is limiting? a growth-optimisation hypothesis. *Functional Plant Biology*, 35(6):521–534.
- Medina-Vega, J. A., Bongers, F., Schnitzer, S. A., and Sterck, F. J. (2021). Lianas explore the forest canopy more effectively than trees under drier conditions. *Functional Ecology*, 35(2):318–329.
- Medina-Vega, J. A., Wright, S. J., Bongers, F., Schnitzer, S. A., and Sterck, F. J. (2022). Vegetative phenologies of lianas and trees in two neotropical forests with contrasting rainfall regimes. *New Phytologist*, 235(2):457–471.
- Meerdink, S. K., Roberts, D. A., King, J. Y., Roth, K. L., Dennison, P. E., Amaral, C. H., and Hook, S. J. (2016). Linking seasonal foliar traits to  $\text{VSWIR-TIR}$  spectroscopy across california ecosystems. *Remote Sensing of Environment*, 186:322–338.
- Mello, F. N., Estrada-Villegas, S., DeFilippis, D. M., and Schnitzer, S. A. (2020). Can functional traits explain plant coexistence? a case study with tropical lianas and trees. *Diversity*, 12(10):397.
- Mengel, K. and Kirkby, E. A. (1987). *Principles of plant nutrition*.

- 
- Merzlyak, M. N., Chivkunova, O. B., Melø, T., and Naqvi, K. R. (2002). Does a leaf absorb radiation in the near infrared (780–900 nm) region? a new approach to quantifying optical reflection, absorption and transmission of leaves. *Photosynthesis Research*, 72:263–270.
- Meunier, F., van Der Heijden, G. M., Schnitzer, S. A., De Deurwaerder, H. P., and Verbeeck, H. (2021). Lianas significantly reduce aboveground and belowground carbon storage: A virtual removal experiment. *Frontiers in Forests and Global Change*, 4:663291.
- Meunier, F., Visser, M. D., Shiklomanov, A., Dietze, M. C., Guzmán Q, J. A., Sanchez-Azofeifa, G. A., De Deurwaerder, H. P., Krishna Moorthy, S. M., Schnitzer, S. A., Marvin, D. C., et al. (2022). Liana optical traits increase tropical forest albedo and reduce ecosystem productivity. *Global change biology*, 28(1):227–244.
- Minotti, P. L., Hankinson, T. J., Grubinger, V. P., and Wien, H. C. (1989). Whole leaves versus petioles for assessing the nitrogen status of tomatoes. *HortScience*, 24(1):84–86.
- Mitchard, E. T. (2018). The tropical forest carbon cycle and climate change. *Nature*, 559(7715):527–534.
- Moss, R. and Loomis, W. (1952). Absorption spectra of leaves. i. the visible spectrum. *Plant physiology*, 27(2):370.
- Muller-Landau, H. C. and Visser, M. D. (2019). How do lianas and vines influence competitive differences and niche differences among tree species? concepts and a case study in a tropical forest. *Journal of Ecology*, 107(3):1469–1481.
- Myers, N. (1988). Tropical forests: much more than stocks of wood. *Journal of tropical ecology*, 4(2):209–221.
- Nam, V. T., Anten, N. P., and van Kuijk, M. (2018). Biomass dynamics in a logged forest: the role of wood density. *Journal of plant research*, 131:611–621.
- Nault, L. and Findley, W. (1981). *Zea diploperennis*: a primitive relative offers new traits to improve corn.
- Neftel, A., Oeschger, H., Schwander, J., Stauffer, B., and Zumbunn, R. (1982). Ice core sample measurements give atmospheric co<sub>2</sub> content during the past 40,000 yr. *Nature*, 295(5846):220–223.
- Nepstad, D. C., Tohver, I. M., Ray, D., Moutinho, P., and Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, 88(9):2259–2269.
- Nobel, P. and Long, S. (1985). Canopy structure and light interception. In *Techniques in bioproductivity and photosynthesis*, pages 41–49. Elsevier.

## BIBLIOGRAPHY

---

- Notch (n.d.). "notch big shot" throw weight launcher. URL: <https://notchequipment.com/notch-big-shot-throw-weight-launcher/>, accessed March 31, 2024.
- Nunes, M. H., Davey, M. P., and Coomes, D. A. (2017). On the challenges of using field spectroscopy to measure the impact of soil type on leaf traits. *Biogeosciences*, 14(13):3371–3385.
- Ogawa, H. (1965). Comparative ecological studies on three main types of forest vegetation in thailand ii. *Structure and floristic composition.: nature & Life in SE Asia*, 4:49–80.
- Ogden, F. L., Crouch, T. D., Stallard, R. F., and Hall, J. S. (2013). Effect of land cover and use on dry season river runoff, runoff efficiency, and peak storm runoff in the seasonal tropics of central panama. *Water Resources Research*, 49(12):8443–8462.
- OpenAI (2024). Chatgpt (gpt-4). URL: <https://www.openai.com/chatgpt>, accessed May 22, 2024.
- Pajares, S. and Bohannan, B. J. (2016). Ecology of nitrogen fixing, nitrifying, and denitrifying microorganisms in tropical forest soils. *Frontiers in microbiology*, 7:1045.
- Paton, S. (2024). 2023 meteorological and hydrological summary for barro colorado island.
- Patton, C. P. (1962). A note on the classification of dry climates in the koppen system.
- Penalosa, J. (1984). Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, pages 1–9.
- Peters, C. M., Gentry, A. H., and Mendelsohn, R. O. (1989). Valuation of an amazonian rainforest. *Nature*, 339:655–656.
- Phillips, O. L., Aragão, L. E., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., et al. (2009). Drought sensitivity of the amazon rainforest. *Science*, 323(5919):1344–1347.
- Phillips, O. L., Vásquez Martínez, R., Arroyo, L., Baker, T. R., Killeen, T., Lewis, S. L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez Vargas, P., et al. (2002). Increasing dominance of large lianas in amazonian forests. *Nature*, 418(6899):770–774.
- Phillips, O. L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T. R., and Núñez Vargas, P. (2005). Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, 86(5):1250–1258.

- 
- Phillips, P. L., Welch, J. B., and Kramer, M. (2004). Seasonal and spatial distributions of adult screwworms (diptera: Calliphoridae) in the panama canal area, republic of panama. *Journal of Medical Entomology*, 41(1):121–129.
- Pickett, S. T. and White, P. S. (2013). *The ecology of natural disturbance and patch dynamics*. Elsevier.
- Poorter, L., van der Sande, M. T., Arets, E. J., Ascarrunz, N., Enquist, B. J., Finegan, B., Licona, J. C., Martínez-Ramos, M., Mazzei, L., Meave, J. A., et al. (2017). Biodiversity and climate determine the functioning of neotropical forests. *Global ecology and biogeography*, 26(12):1423–1434.
- Posit (2024). Rstudio ide. URL: <https://posit.co/downloads/>, accessed May 11, 2024.
- Putz, F. (1991). Silvicultural effects of lianas. *The biology of vines*, pages 493–501.
- Putz, F. et al. (1995). Vines in treetops: consequences of mechanical dependence. *Forest canopies.*, pages 311–323.
- Putz, F. E. (1983). Liana biomass and leaf area of a " tierra firme" forest in the rio negro basin, venezuela. *Biotropica*, pages 185–189.
- Putz, F. E. (1984a). How trees avoid and shed lianas. *Biotropica*, pages 19–23.
- Putz, F. E. (1984b). The natural history of lianas on barro colorado island, panama. *Ecology*, 65(6):1713–1724.
- Putz, F. E. (1990). Liana stem diameter growth and mortality rates on barro colorado island, panama. *Biotropica*, 22(1):103–105.
- R Core Team (2021). R: A language and environment for statistical computing. <https://www.R-project.org/>, accessed May 11, 2024.
- Rabideau, G., French, C., and Holt, A. (1946). The absorption and reflection spectra of leaves, chloroplast suspensions, and chloroplast fragments as measured in an ulbricht sphere. *American Journal of Botany*, pages 769–777.
- Reed, S. C., Townsend, A. R., Taylor, P. G., and Cleveland, C. C. (2011). Phosphorus cycling in tropical forests growing on highly weathered soils. *Phosphorus in action: biological processes in soil phosphorus cycling*, pages 339–369.
- Reich, P. B., Grigal, D. F., Aber, J. D., and Gower, S. T. (1997). Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*, 78(2):335–347.
- Renée Brooks, J., Barnard, H. R., Coulombe, R., and McDonnell, J. J. (2010). Eco-hydrologic separation of water between trees and streams in a mediterranean climate. *Nature Geoscience*, 3(2):100–104.

- Richardson, A. D. and Reeves lii, J. B. (2005). Quantitative reflectance spectroscopy as an alternative to traditional wet lab analysis of foliar chemistry: near-infrared and mid-infrared calibrations compared. *Canadian Journal of Forest Research*, 35(5):1122–1130.
- Roman, A. and Ursu, T. (2016). Multispectral satellite imagery and airborne laser scanning techniques for the detection of archaeological vegetation marks. *Landscape archaeology on the northern frontier of the roman empire at porolissum: an interdisciplinary research project*. Cluj-Napoca: Mega Publishing House, pages 141–152.
- Salzer, J., Matezki, S., and Kazda, M. (2006). Nutritional differences and leaf acclimation of climbing plants and the associated vegetation in different types of an andean montane rainforest. *Oecologia*, 147:417–425.
- Sánchez-Azofeifa, G. and Castro-Esau, K. (2006). Canopy observations on the hyperspectral properties of a community of tropical dry forest lianas and their host trees. *International Journal of Remote Sensing*, 27(10):2101–2109.
- Sánchez-Azofeifa, G. A., Castro, K., Wright, S. J., Gamon, J., Kalacska, M., Rivard, B., Schnitzer, S. A., and Feng, J. L. (2009). Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: Implications for remote sensing in tropical environments. *Remote Sensing of Environment*, 113(10):2076–2088.
- Sandifer, P. A., Sutton-Grier, A. E., and Ward, B. P. (2015). Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation. *Ecosystem services*, 12:1–15.
- Santiago, L. S. and Wright, S. J. (2007). Leaf functional traits of tropical forest plants in telation to growth form. *Functional Ecology*, pages 19–27.
- Schenck, H. (1892). *Beiträge zur Biologie und Anatomie der Lianen im besonderen der in Brasilien einheimischen Arten*. Number 4-5. G. Fischer.
- Schimper, A. F. W. (1898). *Pflanzen-geographie auf physiologischer Grundlage*, volume 2. G. Fischer.
- Schnell, R. (1970). Introduction a la phytogeographie des pays tropicaux: les problemes generaux v. 1.
- Schnitzer, S. A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *The american naturalist*, 166(2):262–276.
- Schnitzer, S. A. and Bongers, F. (2002). The ecology of lianas and their role in forests. *Trends in Ecology & Evolution*, 17(5):223–230.

- 
- Schnitzer, S. A. and Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, 14(4):397–406.
- Schnitzer, S. A. and Carson, W. P. (2001). Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, 82(4):913–919.
- Schnitzer, S. A. and Carson, W. P. (2010). Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology letters*, 13(7):849–857.
- Schnitzer, S. A., Dalling, J. W., and Carson, W. P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of ecology*, 88(4):655–666.
- Schnitzer, S. A., Kuzee, M. E., and Bongers, F. (2005). Disentangling above-and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, 93(6):1115–1125.
- Schnitzer, S. A., Parren, M. P., and Bongers, F. (2004). Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in cameroon. *Forest Ecology and Management*, 190(1):87–98.
- Schnitzer, S. A. and van der Heijden, G. M. (2019). Lianas have a seasonal growth advantage over co-occurring trees. *Ecology*, 100(5):e02655.
- Seibt, U., Rajabi, A., Griffiths, H., and Berry, J. A. (2008). Carbon isotopes and water use efficiency: sense and sensitivity. *Oecologia*, 155:441–454.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., et al. (2017). Forest disturbances under climate change. *Nature climate change*, 7(6):395–402.
- Serbin, S. P., Wu, J., Ely, K. S., Kruger, E. L., Townsend, P. A., Meng, R., Wolfe, B. T., Chlus, A., Wang, Z., and Rogers, A. (2019). From the arctic to the tropics: multi-biome prediction of leaf mass per area using leaf reflectance. *New Phytologist*, 224(4):1557–1568.
- Shapiro, S. S. and Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52(3-4):591–611.
- Shapiro, S. S., Wilk, M. B., and Chen, H. J. (1968). A comparative study of various tests for normality. *Journal of the American statistical association*, 63(324):1343–1372.
- Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., Zhang, W., and Zhang, F. (2011). Phosphorus dynamics: from soil to plant. *Plant physiology*, 156(3):997–1005.
- Smith, J. R., Queenborough, S. A., Alvia, P., Romero-Saltos, H., and Valencia, R. (2017). No strong evidence for increasing liana abundance in the myristicaceae of a neotropical aseasonal rain forest. *Ecology*, 98(2):456–466.

## BIBLIOGRAPHY

---

- Smith-Martin, C. M., Bastos, C. L., Lopez, O. R., Powers, J. S., and Schnitzer, S. A. (2019). Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. *Ecology*, 100(11):e02827.
- Stahl, C., Hérault, B., Rossi, V., Burban, B., Bréchet, C., and Bonal, D. (2013). Depth of soil water uptake by tropical rainforest trees during dry periods: does tree dimension matter? *Oecologia*, 173(4):1191–1201.
- Stoffel, M. A., Nakagawa, S., and Schielzeth, H. (2024). partr2: Partitioning r2 in glmm. R package version 0.9.2, URL: <https://cran.r-project.org/web/packages/partr2/index.html>, accessed May 11, 2024.
- STRI (2024). Barro colorado nature monument. URL: <https://stri.si.edu/facility/barro-colorado>, accessed March 30, 2024.
- Swaine, M. D. and Grace, J. (2007). Lianas may be favoured by low rainfall: evidence from ghana. *Plant Ecology*, 192:271–276.
- Tang, Y., Kitching, R. L., and Cao, M. (2012). Lianas as structural parasites: a re-evaluation. *Chinese Science Bulletin*, 57:307–312.
- Toledo-Aceves, T. and Swaine, M. D. (2008). Above-and below-ground competition between the liana acacia kamerunensis and tree seedlings in contrasting light environments. *Plant Ecology*, 196(2):233–244.
- Trewartha, G. T. and Horn, L. (1980). McGraw-hill. New York, NY.
- Tuckett, R. (2015). The role of atmospheric gases in causing climate change and global warming. *Climate Change: Observed Impacts on Planet Earth, 2nd ed.; Letcher, TM, Ed*, pages 3–20.
- Umaña, M. N., Manzané-Pinzón, E., and Comita, L. S. (2020). Longâ term dynamics of liana seedlings suggest decelerating increases in liana relative abundance over time. *Journal of Ecology*, 108(2):460–469.
- U.S.D.A. (1999). *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. U.S. Government Printing Office. URL: <https://www.nrcs.usda.gov/sites/default/files/2022-06/Soil%20Taxonomy.pdf>, accessed November 25, 2023.
- Van Amstel, A. and Swart, R. (1994). Methane and nitrous oxide emissions: an introduction. *Fertilizer research*, 37:213–225.
- Van der Heijden, G. and Phillips, O. (2009). Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, 6(10):2217–2226.
- Van Der Heijden, G. M. and Phillips, O. L. (2008). What controls liana success in neotropical forests? *Global Ecology and Biogeography*, 17(3):372–383.

- 
- Van Der Heijden, G. M., Powers, J. S., and Schnitzer, S. A. (2015a). Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences*, 112(43):13267–13271.
- Van Der Heijden, G. M., Powers, J. S., and Schnitzer, S. A. (2019). Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: Results from a liana removal experiment in panama. *Journal of Ecology*, 107(4):1890–1900.
- Van Der Heijden, G. M., Schnitzer, S. A., Powers, J. S., and Phillips, O. L. (2013). Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, 6(45):682–692.
- Van Der Heijden, G. M. v. d., Phillips, O. L., and Schnitzer, S. A. (2015b). Impacts of lianas on forest-level carbon storage and sequestration. *Ecology of lianas*, pages 164–174.
- Ventre-Lespiauq, A., Flanagan, N. S., Ospina-Calderón, N. H., Delgado, J. A., and Escudero, A. (2018). Midday depression vs. midday peak in diurnal light interception: contrasting patterns at crown and leaf scales in a tropical evergreen tree. *Frontiers in Plant Science*, page 727.
- Visser, M. D., Detto, M., Meunier, F., Wu, J., Foster, J. R., Marvin, D. C., van Bodegom, P. M., Bongalov, B., Nunes, M. H., Coomes, D., et al. (2021). Why can we detect lianas from space? *bioRxiv*, pages 2021–09.
- Visser, M. D., Muller-Landau, H. C., Schnitzer, S. A., de Kroon, H., Jongejans, E., and Wright, S. J. (2018a). A host–parasite model explains variation in liana infestation among co-occurring tree species. *Journal of Ecology*, 106(6):2435–2445.
- Visser, M. D., Schnitzer, S. A., Muller-Landau, H. C., Jongejans, E., de Kroon, H., Comita, L. S., Hubbell, S. P., and Wright, S. J. (2018b). Tree species vary widely in their tolerance for liana infestation: A case study of differential host response to generalist parasites. *Journal of Ecology*, 106(2):781–794.
- Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 65(1):285–298.
- Vitousek, P. M. (2004). *Nutrient cycling and limitation: Hawai’i as a model system*. Princeton University Press.
- Vitousek, P. M., Walker, L. R., Whiteaker, L. D., and Matson, P. A. (1993). Nutrient limitations to plant growth during primary succession in hawaii volcanoes national park. *Biogeochemistry*, 23:197–215.
- Vogelmann, T. C. and Gorton, H. L. (2014). Leaf: light capture in the photosynthetic organ. In *The structural basis of biological energy generation*, pages 363–377. Springer.

- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., Freidank, M., Cai, J., and Protivinsky, T. (2021). *corrplot*: Visualization of a correlation matrix. R package version 0.92, URL: <https://cran.r-project.org/web/packages/corrplot/index.html>, accessed May 11, 2024.
- W.M.O. (2023). El niño/la niña update (october 2023). URL: [https://wmo.int/sites/default/files/2023-11/WMO\\_ENLN\\_Update-October2023\\_en.pdf](https://wmo.int/sites/default/files/2023-11/WMO_ENLN_Update-October2023_en.pdf), accessed March 30, 2024.
- Wold, H. (1966). Estimation of principal components and related models by iterative least squares. *Multivariate analysis*, pages 391–420.
- Woolley, J. T. (1971). Reflectance and transmittance of light by leaves. *Plant physiology*, 47(5):656–662.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., et al. (2004a). The worldwide leaf economics spectrum. *Nature*, 428(6985):821–827.
- Wright, S. J., Calderón, O., Hernández, A., and Paton, S. (2004b). Are lianas increasing in importance in tropical forests? a 17-year record from panama. *Ecology*, 85(2):484–489.
- Yang, X., Tang, J., Mustard, J. F., Wu, J., Zhao, K., Serbin, S., and Lee, J.-E. (2016). Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests. *Remote Sensing of Environment*, 179:1–12.
- Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., and Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (n, p, k) fertilization in a lowland tropical moist forest, panama. *Austral Ecology*, 36(4):433–445.
- Yorke, S. R., Schnitzer, S. A., Mascaro, J., Letcher, S. G., and Carson, W. P. (2013). Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. *Biotropica*, 45(3):317–324.
- Youngentob, K. N., Zdenek, C., and van Gorsel, E. (2016). A simple and effective method to collect leaves and seeds from tall trees. *Methods in Ecology and Evolution*, 7(9):1119–1123.
- Zeiger, E., Farquhar, G. D., and Cowan, I. (1987). *Stomatal function*. Stanford University Press.
- Zhang, H. and Kovar, J. (2009). Fractionation of soil phosphorus. *Methods of phosphorus analysis for soils, sediments, residuals, and waters*, 2:50–60.
- Zhu, S.-D. and Cao, K.-F. (2009). Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern china. *Plant Ecology*, 204:295–304.

- 
- Zhu, S.-D. and Cao, K.-F. (2010). Contrasting cost–benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern china. *Oecologia*, 163:591–599.
- Zimmerman, M. H., Brown, C. L., et al. (1971). *Trees: structure and function*. New York, USA, Springer-Verlag.
- Zur, Y., Gitelson, A., Chivkunova, O., and Merzlyak, M. (2000). The spectral contribution of carotenoids to light absorption and reflectance in green leaves.

## APPENDIX A

Table A.1: Trees and lianas captured, 42 tree species and 43 liana species.

| Tree species                   | D | W  | Liana species                      | D | W |
|--------------------------------|---|----|------------------------------------|---|---|
| <i>Abarema macradenia</i>      | 1 | 0  | <i>Abuta racemosa</i>              | 0 | 1 |
| <i>Alseis blackiana</i>        | 8 | 11 | <i>Adenocalymma arthropediolum</i> | 0 | 1 |
| <i>Anacardium excelsum</i>     | 3 | 6  | <i>Arrabidaea candicans</i>        | 0 | 2 |
| <i>Andira inermis</i>          | 0 | 1  | <i>Arrabidaea patellifera</i>      | 3 | 0 |
| <i>Apeiba membranacea</i>      | 2 | 8  | <i>Banisteriopsis cornifolia</i>   | 0 | 2 |
| <i>Aspidosperma spruceanum</i> | 1 | 0  | <i>Bauhinia guianensis</i>         | 5 | 6 |
| <i>Brosimum guianense</i>      | 0 | 1  | <i>Bignonia aequinoctialis</i>     | 0 | 1 |
| <i>Casaeria guianensis</i>     | 0 | 1  | <i>Callichlamys latifolia</i>      | 2 | 1 |
| <i>Cecropia insignis</i>       | 1 | 3  | <i>Cayaponia granatensis</i>       | 0 | 1 |
| <i>Ceiba pentandra</i>         | 0 | 2  | <i>Celtis iguanaea</i>             | 1 | 1 |
| <i>Cespedesia spathulata</i>   | 0 | 1  | <i>Chomelia psilocarpa</i>         | 1 | 2 |
| <i>Cordia bicolor</i>          | 1 | 0  | <i>Chondrodendron tomentosum</i>   | 1 | 0 |
| <i>Dipterix oleifera</i>       | 3 | 6  | <i>Clitoria javitensis</i>         | 1 | 0 |
| <i>Ficus insipida</i>          | 2 | 2  | <i>Cnestidium rufescens</i>        | 0 | 1 |
| <i>Ficus spp</i>               | 0 | 1  | <i>Combretum decandrum</i>         | 0 | 2 |
| <i>Guarea grandifolia</i>      | 1 | 3  | <i>Combretum laxum</i>             | 0 | 7 |
| <i>Guarea spp</i>              | 0 | 1  | <i>Connarus panamensis</i>         | 1 | 0 |
| <i>Hasseltia floribunda</i>    | 0 | 1  | <i>Cordia bicolor</i>              | 0 | 2 |
| <i>Heisteria concinna</i>      | 1 | 1  | <i>Davilla nitida</i>              | 0 | 2 |
| <i>Hieronyma alchorneoides</i> | 1 | 5  | <i>Doliocarpus dentatus</i>        | 1 | 1 |
| <i>Inga laurina</i>            | 0 | 1  | <i>Doliocarpus olivaceus</i>       | 2 | 3 |
| <i>Jacaranda copaia</i>        | 1 | 2  | <i>Entada gigas</i>                | 2 | 0 |
| <i>Luehea seemannii</i>        | 0 | 4  | <i>Hasseltia floribunda</i>        | 1 | 0 |
| <i>Mabea occidentalis</i>      | 0 | 1  | <i>Heteropterix laurifolia</i>     | 2 | 0 |
| <i>Mangifera indica</i>        | 0 | 2  | <i>Hippocratea volubilis</i>       | 3 | 1 |
| <i>Miconia minutiflora</i>     | 1 | 0  | <i>Hiraea reclinata</i>            | 0 | 2 |
| <i>Prioria copaifera</i>       | 0 | 2  | <i>Machaerium seemannii</i>        | 0 | 4 |
| <i>Protium tenuifolium</i>     | 1 | 0  | <i>Mansoa kerere</i>               | 0 | 1 |
| <i>Pseudobombax septenatum</i> | 0 | 2  | <i>Maripa panamensis</i>           | 1 | 3 |
| <i>Pseudolmedia spuria</i>     | 2 | 0  | <i>Paullinia fibrigera</i>         | 0 | 2 |
| <i>Simarouba amara</i>         | 2 | 1  | <i>Pleonetoma variabilis</i>       | 0 | 1 |

Continued on next page

Table A.1 continued from previous page

| Tree species                   | D  | W  | Liana species                      | D  | W  |
|--------------------------------|----|----|------------------------------------|----|----|
| <i>Spondias mombin</i>         | 0  | 2  | <i>Prionostemma asperum</i>        | 2  | 1  |
| <i>Spondias radlkoferi</i>     | 0  | 1  | <i>Serjania mexicana</i>           | 0  | 1  |
| <i>Tabebuia guayacan</i>       | 0  | 1  | <i>Serjania paucidentata</i>       | 1  | 0  |
| <i>Tetragastris panamensis</i> | 1  | 8  | <i>Serjania pyramidata</i>         | 0  | 2  |
| <i>Trattinnickia aspera</i>    | 0  | 2  | <i>Stigmaphyllon lindenianum</i>   | 1  | 1  |
| <i>Vatairea erythrocarpa</i>   | 1  | 1  | <i>Stizophyllum inaequilaterum</i> | 0  | 1  |
| <i>Virola surinamensis</i>     | 1  | 0  | <i>Strychnos toxifera</i>          | 0  | 1  |
| <i>Zanthoxylum acuminatum</i>  | 0  | 1  | <i>Tetracera hydrophila</i>        | 0  | 2  |
| <i>Zanthoxylum ekmanii</i>     | 1  | 0  | <i>Tetratpteryx seemannii</i>      | 0  | 1  |
| <i>Zuelania guidonia</i>       | 0  | 2  | <i>Timmabuya myrianta</i>          | 1  | 0  |
| <i>Zygia dinizii</i>           | 1  | 0  | <i>Vitis tiliifolia</i>            | 0  | 2  |
| -                              | -  | -  | unknown                            | 0  | 1  |
| Total trees:                   | 37 | 87 | Total lianas:                      | 32 | 63 |

## APPENDIX B

### B.1 Comparing leaf traits and reflectance bands

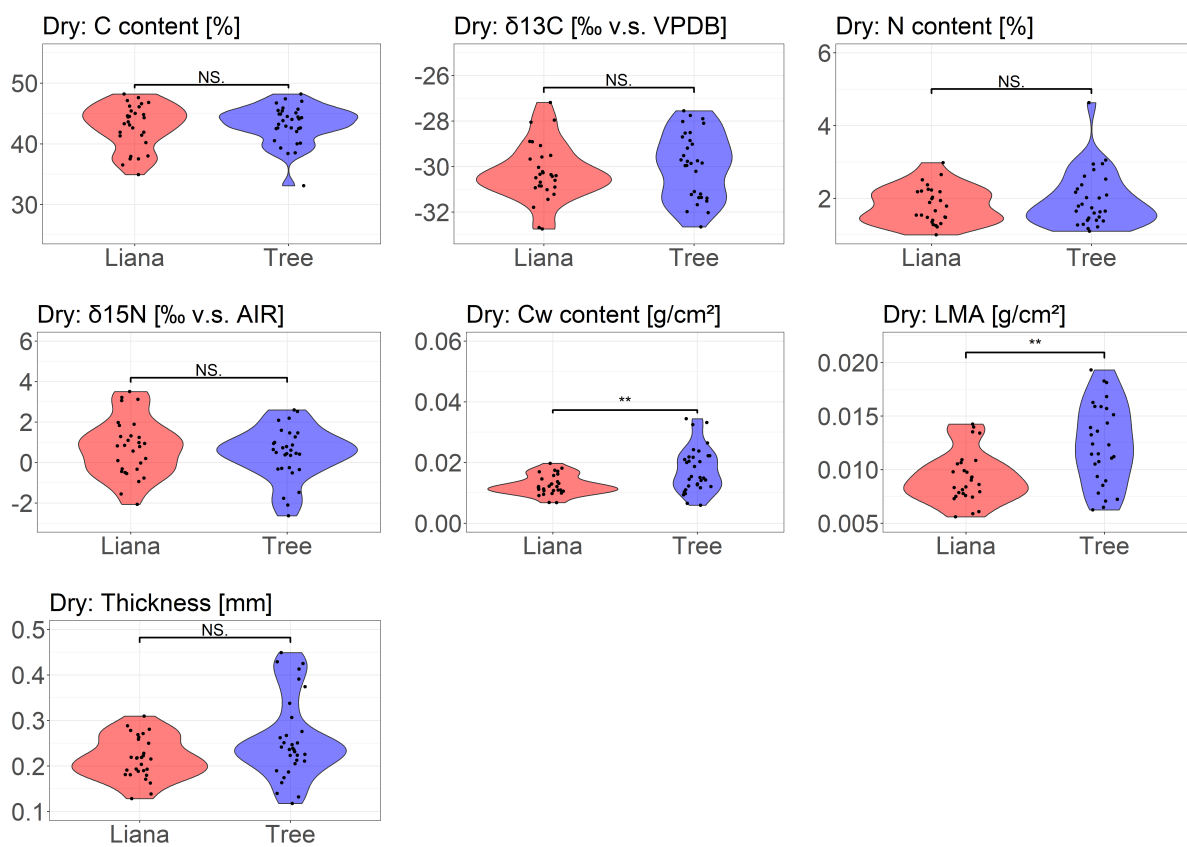


Figure B.1: Violin plots for each variable comparing them between the two growth forms for the dry season. The ANOVA test was implemented to assess possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance.)

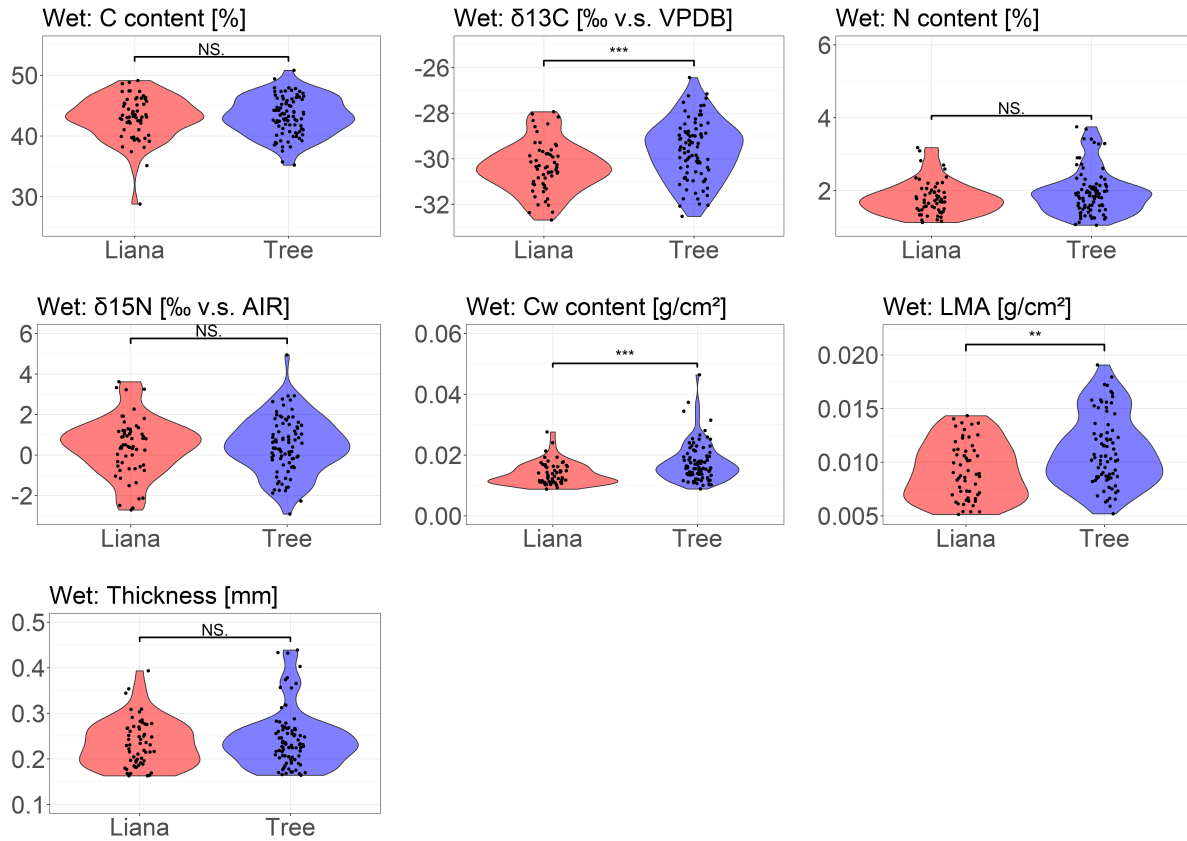


Figure B.2: Violin plots for each variable comparing them between the two growth forms for the wet season. The ANOVA test was implemented to assess possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance.)

B.

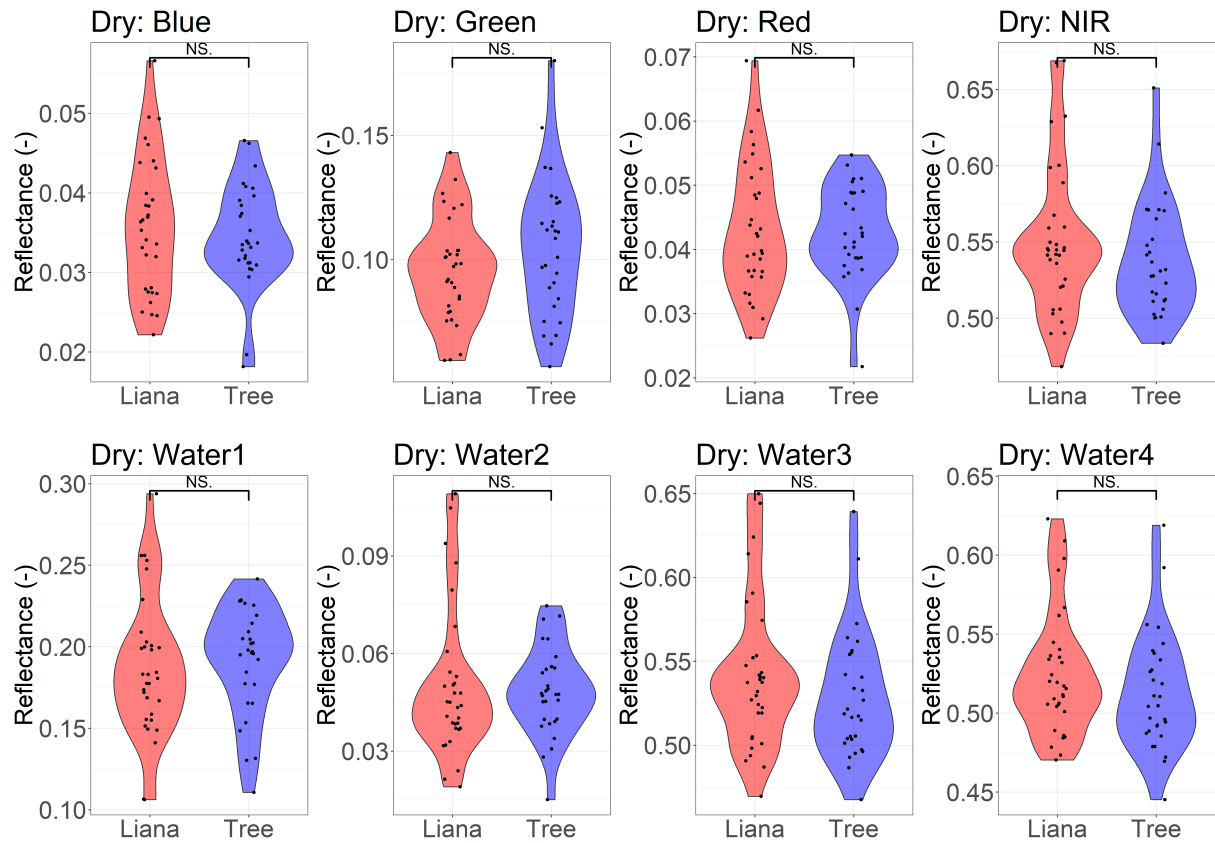


Figure B.3: Violin plots for each band comparing them between the two growth forms in dry season. The ANOVA test was implemented to access possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance). The y-axis varies per band.

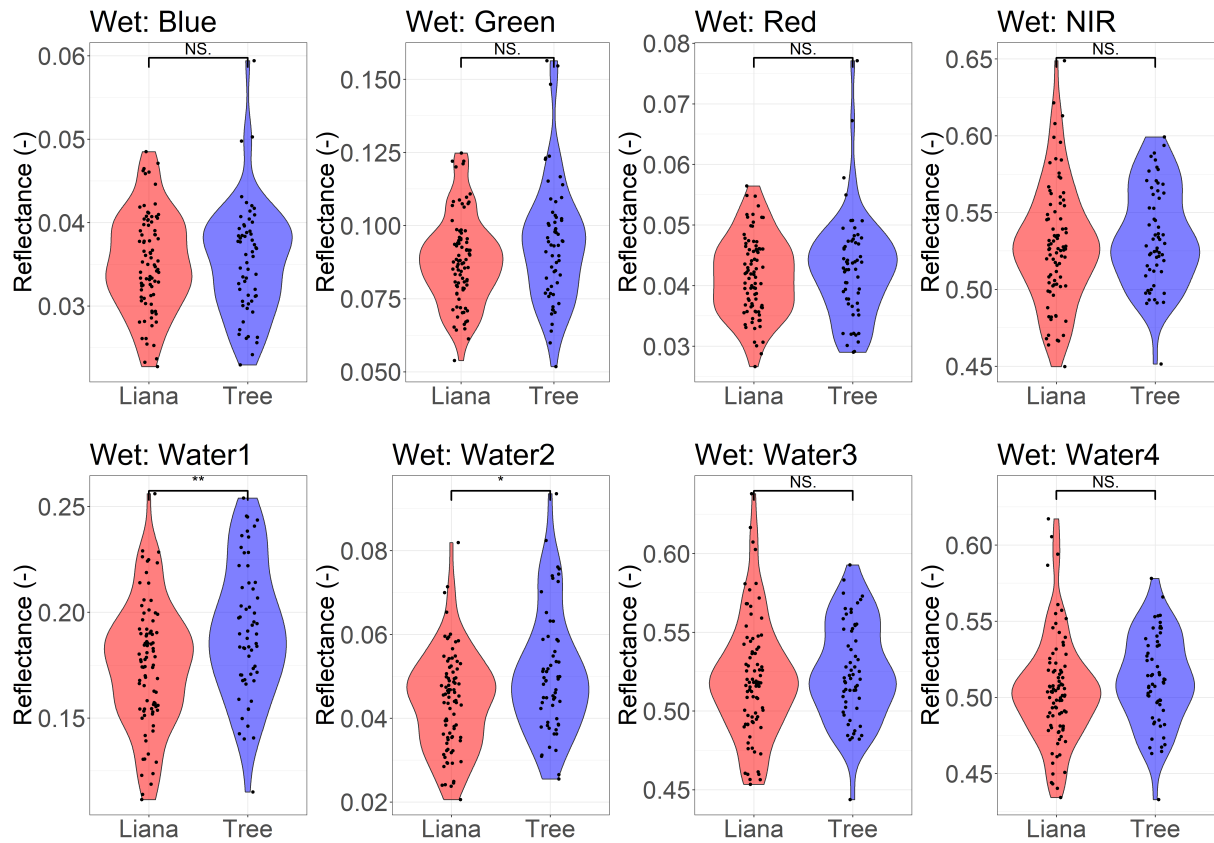


Figure B.4: Violin plots for each band comparing them between the two growth forms in wet season. The ANOVA test was implemented to access possible significant differences in the means of the groups. (Significance: \* 0.05 level, \*\* 0.01 level, \*\*\* 0.001 level, NS. no significance). The y-axis varies per band.

Table B.1: The average reflection of the specific bands for different growth forms and seasons. Columns SL and ST represent the relative, seasonal change in lianas and trees, respectively, when transitioning from the wet to the dry season. Columns D and W indicate the relative change from a tree leaf to a liana leaf during the dry and wet seasons, respectively. The changes that are significant according to the ANOVA and Krustal-Wallis tests are underlined

|        | Liana: |      | Tree: |      | %     | %           | %     | %           |
|--------|--------|------|-------|------|-------|-------------|-------|-------------|
| Band   | Dry    | Wet  | Dry   | Wet  | SL    | ST          | D     | W           |
| Blue   | 0.03   | 0.04 | 0.04  | 0.04 | -2.60 | 1.38        | -3.20 | 0.77        |
| Green  | 0.10   | 0.09 | 0.10  | 0.09 | 11.4  | 8.92        | 9.02  | 6.60        |
| Red    | 0.04   | 0.04 | 0.04  | 0.04 | -0.58 | 3.72        | -1.16 | 3.11        |
| NIR    | 0.54   | 0.53 | 0.55  | 0.53 | 0.77  | <u>4.04</u> | -2.19 | 0.99        |
| Water1 | 0.19   | 0.19 | 0.19  | 0.18 | 0.03  | 6.73        | 2.39  | <u>9.25</u> |
| Water2 | 0.05   | 0.05 | 0.05  | 0.04 | -4.66 | 13.7        | -3.55 | <u>15.0</u> |
| Water3 | 0.53   | 0.53 | 0.54  | 0.52 | 0.65  | <u>4.14</u> | -2.41 | 0.98        |
| Water4 | 0.51   | 0.51 | 0.52  | 0.50 | 0.34  | <u>4.01</u> | -2.22 | 1.36        |

## B.2 Linear mixed-effects models

Table B.2: Statistical tests regarding assumptions linear mixed-effects models. The Durbin-Watson test checks for autocorrelation in the residuals, the Levene test checks if they are homoskedastic and the Shapiro-Wilk checks their normality.

| Test                   | Blue          | Green         | Red           | NIR           | Water1        | Water2        | Water3        | Water4        |
|------------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Durbin-Watson (stat)   | 2.2501        | 2.2457        | 2.2911        | 2.2936        | 2.2091        | 2.3199        | 2.3183        | 2.3350        |
| Levene test (p-value)  | 0.0928        | 0.0618        | 0.3002        | <u>0.0002</u> | <u>0.0318</u> | <u>0.0300</u> | <u>0.0073</u> | 0.5314        |
| Shapiro-Wilk (p-value) | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> | <u>0.0000</u> |

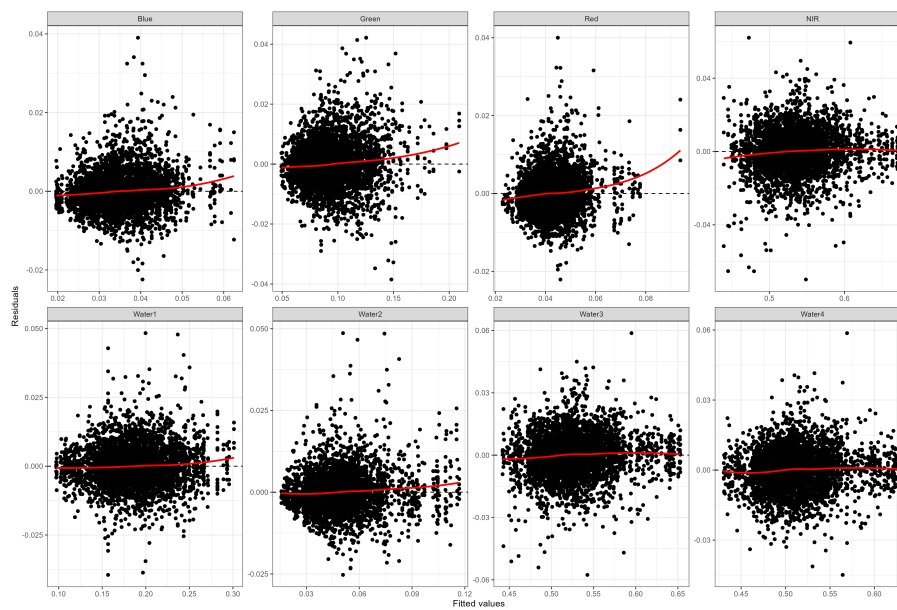


Figure B.5: The residual plots of the linear mixed-effects models of the different bands. The red line is the result of LOESS.

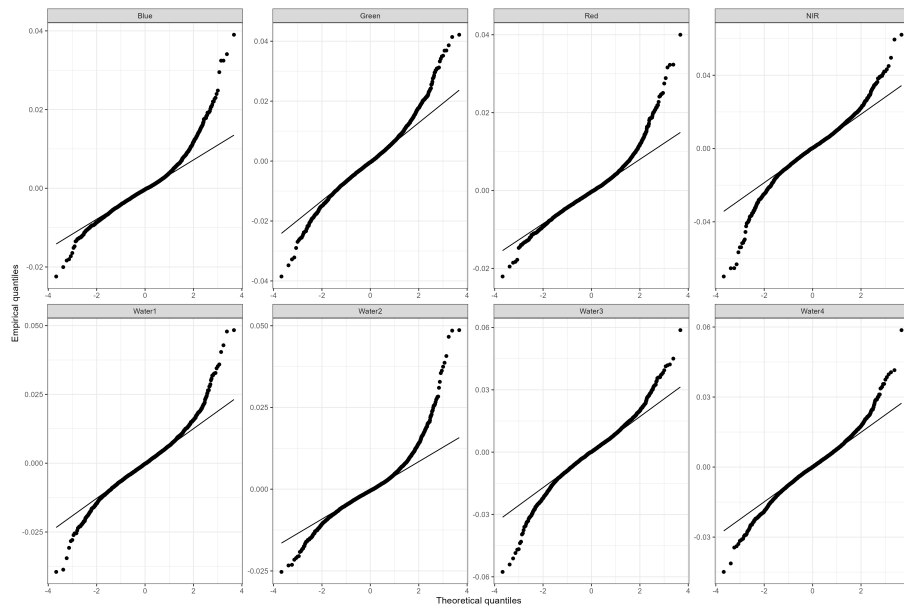


Figure B.6: The Q-Q plots of the linear mixed-effects models of the different bands. There is some tailing present.

Table B.3: P-values of the predictions of the linear mixed-effect model. Significant p-values are underlined

| Band   | Intercept     | Liana  | Wet season    | Second layer | Liana: Wet season |
|--------|---------------|--------|---------------|--------------|-------------------|
| Blue   | <u>0.0000</u> | 0.9941 | 0.1864        | 0.6175       | 0.5268            |
| Green  | <u>0.0000</u> | 0.1349 | <u>0.0336</u> | 0.0824       | 0.4744            |
| Red    | <u>0.0000</u> | 0.7863 | <u>0.0318</u> | 0.2110       | 0.6019            |
| NIR    | <u>0.0000</u> | 0.8718 | 0.0634        | 0.1886       | 0.8584            |
| Water1 | <u>0.0000</u> | 0.4263 | <u>0.0006</u> | 0.0721       | 0.1570            |
| Water2 | <u>0.0000</u> | 0.8036 | <u>0.0005</u> | 0.1797       | <u>0.0298</u>     |
| Water3 | <u>0.0000</u> | 0.6660 | <u>0.0220</u> | 0.1667       | 0.6527            |
| Water4 | <u>0.0000</u> | 0.6822 | <u>0.0062</u> | 0.2381       | 0.4416            |

Table B.4: Variance proportion of all the different variables for each band. Green and red make use of model 2 and the others of model 1.

| Levels                    | Blue | Green | Red  | NIR  | Water1 | Water2 | Water3 | Water4 |
|---------------------------|------|-------|------|------|--------|--------|--------|--------|
| Fixed effects             | 0.64 | 8.17  | 2.73 | 2.33 | 6.93   | 4.52   | 2.99   | 3.47   |
| Species                   | 32.9 | 8.79  | 19.8 | 42.2 | 51.7   | 46.0   | 42.2   | 44.9   |
| Individuals               | 24.8 | 25.8  | 7.18 | 40.3 | 30.0   | 29.6   | 41.0   | 39.1   |
| Leaves                    | 7.02 | 9.10  | 3.04 | 5.94 | 6.69   | 6.52   | 5.65   | 5.55   |
| Residuals                 | 34.7 | 12.9  | 28.6 | 9.25 | 4.99   | 13.3   | 8.10   | 6.98   |
| Growth form ~ Species     | -    | 20.5  | 2.35 | -    | -      | -      | -      | -      |
| Growth form ~ Individuals | -    | 10.5  | 22.1 | -    | -      | -      | -      | -      |
| Growth form ~ Leaves -    | -    | 4.24  | 14.2 | -    | -      | -      | -      | -      |

### B.3 Partial least squares regression

Table B.5: Performance of the partial least squares regression (PLSR) models expressed in r-square, root mean squared error of prediction (RMSEP) and its percentage (%RMSEP).

| Variable               | # components | R <sup>2</sup> | RMSEP | %RMSEP |
|------------------------|--------------|----------------|-------|--------|
| Trees in both seasons  |              |                |       |        |
| C                      | 14           | 0.34           | 2.51  | 14.19  |
| $\delta^{13}\text{C}$  | 14           | 0.53           | 0.99  | 13.35  |
| N                      | 16           | 0.74           | 0.34  | 8.81   |
| $\delta^{15}\text{N}$  | 13           | 0.36           | 1.18  | 14.1   |
| $C_w$                  | 15           | 0.68           | 0     | 9.34   |
| LMA                    | 14           | 0.72           | 0     | 14.27  |
| Thickness              | 15           | 0.82           | 0.03  | 8.49   |
| Lianas in both seasons |              |                |       |        |
| C                      | 13           | 0.44           | 2.77  | 13.65  |
| $\delta^{13}\text{C}$  | 14           | 0.36           | 0.97  | 16.13  |
| N                      | 15           | 0.67           | 0.29  | 12.62  |
| $\delta^{15}\text{N}$  | 14           | 0.38           | 1.14  | 18.07  |
| $C_w$                  | 14           | 0.72           | 0     | 8.97   |
| LMA                    | 12           | 0.73           | 0     | 14.04  |
| Thickness              | 11           | 0.74           | 0.03  | 9.63   |
| Trees in dry season    |              |                |       |        |
| C                      | 15           | 0.71           | 1.63  | 10.82  |
| $\delta^{13}\text{C}$  | 16           | 0.81           | 0.67  | 10.70  |
| N                      | 15           | 0.78           | 0.36  | 9.56   |
| $\delta^{15}\text{N}$  | 15           | 0.61           | 0.94  | 15.63  |
| $C_w$                  | 15           | 0.82           | 0     | 11.25  |
| LMA                    | 15           | 0.87           | 0     | 9.68   |
| Thickness              | 15           | 0.93           | 0.03  | 7.3    |
| Trees in wet season    |              |                |       |        |
| C                      | 15           | 0.49           | 2.23  | 14.28  |
| $\delta^{13}\text{C}$  | 14           | 0.55           | 0.92  | 12.36  |
| N                      | 16           | 0.82           | 0.27  | 9.06   |
| $\delta^{15}\text{N}$  | 15           | 0.45           | 1.07  | 13.21  |
| $C_w$                  | 15           | 0.73           | 0     | 8.82   |
| LMA                    | 13           | 0.56           | 0     | 12.68  |
| Thickness              | 15           | 0.77           | 0.03  | 8.85   |
| Lianas in dry season   |              |                |       |        |
| C                      | 15           | 0.80           | 1.72  | 12.9   |
| Continued on next page |              |                |       |        |

Table B.5 continued from previous page

| Variable              | # components | R <sup>2</sup> | RMSEP | %RMSEP |
|-----------------------|--------------|----------------|-------|--------|
| $\delta^{13}\text{C}$ | 15           | 0.83           | 0.55  | 9.86   |
| N                     | 14           | 0.86           | 0.22  | 10.77  |
| $\delta^{15}\text{N}$ | 15           | 0.67           | 0.81  | 14.6   |
| $C_w$                 | 13           | 0.81           | 0     | 9.7    |
| LMA                   | 13           | 0.81           | 0     | 10.77  |
| Thickness             | 14           | 0.84           | 0.02  | 10.06  |
| Lianas in wet season  |              |                |       |        |
| C                     | 14           | 0.48           | 2.61  | 12.87  |
| $\delta^{13}\text{C}$ | 14           | 0.51           | 0.81  | 15.4   |
| N                     | 14           | 0.61           | 0.28  | 13.57  |
| $\delta^{15}\text{N}$ | 14           | 0.55           | 0.98  | 15.51  |
| $C_w$                 | 13           | 0.81           | 0     | 8.55   |
| LMA                   | 14           | 0.85           | 0     | 11.08  |
| Thickness             | 12           | 0.78           | 0.03  | 9.77   |

B.

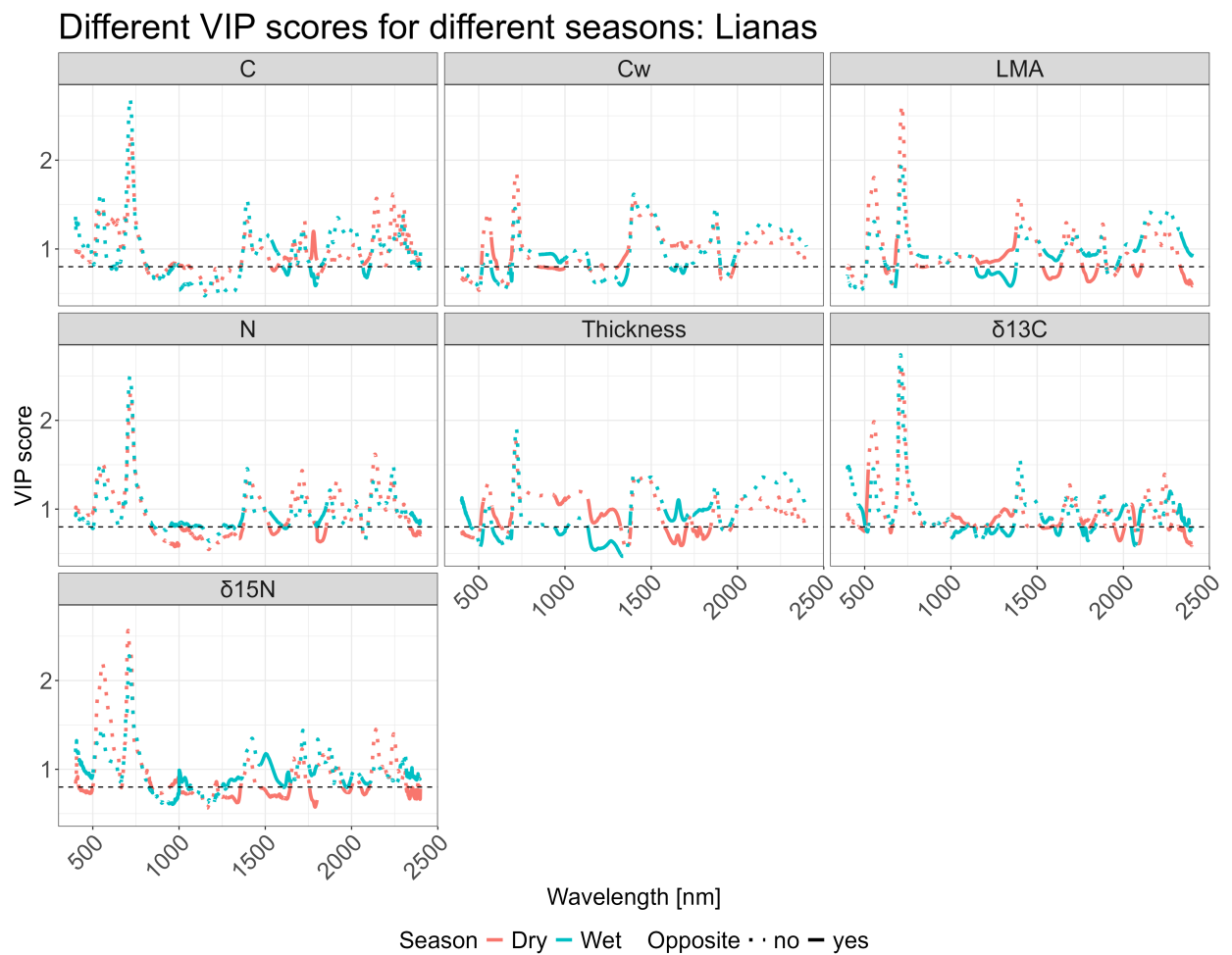


Figure B.7: The VIP scores for all wavelengths. When they are important ( $> 0.80$ ; above the black dashed line) for one growth form and unimportant ( $< 0.80$ ; below the black line) for the other growth form, the lines are solid and otherwise the lines are dotted. From left to right and top to bottom the variables are C, C<sub>w</sub>, LMA, N, Thickness, δ<sup>13</sup>C and δ<sup>15</sup>N

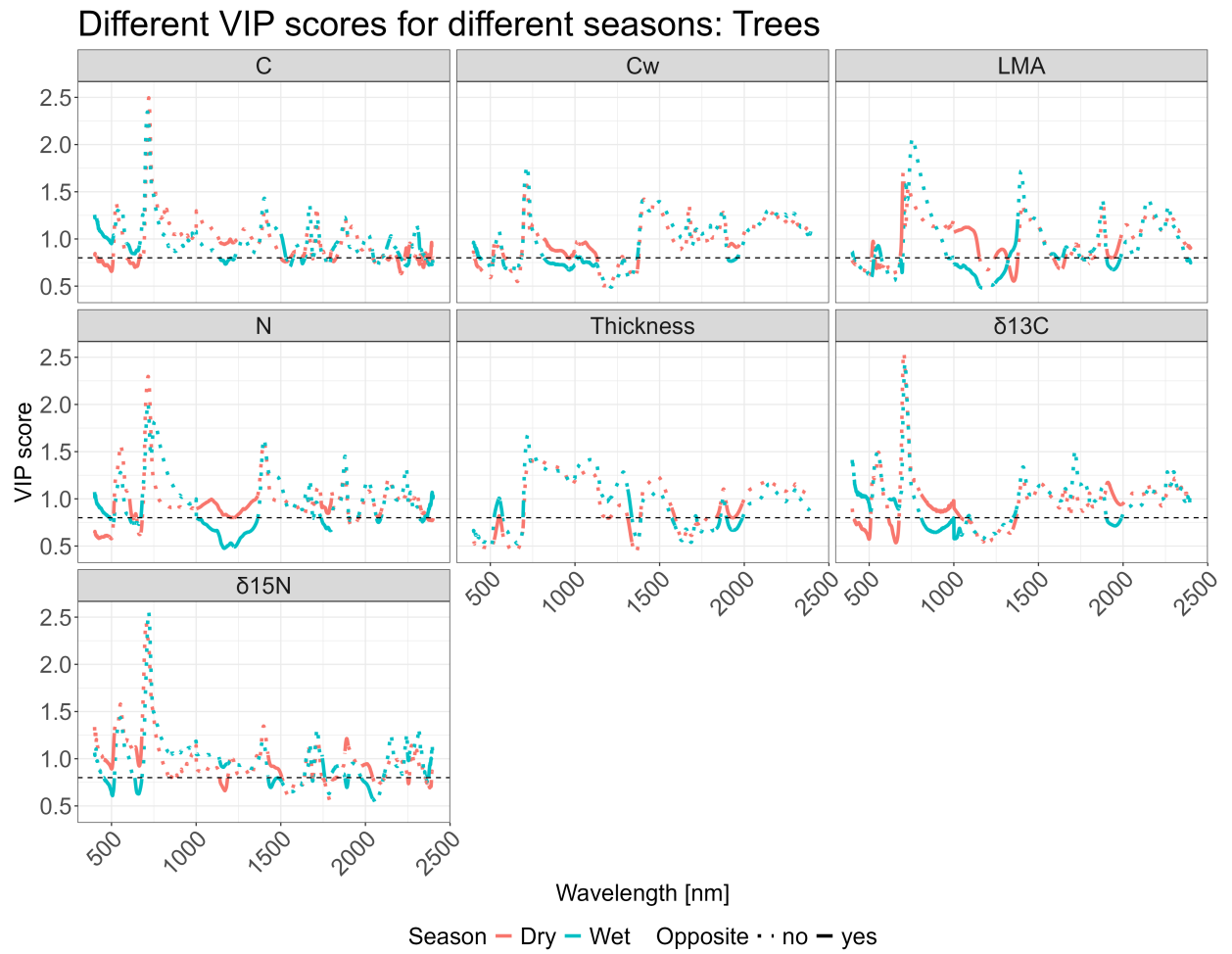


Figure B.8: The VIP scores for all wavelengths. When they are important ( $> 0.80$ ; above the black dashed line) for one growth form and unimportant ( $< 0.80$ ; below the black line) for the other growth form, the lines are solid and otherwise the lines are dotted. From left to right and top to bottom the variables are C, C<sub>w</sub>, LMA, N, Thickness,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$