

COMPARISON OF LEAF-LEVEL PHOTOSYNTHETIC CAPACITY OF TROPICAL LOWLAND FORESTS FROM THE CONGO AND AMAZON BASIN

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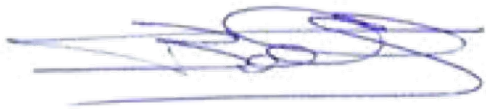
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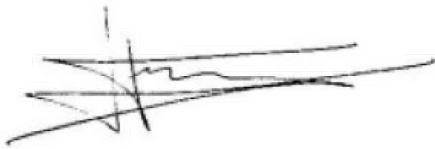
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ABBREVIATIONS

Abbreviation	Meaning
[]	Concentration
A	Net photosynthesis, or CO ₂ assimilation
A_c	A for Rubisco limitation
A_j	A for RuBP regeneration limitation
A_{leaf}	Leaf area
A_{max}	Maximum CO ₂ assimilation rate
ANCA-SL	Automated Nitrogen Carbon Analyser – Solids and Liquids
A_p	A for TPU limitation
C_a	Ambient CO ₂ concentration
C_{atm}	Atmospheric CO ₂ concentration
C_c	CO ₂ partial pressure at Rubisco
CFE	CO ₂ fertilization effect
C_i	CO ₂ concentration in the intercellular airspaces of the leaf
C_{leaf}	CO ₂ concentration inside the leaf
CRT	Carbon residence time
D	Deciduous
DGVM	Dynamic Global Vegetation Model
DRC	Democratic Republic of the Congo
E	Evergreen
EA-IRMS	Elemental Analyser - Isotope Ratio Mass Spectrometer
ENSO	El Niño-Southern Oscillation
ETC	Electron transport chain
FVCB	Farquhar-von Caemmerer-Berry
GHG	Greenhouse gas
GPP	Gross primary productivity
g_s	Stomatal conductance
I	Photosynthetic photon flux density
ICP-OES	Inductively Coupled Plasma Optical Emission Spectroscopy
INERA	Institut national pour l'étude et la recherche agronomique
ISOFYS	Isotope Bioscience Laboratory
ITCZ	Intertropical Convergence Zone
J	Rate of electron transport
J_{max}	Maximum rate of electron transport
J_{max}^{25}	Maximum rate of electron transport at 25°C
K_c	Michaelis constant of Rubisco for CO ₂

K_o	Inhibition constant
L	Liana
LCA	Laboratory for Chemical Analyses
LD	Light-demanding
LES	Leaf economics spectrum
LL	Leaf lifespan
LMA	Leaf mass per area
m_{dry}	Leaf dry mass
N_{area}	Area-based nitrogen content
NEE	Net ecosystem CO ₂ exchange
NPLD	Non-pioneer light-demanding
O	Partial pressure of O ₂ at Rubisco
P	Photosynthesis
P	Pioneer
PAR	Photosynthetic Active Radiation
P_{area}	Area-based phosphorus content
PFT	Plant functional type
PGA	3-phosphoglycerate
PGAL	3-phosphoglyceraldehyde
R	Rate of mitochondrial respiration
r^2	Coefficient of determination
R_d, R_{dark}	Dark respiration rate
R_l	Leaf's respiration
RUBP	Ribulose-1,5-biphosphate
SB	Shade-bearing
SD	Standard deviation
SE	Standard error
SLA	Specific leaf area
SMA	Standardized Major Axis
SST	Sea surface temperature
TPU	Triose phosphate use
USB	Understory shade-bearing
V_c	Rate of carboxylation
V_{cmax}	Maximum carboxylation capacity
V_{cmax}^{25}	Maximum carboxylation capacity at 25°C
V_o	Rate of oxygenation, or photorespiration
WUE	Water use efficiency
Γ	CO ₂ compensation point
Γ^*	Photorespiratory compensation point

ABSTRACT

Tropical forests play a critical role in the global carbon cycle, acting as major carbon sinks through large-scale CO₂ fixation. Accurately representing these forests in Dynamic Global Vegetation Models (DGVMs) is crucial for predicting future climate change and its impact on vegetation. However, DGVMs often use uniform parameterizations for tropical forests, particularly in the two largest regions – the Amazon and Congo Basin – despite potential ecological differences. This study aims to assess whether such generalizations are valid by comparing leaf-level photosynthetic capacity and associated functional traits of dominant species from lowland tropical forests in these regions.

Leaf photosynthetic (maximum carboxylation capacity – V_{cmax} , and maximum rate of electron transport – J_{max}), leaf chemical (area-based nitrogen content – N_{area} , area-based phosphorus content – P_{area}) and leaf structural (specific leaf area – SLA) traits were measured on 23 species at the CongoFlux research site of Yangambi, situated in the central Congo Basin, and compared with data on 34 species from the Paracou and Nouragues sites (French Guiana) in the Amazon Basin. In order to get a more complete view over the examined sites, species were categorized into plant functional types (PFTs), based on light requirement and leaf phenology, with measurements taken at both top and bottom crown positions.

All measured parameters were strikingly higher in Yangambi than in the Amazonian sites. These differences were partly due to methodological issues (e.g. an unequal PFT distribution between the sites). However, there appear to be significant (a)biotic differences between the sites as well, since the measured parameters were consistently higher in Yangambi for each PFT (with the exception of J_{max} and N_{area} for the lianas). Lastly, positive correlations were found between V_{cmax} and N_{area} , P_{area} , and stomatal conductance (g_s) at all sites. All correlations were stronger in Yangambi than in the Amazonian sites.

Furthermore, photosynthetic capacity differed substantially between PFTs of all sites combined, being highest for pioneer species, and lowest for understory species. Lianas showed a generally lower photosynthetic capacity than trees. Leaf functional traits varied less among PFTs, with the exception of understory species, having low N_{area} and P_{area} and high SLAs. Additionally, deciduous species showed higher V_{cmax} and J_{max} values than evergreen species. Photosynthetic capacity, N_{area} , and P_{area} were higher at the top of the crown compared to the bottom, while SLA was lower. Crown position had the biggest effect on photosynthetic capacity, followed by species' light requirement.

These findings suggest that photosynthetic capacity may be inherently higher in the Congo Basin than in the Amazon Basin, indicating that region-specific parametrisation in DGVMs is advisable for improved climate predictions. Further research, particularly in the Congo Basin, is needed to validate this conclusion and refine model inputs.

SAMENVATTING

Tropische regenwouden spelen een cruciale rol in de globale koolstofcyclus en fungeren als belangrijke koolstofsinks door grootschalige CO₂-fixatie. Een nauwkeurige weergave van deze bossen in Dynamic Global Vegetation Models (DGVM's) is cruciaal voor het voorspellen van toekomstige klimaatveranderingen en de invloed daarvan op vegetatie. DGVM's gebruiken echter vaak uniforme parametrisaties voor tropische wouden, vooral in de twee grootste regio's – het Amazone- en het Congobekken – ondanks mogelijke ecologische verschillen. Deze studie heeft als doel om te beoordelen of dergelijke generalisaties geldig zijn, door de fotosynthetische capaciteit op bladniveau en bijbehorende functionele eigenschappen van dominante soorten uit laagland tropische bossen in deze regio's te vergelijken.

Fotosynthetische (de maximale carboxylatiecapaciteit – V_{cmax} , en de maximale snelheid van elektronentransport – J_{max}), chemische (het stikstofgehalte per oppervlakte-eenheid – N_{area} , het fosforgehalte per oppervlakte-eenheid – P_{area}) en structurele (de specifieke bladoppervlakte – SLA) eigenschappen van de bladeren werden gemeten op 23 soorten in de CongoFlux-onderzoekssite in Yangambi, centraal gelegen in het Congobekken, en vergeleken met gegevens over 34 soorten op de sites van Paracou en Nouragues (Frans-Guyana) in het Amazonebekken. Om een completer beeld te krijgen van de onderzochte sites, werden de soorten ingedeeld in functionele planttypes (PFT's) op basis van lichtbehoefte en bladfenologie, met metingen zowel bovenaan als onderaan de kroon.

Alle gemeten parameters waren opvallend hoger in Yangambi dan in de Amazonesites. Deze verschillen waren deels te wijten aan methodologische problemen (bijvoorbeeld een ongelijke verdeling van PFT's tussen de locaties). Er lijken echter ook significante (a)biotische verschillen tussen de locaties te zijn, aangezien de gemeten parameters consistent hoger waren in Yangambi voor elke PFT (met uitzondering van J_{max} en N_{area} voor de lianen). Tot slot werden positieve correlaties gevonden tussen V_{cmax} en N_{area} , P_{area} en stomatale geleiding (g_s) op alle sites. Alle correlaties waren sterker in Yangambi dan in de Amazonesites.

Bovendien verschilde de fotosynthetische capaciteit aanzienlijk tussen de PFT's voor alle sites samen, en was het hoogst voor pioniersoorten en het laagst voor soorten die permanent onder het kronendak leven. Lianen vertoonden over het algemeen een lagere fotosynthesecapaciteit dan bomen. De functionele eigenschappen van de bladeren verschilden minder tussen de PFT's, met uitzondering van de soorten onder het kronendak, die een lage N_{area} en P_{area} en een hoge SLA hadden. Daarnaast vertoonden bladverliezende soorten hogere V_{cmax} - en J_{max} -waarden dan groenblijvende soorten. Bladeren bovenin de kroon hadden een hogere fotosynthesecapaciteit, een hogere N_{area} en P_{area} en een lagere SLA dan bladeren onderin de kroon. De kroonpositie had het grootste effect op de fotosynthesecapaciteit, gevolgd door de lichtbehoefte van de soort.

Deze bevindingen suggereren dat de fotosynthetische capaciteit inherent hoger kan zijn in het Congobekken dan in het Amazonebekken, wat aangeeft dat regiospecifieke parametrisering

in DGVM's raadzaam is voor betere klimaatvoorspellingen. Verder onderzoek, met name in het Congobekken, is nodig om deze conclusie te valideren en de modelinput te verfijnen.

RÉSUMÉ

Les forêts tropicales jouent un rôle essentiel dans le cycle mondial du carbone, en agissant comme des puits de carbone majeurs par la fixation du CO₂ à grande échelle. La représentation précise de ces forêts dans les modèles dynamiques de végétation mondiale (DGVM) est essentielle pour prévoir les changements climatiques futurs et leur impact sur la végétation. Cependant, ces modèles utilisent souvent des paramétrages uniformes pour les forêts tropicales, en particulier dans les deux plus grandes régions – l'Amazonie et le Bassin du Congo – malgré les différences écologiques potentielles. Cette étude vise à évaluer la validité de ces généralisations en comparant la capacité photosynthétique au niveau des feuilles et les traits fonctionnels associés des espèces dominantes des forêts tropicales de plaine dans ces régions.

Les caractéristiques photosynthétiques (la capacité maximale de carboxylation – V_{cmax} , et le taux maximal de transport d'électrons – J_{max}), chimiques (la teneur en azote basée sur la surface – N_{area} , la teneur en phosphore basée sur la surface – P_{area}) et structurales (surface foliaire spécifique - SLA) des feuilles ont été mesurées sur 23 espèces sur le site de recherche CongoFlux de Yangambi, situé dans le centre du Bassin du Congo, et comparées aux données de 34 espèces des sites de Paracou et de Nouragues (Guyane française) dans le Bassin de l'Amazonie. Afin d'obtenir une vue plus complète des sites examinés, les espèces ont été classées en types fonctionnels de plantes (TFP) sur la base des besoins en lumière et de la phénologie des feuilles, les mesures étant prises à la fois au sommet et à la base de la couronne.

Tous les paramètres mesurés étaient étonnamment plus élevés à Yangambi que dans les sites amazoniens. Ces différences sont en partie dues à des problèmes méthodologiques (par exemple, une distribution inégale des TFP entre les sites). Cependant, il semble qu'il y ait également des différences (a)biotiques significatives entre les sites, puisque les paramètres mesurés étaient systématiquement plus élevés à Yangambi pour chaque TFP (à l'exception de J_{max} et N_{area} pour les lianes). Enfin, des corrélations positives ont été trouvées entre V_{cmax} et N_{area} , P_{area} , et la conductance stomatique (g_s) sur tous les sites. Toutes les corrélations étaient plus fortes à Yangambi que dans les sites amazoniens.

En outre, la capacité photosynthétique différait considérablement entre les TFP de tous les sites combinés, étant la plus élevée pour les espèces pionnières, et la plus faible pour les espèces du sous-étage. La capacité photosynthétique des lianes était généralement inférieure à celle des arbres. Les traits fonctionnels des feuilles varient moins entre les TFP, à l'exception des espèces de sous-bois, qui présentent des N_{area} et P_{area} faibles et des SLA élevés. En outre, les espèces à feuilles caduques présentaient des valeurs V_{cmax} et J_{max} plus élevées que les espèces à feuilles persistantes. Les feuilles situées au sommet de la couronne avaient des capacités photosynthétiques plus élevées, des N_{area} et P_{area} plus élevés et des SLA plus faibles que les feuilles situées au bas de la couronne. La position de la couronne a eu l'effet le plus important sur la capacité photosynthétique, suivi par les besoins en lumière des espèces.

Ces résultats suggèrent que la capacité photosynthétique peut être intrinsèquement plus élevée dans le bassin du Congo que dans le bassin de l'Amazonie, ce qui indique que la paramétrisation spécifique à la région dans les DGVM est conseillée pour améliorer les prévisions climatiques. D'autres recherches, en particulier dans le bassin du Congo, sont nécessaires pour valider cette conclusion et affiner les données d'entrée du modèle.

1. INTRODUCTION

Tropical forests play a crucial role in the battle against climate change, but they are increasingly fragile. They contribute about 34% to the global terrestrial CO₂ fixation through photosynthesis, making them the largest component in the terrestrial carbon sink (Anderson-Teixeira et al., 2016; Beer et al., 2010). Yet tropical forests are poorly studied (Anderson-Teixeira et al., 2016). Dynamic Global Vegetation Models (DGVMs) are tools which allow us to make predictions of the future climate and to gain better understanding in the responses of vegetation to climate change (Krinner et al., 2005). However, these models require a good parametrisation. Measurements of leaf-level photosynthesis are essential in this regard (Rogers et al., 2017). Given their crucial role in the global carbon cycle, tropical forests must be accurately represented in DGVMs.

Up until now, not much photosynthetic data has been gathered in the tropics. Often the same parameters are used in DGVMs for all tropical forests (e.g. Potter & Klooster, 1999; Sich et al., 2008), including the two largest, located in the Amazon and Congo Basin. Especially in the Congo Basin a large data gap is present (Malhi et al., 2013). Leaf-level photosynthesis has never been measured there. However, many differences exist between the Neotropical and African rainforests, including in climate (e.g. Sullivan et al., 2020), vegetation (e.g. Bastin et al., 2015; Luambua et al., 2021; Slik et al., 2015) and carbon dynamics (e.g. Brienen et al., 2015; Hubau et al., 2020; Sullivan et al., 2017). They show different responses to climate change as well, since Hubau et al. (2020) observed an asynchronous carbon sink saturation, with the African saturation occurring delayed to the Amazonian saturation. This study intends to analyse the photosynthetic capacity of sites from both the Amazon and Congo Basin, and look for potential differences.

Two of the most important parameters to estimate the photosynthetic capacity of a plant are the maximum carboxylation capacity (V_{cmax}) and the maximum rate of electron transport (J_{max}). These can be obtained by measuring CO₂ response curves (Sharkey et al., 2007). Besides, it is important to collect parameters on several species, since there is much variation in photosynthetic capacity between them (e.g. Rijkers et al., 2000; Zhang et al., 2018). However, tropical forests are incredibly diverse ecosystems (Slik et al., 2015), making it impossible to measure all species. That's why species are often divided into plant functional types (PFTs) (Box, 1996; Yang et al., 2015), and only dominant species representative for certain PFTs are measured. Popular ways of categorizing tropical species into PFTs are light requirement + regeneration (Hawthorne, 1995) and leaf phenology (e.g. Pringle et al., 2011). Furthermore, photosynthetic capacity typically differs between the top and the bottom of the crown of woody species (e.g. Lambers & Oliveira, 2019; Niinemets, 2023). In order to get representative values for species, parameters have to be measured at different positions in the crown. Lastly, photosynthetic parameters are often linked with leaf functional traits, such as leaf nutrient concentrations and specific leaf area (SLA) (Wright et al., 2004). Hence, these other leaf traits need to be measured as well, since they reveal valuable information about the strategy of the

investigated species (Díaz et al., 2016; Reich, 2014). This thesis aims at getting a representative view of the photosynthetic capacity of lowland tropical forest sites from the Amazon and Congo Basin, by measuring photosynthetic parameters (V_{cmax} and J_{max}) and leaf traits (leaf nitrogen and phosphorous content, SLA and stomatal conductance) of dominant species from several PFTs (including lianas and understory species) at different crown positions.

This master's thesis tries to answer the following research questions:

1. How do important photosynthetic parameters differ between several PFTs of three tropical lowland forest sites examined together? Can these potential differences be linked to differences in leaf functional traits (SLA and nutrient content)?
2. How do important photosynthetic parameters differ between the top and the bottom of the crown for species of three tropical lowland forest sites examined together? Can this potential difference be linked to a difference in leaf functional traits?
3. How do important photosynthetic parameters differ between species of two tropical lowland forest sites in the Amazon Basin on one hand, and species of one tropical lowland forest site in the Congo Basin on the other hand, including potential variation between PFTs and between bivariate relationships with leaf functional traits?

The following section is a literature review, in which the observed differences between the Amazon and Congo Basin are discussed in more detail. It also contains a closer look into leaf-level photosynthesis and measuring CO_2 response curves. It ends with discussing photosynthetic variation between species, by looking at bivariate relationships with leaf functional traits and at PFTs. Section 3 contains the materials and methods used to answer the research questions. In section 4 the results are disposed, with a visual overview of the data and statistical analysis. Thereafter, a thorough discussion of the results follows, in which the research questions are answered. In the end, a conclusion is formulated, with the most important results of the thesis, followed by proposals for further research.

This explorative study tries to gain a better understanding of possible differences in photosynthetic parameters between two crucial tropical biomes. Additionally, it aids at partially closing the existing data gap in the Congo Basin. This could potentially allow for a better parametrisation of DGVMs and by consequence better predictions of climate change and its impacts on tropical forests.

2. LITERATURE REVIEW

2.1. Importance of tropical rainforests in the global carbon cycle

The most recent Global Carbon Budget report (Friedlingstein et al., 2023) shows that we're far from reaching the goal of the Paris Agreement to limit global warming to 1.5°C. Global fossil CO₂ emissions continue to grow. In 2022, the fossil emissions amounted to 9.9 ± 0.5 Gt carbon yr⁻¹, which is 0.9% higher than in 2021. When emissions from land-use change (mainly deforestation) are included, total anthropogenic emissions in 2022 were 11.1 Gt C yr⁻¹.

The most important sink of CO₂ is the terrestrial sink (Friedlingstein et al., 2023): vegetation removing CO₂ from the atmosphere and storing it in biomass through the process of photosynthesis. In 2022, this sink counted for 3.8 ± 0.8 Gt C yr⁻¹ (Friedlingstein et al., 2023). Pan et al. (2011) found a large and persistent C sink in the world's forests of 2.41 ± 0.42 Gt C yr⁻¹ over the period 1990-2007. Among all forest biomes, the tropical forests play a crucial role in the global carbon cycle, since they store $\pm 45\%$ of terrestrial C (Anderson-Teixeira et al., 2016).

Tropical forests are distributed around the equator close to the Intertropical Convergence Zone (ITCZ). They are characterised by the absence of thermal seasons (Peters, 2014), which means they have a very uniform, warm temperature across the year, typically higher than 20°C (Corlett, 2011). Tropical rainforests experience a high precipitation throughout the year, with values ranging between roughly 1100 and > 4000 mm yr⁻¹, with sometimes a short dry season (Peters, 2014). They cover around 10% of the Earth's land surface (Pan et al., 2011). The dominant life forms are trees, lianas and epiphytes. They are usually very complex, dense, productive and diverse ecosystems.

Tropical forests contribute about 41 Gt C yr⁻¹ to the global terrestrial GPP (gross primary productivity, i.e. the rate of CO₂ fixation by photosynthesis) (Beer et al., 2010). This is 34% of the global total, making tropical forests the largest component in the terrestrial C sink (Anderson-Teixeira et al., 2016). Boreal and temperate forests account for a GPP of approximately 8 and 10 Gt C yr⁻¹, respectively (Beer et al., 2010). All tropical biomes together (savannahs and grasslands added) account for about 60% of the global GPP (Beer et al., 2010). It is safe to say that we live on a predominantly tropical planet, in terms of terrestrial metabolism. However, eddy covariance studies showed that per unit of light, tropical forests don't have a higher productivity than temperate broadleaf forests in their peak growing season (Malhi, 2012). The high productivity of wet tropical forests is almost entirely linked with the absence of a dormant period (winter or dry season), rather than that they have an intrinsic high productivity associated with for example high temperatures or high diversity (Malhi, 2012).

Next to their impact on the global C cycle, tropical forests have other important functions, as explained by Lewis et al. (2015). They play an important part in regulating the global water cycle, e.g. via transpiration. They contain over half of Earth's biodiversity. Besides, more than one billion people directly depend on tropical forests for food, timber and medicines.

There are many threats to the rainforest carbon sinks. First of all, there is deforestation. While undisturbed tropical forests act as carbon sinks, the overall carbon balance in tropical forests tilts towards being a carbon source. This is due to the emissions from deforestation and forest degradation outweighing the carbon uptake in undisturbed forests (Baccini et al., 2017; Pan et al., 2011). Only 24% of tropical forests are still intact (Lewis et al., 2015). Furthermore, extreme droughts will occur more frequently due to climate change, related to El Niño-Southern Oscillation (ENSO) events and rising equatorial sea surface temperatures (Hua et al., 2016; Lewis et al., 2011). This can cause big C losses, e.g. due to tree mortality (Phillips et al., 2009). A last threat is the global temperature increase. Sullivan et al. (2020) found that tropical forest C stocks decrease with $\pm 6\%$ per 1°C increase in mean daily maximum temperature in the warmest month. The main cause is reduced woody productivity. They also found a thermal threshold: above 32.2°C , the decrease becomes even stronger. They predicted that a 2°C increase in global temperatures above preindustrial levels would push 71% of the tropical forest biome beyond the thermal threshold. This would lead to a 20% decrease of the C stocks. In general, there is an ongoing decline of the tropical forest carbon sink (due to reasons as mentioned above): the pan-tropical sink evolved from $0.99 \text{ Pg C yr}^{-1}$ in 2000-2010 to $0.68 \text{ Pg C yr}^{-1}$ in the following decade (Hubau et al., 2020). However, Huntingford et al. (2013) did simulations with several climate models and they found evidence for resilience of the C stock of tropical rainforests to climate change.

Despite their importance in the global C cycle, tropical forests and their C dynamics remain understudied (Anderson-Teixeira et al., 2016). Some factors make fieldwork in the tropics challenging, such as the remoteness, climate, high diversity and structural complexity, political instability and lack of resources (Verryckt et al., 2022). In summary, tropical forests are indispensable in the fight against climate change, yet they are exceedingly fragile and at great risk. They are both strongly influencing and being influenced by the global climate. Therefore, it is essential to collect more data and to protect and restore them, together with drastically reducing CO_2 emissions.

2.2. Two major tropical rainforests in the world

2.2.1. Geographic location

The Amazon Basin is located in northern equatorial South America (Figure 2.1) and has an approximate area of 6.3 million km^2 (Albert et al., 2021). It encompasses various countries, such as Brazil, French Guiana and Colombia. The Amazon River runs through the basin and is the second longest river in the world with by far the biggest discharge, representing 15% of the global discharge to the oceans (Marengo et al., 2018). The Amazon Basin is home to the largest continuous tropical moist forest, with an area of around 5.5 million km^2 or 550 Mha (Sibret et al., 2022).

The Congo Basin is situated in central equatorial Africa (Figure 2.1) and has an approximate area of 3 687 000 km² (Alsdorf et al., 2016). It covers several African countries, such as the Democratic Republic of the Congo (DRC), the Central African Republic and parts of Angola and Cameroon. The biggest part is located in DRC. The Congo River runs through the basin and is the fifth longest river in the world. The Congo Basin encompasses the world's second largest continuous rainforest, spanning an area of roughly 1.8 million km² or 180 Mha (Sorí et al., 2017). The central area is known as the Cuvette Centrale, an immense depression that contains a forest swamp. This is the tropics' most extensive peatland complex (Dargie et al., 2017).



Figure 2.1: Location of the Amazon and Congo Basin. Taken from Kurek et al. (2022).

2.2.2. Climate

Since there are no distinct thermal seasons, rainfall distribution becomes a critical factor in distinguishing climate types in the tropics (Peters, 2014). According to the classification of Lauer, as explained by Peters (2014), there are two important climate types in tropical forests: the humid and semi-humid climate type. Both climate types dominate the Amazon and Congo Basin rainforests. The humid climate type can be found closest to the equator within the ITCZ. It is characterized by a clear water surplus, with a maximum of two arid months, where the monthly precipitation sum is lower than the monthly landscape evaporation rate (Peters, 2014). Nevertheless, the monthly levels of precipitation frequently show significant variability throughout the year. The semi-humid climate type is typically situated a little further from the equator. It has a short distinct dry season, with 3 – 5 arid months (Peters, 2014).

Although the Amazon and Congo Basin share similar climate types, considerable differences exist between them when averaging climatic variables. African tropical forests are on average drier and cooler than South American tropical forests, because they are located at higher altitudes (Banin et al., 2012; Hubau et al., 2020). The recent mean annual temperature is 25–25.5°C in the African rainforests and 26.5–27°C in the Amazon rainforests (Hubau et al., 2020). This means the Amazon forest is closer to the thermal threshold of 32.2°C (see section 1). Indeed, Sullivan et al. (2020) predict the biggest long-term reductions in carbon stocks, linked

to temperature increase, in South America. The average mean annual precipitation across the Amazon Basin (Figure 2.2 A) is around 2200-2500 mm (Banin et al., 2012; Marengo et al., 2018). The northwestern and western parts of Amazonia receive the most rainfall, with values as high as 4200 mm yr⁻¹ (Peters, 2014). In the semi-humid parts typical values are 1900 mm yr⁻¹ (Peters, 2014). Across the Congo Basin mean annual precipitation estimates (Figure 2.2 B) range from 1500 to 1900 mm (Alsdorf et al., 2016; Banin et al., 2012; Guan et al., 2015), which is considerably less than in the Amazon Basin. The wettest part of the Congo Basin is situated at the northwestern Atlantic coast, with precipitation values of 3000 mm yr⁻¹ (Peters, 2014). The driest parts receive around 900-1000 mm yr⁻¹ (Alsdorf et al., 2016). Besides the overall lower rainfall in the African tropical forests, the precipitation in the humid climate types also shows more seasonality than in Amazonia (Peters, 2014). The humid evergreen Amazon forests in the northwest show very little variation in monthly precipitation amounts (Marengo et al., 2018). In the equatorial Congo Basin however, there is a bimodal rainfall regime with two precipitation peaks each year: a lesser peak during March–May and a greater peak during September–November (Alsdorf et al., 2016; Bush et al., 2020). This pattern is traditionally explained by the seasonal migration of the ITCZ (Alsdorf et al., 2016; Bush et al., 2020).

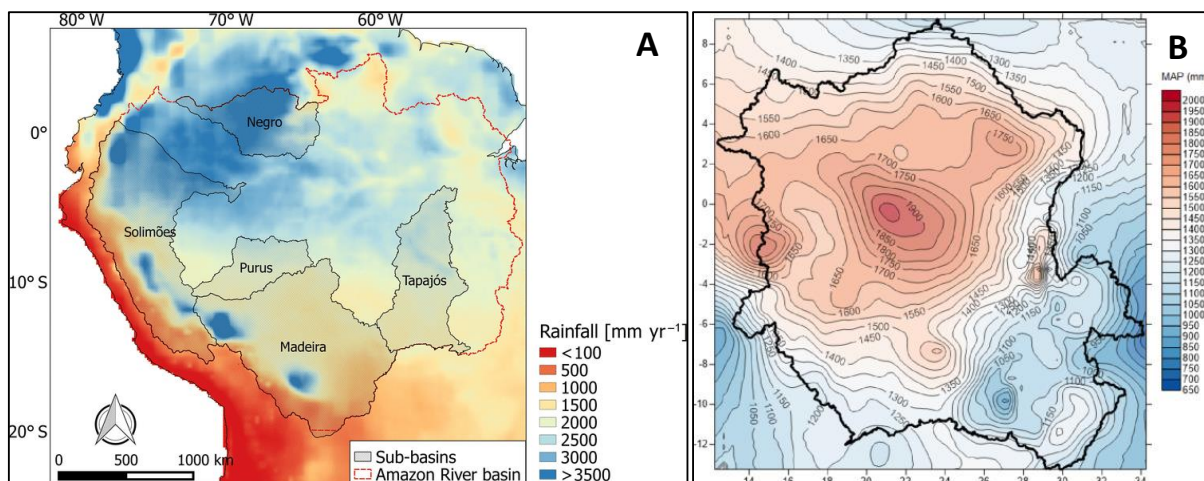


Figure 2.2: Distribution of the mean annual rainfall throughout the Amazon Basin (A) and the Congo Basin (B). A) From Maeda et al. (2017), B) From Tshimanga et al. (2016)

The climate is changing in the tropics. Both continents show a warming and drying trend (Hubau et al., 2020). In the Amazon region, mean air temperature has increased with 0.6°C from 1973 to 2013 (Marengo et al., 2018). Kasongo Yakusu et al. (2023) found a 0.18°C increase in mean daily temperature per decade in Yangambi, central Congo Basin. Since the early 1990s, the rise in temperature and temperature extremes accelerated. In Lopé National Park in Gabon (western Congo Basin) minimum daily temperature increased by 0.25°C per decade (Bush et al., 2020). There is no consistent long-term trend in total precipitation within the Amazon Basin (Marengo et al., 2018). However, rainfall variability has increased with more extreme droughts and floods occurring. “Mega-droughts” were recorded in 2005, 2010 and 2016 (Marengo et al., 2018). There are two causes, as explained by Lewis et al. (2011). On one hand, there are the rising Pacific sea surface temperatures (SSTs), which may intensify El Niño events and associated periodic Amazon droughts. On the other hand, warming SSTs in the tropical Atlantic displace the ITCZ northwards, prolonging and intensifying the dry season,

especially in southern Amazonia (Marengo et al., 2018). Similar trends are witnessed in the Congo Basin. In Yangambi, there is no long-term change in precipitation, although post 2000 a drying trend of -87 mm per decade has been observed (Kasongo Yakusu et al., 2023). In Gabon total annual rainfall has decreased with 75 mm per decade (Bush et al., 2020). There has also been witnessed a stronger seasonality in the central Congo Basin (e.g. Yangambi), with less rainfall in the dry season and more and intensified rainfall in the wet season (Kasongo Yakusu et al., 2023). The drying trend that has been observed over the past two decades in central equatorial Africa is likely the consequence of increasing SSTs in the western edge of the Indian Ocean, which enhanced and extended the Indo-Pacific Walker circulation westward (Hua et al., 2016).

2.2.3. Vegetation

In the humid climate type the dominant vegetation type is evergreen tropical forest, while in the semi-humid climate type this is semi-evergreen monsoon forest (Peters, 2014). The latter have lower tree formations, reduced species diversity and less biomass, in comparison with evergreen tropical forests. However, both forest types can be considered as tropical rainforests, with high amounts of precipitation (Peters, 2014).

Using inventory data, Sullivan et al. (2017) found an average of 152 tree species ha⁻¹ in the Amazon tropical forests. Ter Steege et al. (2013) estimated there is a total of $\pm 16\,000$ tree species in lowland Amazonia. A more recent study by Slik et al. (2015) estimates that the Neotropics (i.e. tropical South America) harbour $\pm 19\,000 - 25\,000$ tree species. In comparison, temperate Europe has only 124 tree species (Slik et al., 2015). Remarkable is that only 283 species, or 1.8% of the estimated 16 000 total species pool, collectively account for 50% of the total number of stems (Fauset et al., 2015). This means most Amazonian species are very rare. Some of the most abundant tree species in the Amazon rainforests are *Iriartea deltoidei* (from the Arecaceae family), *Eschweilera coriacea* (Lecythidaceae), *Pseudolmedia laevis* (Moraceae) and *Eperua falcata* (Fabaceae) (Fauset et al., 2015). The study of Fauset et al. (2015) also shows that around 1.1% of the species in the Amazonian species pool together account for 50% of the total carbon gains. These species are called productivity hyperdominants. Another finding is that $\pm 1.1\%$ of the species in the Amazonian species pool are collectively responsible for 50% of the total C stock. These are called biomass hyperdominants. Furthermore, these biomass and productivity hyperdominant species are often not among the most abundant species (in stem number). They conclude that dominance of forest function is concentrated in a few species with a large diameter and high wood density. Esquivel-Muelbert et al. (2019) analysed long-term changes in the species composition in lowland Amazonian forests, having witnessed an intensification of the dry season. They found that dry-associated tree genera have become more abundant among newly recruited trees, together with an increased mortality of wet-affiliated genera. Thus, a gradual transition towards a drier affiliated Amazonia is currently unfolding.

African tropical forests have a much lower species richness in comparison with Neotropical ones: on average 74 tree species ha⁻¹ (Sullivan et al., 2017). In total the Congo Basin has an estimated number of $\pm 4500 - 6000$ tree species (Slik et al., 2015). Not many species are

shared among both continents (Slik et al., 2015). A key structural feature of African tropical forests is their low stem density (426 stems ha^{-1}), in comparison with Amazonian forests (around 600 stems ha^{-1}) (Lewis et al., 2013). Bastin et al. (2015) found there are only 18 biomass hyperdominant species (collectively accounting for half of the total biomass) in the Congo Basin, which is only 0.3% of the estimated 6000 tree species pool. One species, *Gilbertiodendron dewevrei* (Fabaceae), even accounts for $\pm 20\%$ of the total C stock. Out of these 18 species examined in this study, 7 are typically middle-sized trees that rarely develop large diameters (e.g. 70 cm). Thus, Fauset et al. (2015) demonstrated that Amazonian biomass hyperdominant species generally attain large maximum sizes, whereas Bastin et al. (2015) highlighted the crucial contribution of very common and abundant middle-sized tree species to the African forest carbon budget. Some of the most abundant tree genera in the Congo Basin are *Celtis* (Ulmaceae), *Petersianthus* (Lecythidaceae), *Entandrophragma* (Meliaceae) and *Anonidium* (Annonaceae) (Fayolle et al., 2014). Another important difference with the Amazon, is the relatively higher amount of deciduous, light demanding and dry tolerant species witnessed in the Congo Basin (Biwolé et al., 2015; Luambua et al., 2021). Climate change is also inducing a vegetation shift in the Congo Basin. Aguirre-Gutiérrez et al. (2020) showed that the recent long-term droughts in the Congo Basin led to a significant decline in taxonomic, phylogenetic and functional diversity. Fauset et al. (2012) observed a consistent increase in deciduous (drought-tolerant) canopy specialist species, accompanied by a decrease in evergreen (wet-affiliated) sub-canopy specialist species. By favouring drought-tolerant species in their composition, the biomass stocks of African tropical forests may be more resilient to prolonged droughts compared to what short-term studies of severe individual droughts imply (Fauset et al., 2012).

2.2.4. Carbon pool and sink

The Amazon forests account for 17% of the terrestrial vegetation carbon stock (Fauset et al., 2015). Sullivan et al. (2017) found a mean carbon stock of 140 Mg ha^{-1} in the Amazonian forests. In 1998, Phillips et al. found the first evidence, supported by plot inventory data, that Neotropical forests are a significant C sink, sequestering 0.71 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (from 1975 to 1996). A more recent study by Brien et al. (2015) estimated that during the 1990s the average C sink of intact Amazonian forests was 0.53 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ and during the 2010s 0.24 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, indicating a substantial decline in the Amazonian carbon sink (Figure 2.3 A). This can be explained by the recent stabilization in woody productivity (Figure 2.3 B) alongside persistent increases in woody mortality (Figure 2.3 C), resulting in shortened carbon residence times (Brien et al., 2015). Potential factors driving the mortality increase include higher climate variability and feedbacks of accelerated growth leading to higher mortality rates, thereby reducing tree longevity. The 2005 Amazon drought for example lead to a total carbon loss of 1.2 to 1.6 Pg, reversing the large long-term carbon sink in affected forests (Phillips et al., 2009).

The African tropical forests have a mean carbon stock of 183 Mg ha^{-1} (Sullivan et al., 2017). Per unit of area, this stock is significantly higher than the Amazonian one. So the Congo Basin forests have fewer, but bigger stems per area (Lewis et al., 2013). Supported by plot inventory

data, Lewis et al. (2009) were the first to assert that African tropical forests serve as a notable carbon sink, sequestering $0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (during the period 1968-2007). Hubau et al. (2020) showed that while the Amazon C sink continued to decline, the C sink of intact African tropical forests had been stable for the three decades to 2015, at $0.66 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Figure 2.3 A). However, after 2010 they also witnessed a decline of the C sink in the Congo Basin. This indicates that the two major tropical forests of the world show different reactions to global climate change.

Hubau et al. (2020) combined data of inventory plots of structurally intact old-growth forests on both continents. The divergence in the C sink is primarily related to carbon losses from tree mortality, showing no discernible multi-decadal trend in Africa and a long-term rise in Amazonia (Figure 2.3 C). However, after 2010 Hubau et al. (2020) also witnessed an increase in C losses in the Congo Basin. These increases are delayed in comparison to Amazonia, which indicates there is an asynchronous C sink saturation of the two forests (Figure 2.3 A). Hubau et al. (2020) saw that increasing C losses were found in plots with high long-term productivity (or with a short carbon residence time = CRT), while no increase was found in low-productivity plots (with a long CRT). Periods of higher productivity are followed by periods of higher tree mortality, through internal feedback mechanisms (Hubau et al., 2020). This explains the diverging sink: Amazon forests exhibit higher long-term woody productivity (relative to their lower carbon stocks), leading to accelerated mortality feedbacks compared to African tropical forests (Hubau et al., 2020). Simplified, Amazon forests are “fast” (shorter CRT), African forests are “slow” (higher CRT).

This diverging trend further accentuates the importance of the Congo Basin rainforests. Although they have a smaller area, the total C sink of the intact African tropical forests even surpassed the one of the intact Amazonian forests after 2010, with levels of 0.4 Pg C yr^{-1} and $0.27 \text{ Pg C yr}^{-1}$, respectively (Hubau et al., 2020). Despite its global and regional importance, The Congo Basin has been studied considerably less, in comparison to the Amazon Basin. The Congo Basin (especially the centre) has some of the least environmental observations worldwide, due to lack of access or security and political instability (Malhi et al., 2013). This data gap needs to be filled to gain a better understanding of the contribution of this region to the global carbon (and water) cycle (López-Ballesteros et al., 2018). It is certain that the Congo Basin will play a crucial role in the future of our planet and therefore needs more attention.

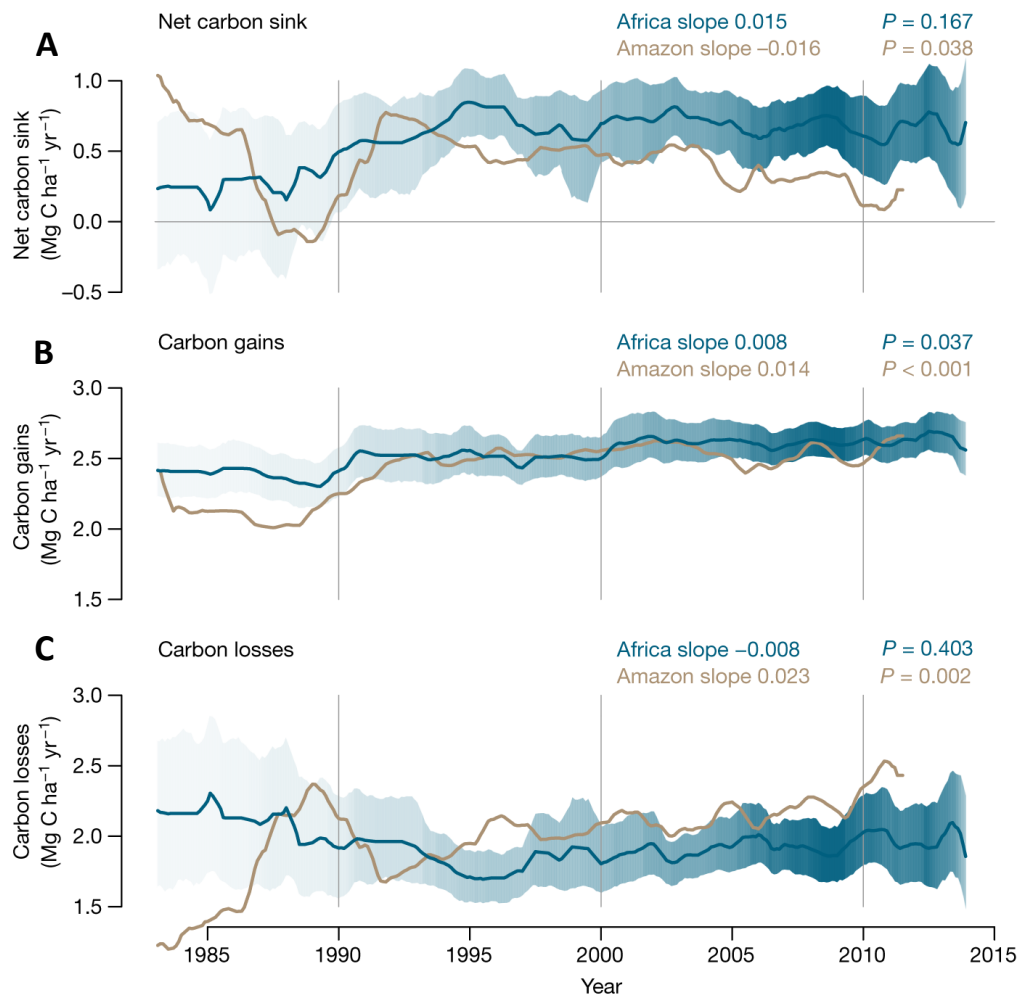


Figure 2.3: Long-term carbon dynamics of structurally intact old-growth tropical forests in Africa and Amazonia. Trends in net aboveground live biomass carbon (A), carbon gains from wood production (B), and carbon losses from tree mortality (C). Shading corresponds to the 95% confidence interval. Taken from (Hubau et al., 2020). Amazonian data from Brien et al. (2015).

2.3. Measuring photosynthesis

Hubau et al. (2020) made use of permanent inventory plots to gain better understanding of the reaction of both tropical forest to global changes. A different way to fill this data gap is the use of Dynamic Global Vegetation Models (DGVMs). DGVMs simulate changing vegetation dynamics, coupled to climate models (Krinner et al., 2005). They are used to make more accurate predictions of future vegetation responses to climate change. They are based on photosynthetic models, which need photosynthetic measurements to be parametrised (Rogers et al., 2017). Given their crucial role in the global carbon cycle and scarce measurements, more photosynthetic data of tropical forests is needed to better parametrise DGVMs for the tropics and make more accurate predictions. Photosynthesis is mostly represented in DGVMs with the Farquhar-von Caemmerer-Berry model (Farquhar et al., 1980). This master's thesis will compare the photosynthetic parameters that are used in these models between sites of the two major tropical rainforests.

2.3.1. Photosynthesis in C3 plants

Net photosynthesis, or CO₂ assimilation (A), is the difference between the biochemical CO₂ fixation (P) and the leaf's respiration (R_l) (Schulze et al., 2019):

$$A = P - R_l \quad (2.1)$$

Photosynthesis (P) itself is a diffusion process driven by the stomatal conductance (g_s) and the gradient of the CO₂ concentration between the atmosphere (C_{atm}) and the leaf (C_{leaf}) (Schulze et al., 2019):

$$P = (C_{atm} - C_{leaf}) g_s \quad (2.2)$$

The stomatal conductance is a measure of the rate of gas exchange and transpiration through the leaf stomata as determined by the degree of stomatal aperture (Pietragalla & Pask, 2012). The more the stomata are opened (higher g_s), the more CO₂ can enter the leaf and the higher the photosynthetic rate.

Photosynthesis encompasses a complex set of biophysical and biochemical processes. This section wants to give a simplified overview, derived from Raven et al. (2013). In general photosynthesis is the process where light energy (photons) is used to create carbohydrates (generalized as CH₂O) from carbon dioxide (CO₂) and water (H₂O), with oxygen (O₂) formed as a side product:



Light energy is transformed into chemical energy, under the form of sugars. This process is the route by which virtually all energy enters our biosphere. The photosynthetic process can be divided into the light reactions and the dark reactions, as explained by Raven et al. (2013).

Light reactions (adapted from Raven et al. (2013))

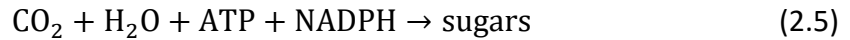
The light reactions are energy-transduction reactions: they require light, are light-dependent. They take place in the thylakoid membranes of the chloroplasts in the plant cell. The overall reaction occurring is (Figure 2.4):



Solar energy is absorbed by pigment molecules, of which the chlorophylls are the most important ones. This sets an electron transport chain (ETC) in motion, in which chemical energy is created under the form of the molecules ATP and NADPH. The amount of NADPH and ATP produced depends on the rate of electron transport J (μmol of electrons m⁻² s⁻¹). Water molecules deliver electrons for the ETC and O₂ is produced (water photolysis). Only a portion of the sunlight spectrum can be used by the pigment molecules of plants for photosynthesis, being the Photosynthetic Active Radiation (PAR). The PAR ranges from wavelengths of 400 to 700 nm. The amount of sunlight available for the plant is often expressed as the photosynthetic photon flux density I (μmol of photons m⁻² s⁻¹).

Dark reactions (adapted from Raven et al. (2013))

The dark reactions are light independent and occur in the stroma of the chloroplasts. The overall reaction is:



The dark reactions are carbon-fixation reactions: NADPH and ATP produced in the light reactions are used to reduce carbon dioxide to organic carbon. In many plant species this happens in the Calvin cycle, a series of reactions in which CO_2 is converted to sugars. The Calvin cycle consists of three major stages (Figure 2.4):

- First stage = carboxylation (fixation of CO_2):
 CO_2 is combined with ribulose-1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglycerate (PGA). This reaction is catalysed by the enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase). Each PGA molecule – the first detectable product of the Calvin cycle – contains three carbon atoms. Plants in which the Calvin cycle is the only carbon-fixation pathway, are therefore called C3 plants. (Almost) all trees are C3 plants. The amount of CO_2 fixated in the Calvin cycle depends on the rate of carboxylation (V_c).
- Second stage = reduction:
PGA is reduced to 3-phosphoglyceraldehyde (PGAL), also known as triose phosphate (TP), with the use of NADPH and ATP.
- Third stage = regeneration:
Part of the produced PGAL is used to form sugars and part is used for the regeneration of RuBP, such that the cycle can continue.

Although the dark reactions do not directly need light, they can only occur in the presence of light, because of its need for NADPH and ATP produced in the light reactions.

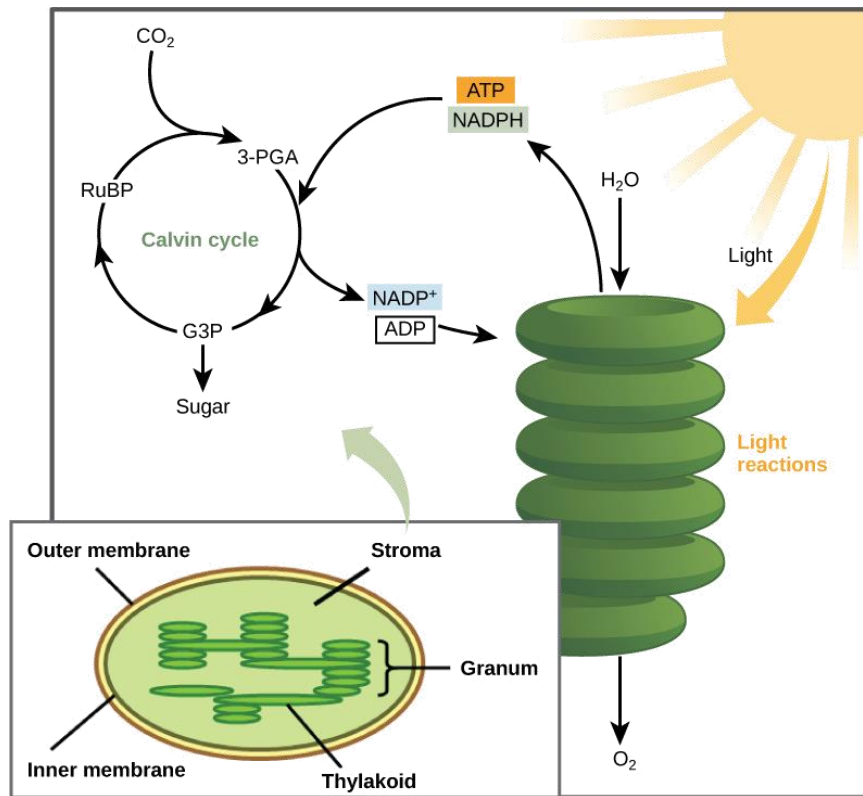


Figure 2.4: Schematic representation of the photosynthetic process of coupled light and dark (Calvin cycle) reactions (G3P = PGAL) in the chloroplasts (bottom left). Taken from Fowler et al. (2013).

Net photosynthesis

To calculate net photosynthesis or CO₂ assimilation of the leaf, the amount of respiration needs to be known (Formula 2.1). There are two types of respiration described by Raven et al. (2013):

- Type 1 = photorespiration:
The enzyme Rubisco can also use O₂ (i.e. Rubisco's oxygenase activity) instead of CO₂ (i.e. Rubisco's carboxylase activity) as a substrate and oxidate RuBP. For each molecule of RuBP oxidated, half a molecule of CO₂ is released (Farquhar et al., 1980). As photorespiration is coupled to the Calvin cycle, it can only occur in the presence of light.
- Type 2 = mitochondrial respiration:
Respiration happening in the mitochondria, releasing CO₂. This respiration occurs at any time, also in absence of light. Therefore, it is often referred to as dark respiration.

Farquhar et al. (1980) describe the amount of net photosynthesis (A) as:

$$A = V_c - 0.5V_o - R \quad (2.6)$$

with V_c = rate of carboxylation, V_o = the rate of oxygenation (photorespiration) and R = the rate of mitochondrial respiration.

2.3.2. CO₂ response curves

Increased concentrations of atmospheric CO₂ enhance vegetation productivity (Wang et al., 2020). In other words, increasing [CO₂] leads to higher CO₂ assimilation (A) (Sharkey et al., 2007). This is called the CO₂ fertilization effect. The reasons behind this global phenomenon are explained by Sharkey et al. (2007). First of all, CO₂ is a substrate for the photosynthesis reaction and is currently a limiting factor. Secondly, increasing [CO₂] increases the carboxylation activity and decreases the oxygenation activity of Rubisco, thereby reducing CO₂ release by photorespiration and increasing light use efficiency. But photosynthesis does not keep increasing endlessly with increasing [CO₂]. The relationship between the CO₂ concentration and photosynthesis is described through the CO₂ response curve.

A CO₂ response curve (in short: $A:C_i$ curve) describes the net CO₂ uptake by a plant leaf (A) as a function of the CO₂ concentration in the intercellular airspaces of the leaf (C_i) (Sharkey et al., 2007). The response of A to ambient CO₂ concentrations (C_a) cannot be easily interpreted since it is affected by boundary layer, stomatal, and mesophyll processes (Long & Bernacchi, 2003). This is why C_i is used instead of C_a . The curve is made under light saturated conditions to eliminate the influence of light on A .

A CO₂ response curve consists of three distinct phases, as summarised by Sharkey et al. (2007). Each of these phases represents a limiting factor of light-saturated photosynthesis (Figure 2.5):

- Phase 1 = Rubisco limited phase:
In this phase, A is determined by the Rubisco activity, assuming the enzyme has a saturating supply of the substrate RuBP. With higher [CO₂], Rubisco has more substrate and a higher carboxylation activity (so less photorespiration), leading to higher net photosynthesis. This state typically occurs at low CO₂ concentrations, usually < 20 Pa or 200 ppm. Photosynthetic rate increases linearly with C_i .
- Phase 2 = RuBP regeneration limited phase:
In this phase, RuBP is used at a constant rate by Rubisco, so photosynthesis is limited by the regeneration of RuBP. The RuBP regeneration is limited by the supply of NADPH and ATP, which in turn is limited by the electron transport rate (J). This state occurs at higher CO₂ concentrations, usually > 30 Pa or 300 ppm. CO₂ assimilation increases with increasing [CO₂], only because of the higher carboxylation activity of Rubisco, reducing CO₂ release by photorespiration. By consequence, the curve has a smaller slope than in phase 1.
- Phase 3 = triose phosphate use (TPU) limited phase:
In this phase the capacity of the leaf to use the products of the chloroplasts (primarily triose phosphate) is lower than the capacity of the reactions taking place in the chloroplasts. The photosynthetic rate is limited by the TPU and will not respond anymore to increasing CO₂ concentration. The curve reaches a plateau. But this third state is not always present and of less importance.

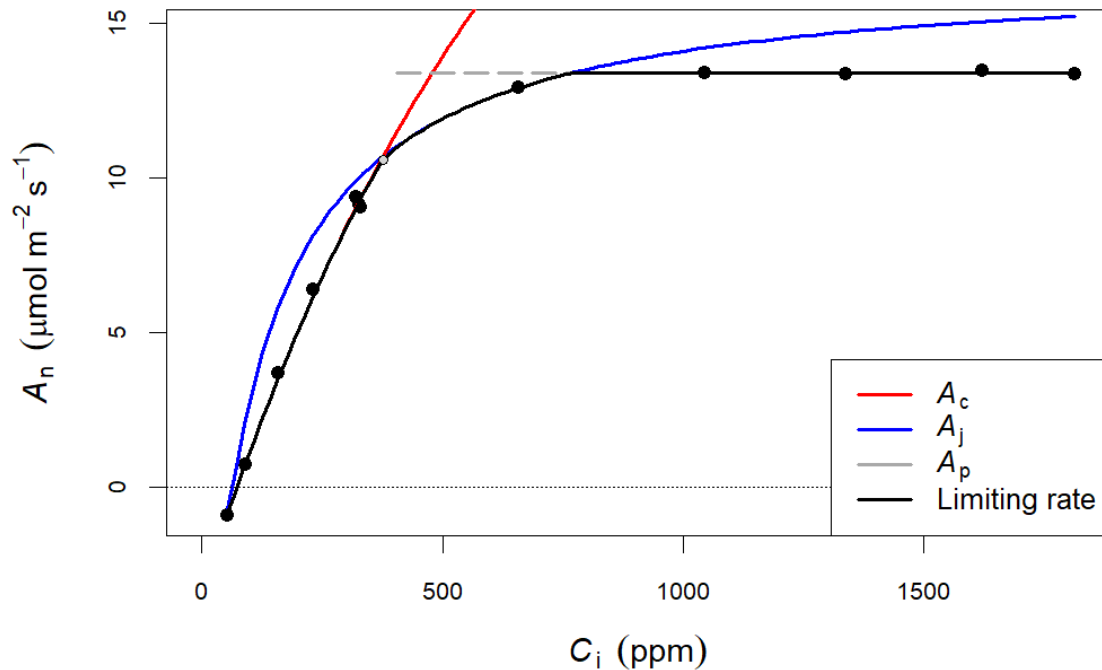


Figure 2.5: A CO_2 response curve of the species *Petersianthus macrocarpus*, measured in Yangambi (DRC) in August 2023 and fitted with the “Plantecophys” R package (Duursma, 2015). Net CO_2 uptake (A_n) is plotted in function of the intercellular CO_2 concentration (C_i). The black A - C_i curve is the minimum of three potential limiting factors of net photosynthesis: Rubisco (A_c), RuBP (A_j), or TPU (A_p).

From this CO_2 response curve, four photosynthetic parameters can be derived (Farquhar & Sharkey, 1982; Sharkey et al., 2007):

- The CO_2 compensation point (Γ):
This is the CO_2 concentration at which no net CO_2 assimilation occurs. Photosynthesis equals total respiration (photorespiration + mitochondrial respiration), i.e. the carboxylation rate equals the respiration rate ($V_c = 0.5 \cdot V_o + R$, see Formula 2.6). On the CO_2 response curve, Γ can be derived as the intersect with the x-axis. Γ^* refers to the photorespiratory compensation point, where photosynthetic uptake of CO_2 is exactly compensated by photorespiratory CO_2 release. So Γ^* is the compensation point in the absence of “dark respiration”. The carboxylation rate equals half the oxygenation rate ($V_c = 0.5 \cdot V_o$). When air around the leaf has a concentration of Γ^* , there is still a net release of CO_2 , because of the non-photorespiratory mitochondrial respiration. Consequently, Γ^* is slightly lower than Γ .
- The maximum CO_2 assimilation rate ($A_{\max}$):
 $A_{\max}$ is reached under light and CO_2 saturation and can be derived from the $A:C_i$ curve as the assimilation rate at the plateau. This value is often determined by the TPU and, therefore, rarely occurs in natural conditions.
- The maximum carboxylation rate ($V_{c\max}$):
The maximum rate of carboxylation is determined by the amount and the carboxylation activity of Rubisco and is derivable from the CO_2 response curve as the slope of the curve at 0 ppm.
- The maximum rate of electron transport ($J_{\max}$):

$J_{\max}$ is reached under light saturated conditions and ensures a maximum speed of RuBP regeneration. It is not directly readable from the curve.

These photosynthetic parameters (especially $V_{\max}$ and $J_{\max}$) are used to parametrise DGVMs, so accurate predictions of global carbon fluxes can be made (Walker et al., 2014). $J_{\max}$ is tightly coupled with $V_{\max}$. This is traditionally explained by an optimal resource allocation between electron transport and the Calvin cycle. Walker et al. (2014) suggest this positive correlation exists to protect the plant against photoinhibition, when Rubisco carboxylation is limiting. Photoinhibition is an excess of absorbed light which causes oxidative damage to the photosynthetic system, reducing photosynthetic capacity (Keren & Krieger-Liszky, 2011).

Fitting of CO₂ response curve models

The most frequently used model to describe the response of the net photosynthetic rate to increasing CO₂ concentrations in C3 species, is the Farquhar-von Caemmerer-Berry (FvCB) model (Farquhar et al., 1980), as summarised by Sharkey et al. (2007). This model is the basis for calculating important photosynthetic parameters, such as $V_{\max}$ and $J_{\max}$, used in DGVMs.

When the CO₂ assimilation rate (A) is Rubisco-limited (phase 1; Figure 2.5), its response to [CO₂] can be described by the following formula:

$$A = V_{\max} \left[\frac{C_c - \Gamma^*}{C_c + K_c(1 + O/K_o)} \right] - R_d \quad (2.7)$$

where A is the net photosynthetic rate, $V_{\max}$ is the maximum carboxylation velocity of Rubisco, C_c is the CO₂ partial pressure at Rubisco, Γ^* is the photorespiratory CO₂ compensation point, K_c is the Michaelis constant of Rubisco for CO₂, O is the partial pressure of O₂ at Rubisco, K_o is the inhibition constant (usually taken to be the Michaelis constant) of Rubisco for oxygen and R_d is the dark respiration.

When A is limited by RuBP regeneration (phase 2; Figure 2.5),

$$A = J \left[\frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} \right] - R_d \quad (2.8)$$

where J is the rate of electron transport.

When A is TPU-limited (phase 3; Figure 2.5), its evolution in function of [CO₂] can be described with the following equation:

$$A = 3 \text{ TPU} - R_d \quad (2.9)$$

where TPU is the rate of triose phosphate use.

The (light saturated) photosynthetic rate at a certain CO₂ concentration is determined by the biochemical factor that is most limiting at that concentration and, therefore, can be determined as the minimum photosynthetic rate of those three limiting factors (Figure 2.5):

$$A = \min(|A_c|, |A_j|, |A_p|) \quad (2.10)$$

where A_c is A for Rubisco limitation, A_j is A for RuBP regeneration limitation and A_p is A for TPU limitation.

Limitations to the CO₂ fertilization effect

Because of the CO₂ fertilization effect (CFE), rising atmospheric CO₂ concentrations could be seen as a positive trend, stimulating photosynthesis. It is demonstrated by the CO₂ response curves that indeed a higher [CO₂] leads to a higher A until a maximum is reached. But there are some further limitations to the CFE in the long term.

A recent study by Wang et al. (2020) showed that global CFE has declined across most terrestrial regions of the globe from 1982 to 2015, using multiple long-term satellite- and ground-based datasets. The two main explanations for this trend are emerging nutrient limitations and the underestimated sensitivity of photosynthesis to water availability. The growing atmospheric CO₂ concentration increases C assimilation in plants. To cope with the higher amount of carbohydrates, formed through photosynthesis, plants will have a higher demand for other nutrients, most importantly N and P. This demand cannot be met, leading to lower N and P concentrations in leaves, limiting photosynthesis and thereby CFE. The study of Ainsworth & Rogers (2007) concludes the same, stating there is an acclimation of the carboxylation capacity of Rubisco, because of photosynthetic downregulation by nitrogen supply. Furthermore, a plant requires more water if photosynthesis increases, as seen by Formula 2.3. As there is not suddenly more water available, CO₂ assimilation is limited (Wang et al., 2020). Another limitation to the CFE is that elevated [CO₂] reduces stomatal conductance (g_s), i.e. there is a higher stomatal closure (Ainsworth & Rogers, 2007). According to Formula 2.2, a lower g_s reduces photosynthesis. Current carbon cycle models don't take the declining CFE trend enough into account (Wang et al., 2020), leading to underestimation of future global warming.

2.4. Photosynthetic variation between species

2.4.1. Bivariate relationships with leaf functional traits

Photosynthetic capacities differ between species. This needs to be accounted for in DGVMs, but photosynthesis cannot be quantified for all species. One (more recent) way to deal with this problem in DGVM parameterisation is to study empirical relationships between photosynthetic parameters and leaf functional traits. Wright et al. (2004) describe these relationships in the leaf economics spectrum (LES) and they are further quantified for several global vegetation types by Kattge et al. (2009).

The LES concept (Wright et al., 2004) states there are trade-offs between various leaf functional traits, resulting in a spectrum of chemical, structural and physiological properties of leaves. Plants use photosynthate and minerals to construct leaves, which in turn produce photosynthate over their lifetimes. These photosynthetic products are used to acquire mineral nutrients, to support plant metabolism and to re-invest in leaves, their supporting stems and other plant parts. Wright et al. (2004) state these processes of investment and re-investment of nutrients (carbon and minerals) are inherently economic in nature. The LES ranges from quick to slow return on investments of nutrients and dry mass in leaves. This phenomenon can be observed globally.

There are six key features of leaves, essential to describe the worldwide LES (Wright et al., 2004):

- The leaf mass per area (LMA) is the ratio of leaf dry mass to light-intercepting leaf area. More often, the reverse leaf trait is used: specific leaf area (SLA), i.e. leaf area per unit of leaf dry mass. A leaf with a low SLA (or high LMA) is thick and/or dense.
- Photosynthetic assimilation rate or photosynthetic capacity (A)
- Leaf nitrogen (N)
- Leaf phosphorus (P)
- The dark respiration rate (R_{dark}) reflects how fast photosynthetic products are consumed by the plant.
- Leaf lifespan (LL): Leaves with a high lifespan need a robust construction in the form of a low SLA.

The ecophysiological leaf characteristics (such as N, P, A and R_{dark}) can be expressed on an area basis and on a mass basis. Light capture and transactions through surfaces can be best described per leaf area, while leaf economics in terms of revenues and expenditures per unit investment, measured as biomass or C, N or P, are quantified per unit of leaf dry mass (Wright et al., 2004). In this master's thesis, the choice has been made to work on area-based relationships (e.g. N_{area} and P_{area} = leaf N and P concentration on an area basis). This decision aligns with the fact that photosynthetic parameters used in DGVMs (such as V_{cmax} and J_{max}) are mostly expressed per unit of leaf area.

The global dataset of Wright et al. (2004) clearly shows that photosynthetic capacity (A) increases with leaf nitrogen, both on mass and area basis. This can be explained by the fact that N is an essential component of the photosynthetic proteins, especially Rubisco. Other studies also find a positive relationship between the photosynthetic parameters A_{max} , V_{cmax} and J_{max} , and N (Bahar et al., 2017; Domingues et al., 2010; Ellsworth et al., 2022; Reich et al., 2009; Walker et al., 2014).

Several studies indicate that leaf phosphorus content has a significant impact on the relationship between photosynthesis and N, rather than it affects A directly (Domingues et al., 2010; Ellsworth et al., 2022; Reich et al., 2009; Walker et al., 2014). The interaction between N and P is more important than the influence of P alone. With increasing leaf P, the response of A (A_{max} , V_{cmax} and J_{max}) to leaf N gets stronger. Or, in sites with low P, A is less sensitive to N, which significantly decreases photosynthesis. However, the research of Ellsworth et al. (2022) concludes there is also a direct influence of leaf P on V_{cmax} and J_{max} . They even found that in their (predominantly pan-tropical) dataset P on its own had a higher impact on the photosynthesis rates (especially on J_{max}) than N.

P is an essential nutrient to plants, since it is an important compound in nucleic acids, phospholipid membranes and bioenergetic molecules such as ATP (Wright et al., 2004). The supply of P is necessary for the electron transport capacity of leaves (J) and for the regeneration of RuBP (Ellsworth et al., 2022), since ATP and NADP – crucial molecules in these processes – are rich in P (section 2.3.1).

Domingues et al. (2010) highlight that photosynthesis is determined by the most limiting leaf nutrient, nitrogen or phosphorus. Plants gain P from weathered soil minerals, while N can be largely fixed from the atmosphere (Wright et al., 2004). Temperate and boreal ecosystems are generally considered to be N limited. On the contrary, many tropical forests have an excess of N and are limited by plant available P, since tropical soils are old and thus highly weathered (Domingues et al., 2010; Reich et al., 2009). So, in tropical biomes a weaker relationship between A and N is expected and a stronger relationship between A and P, compared to younger biomes (temperate and arctic) (Domingues et al., 2010; Reich et al., 2009). Regarding the importance of tropical forests in regulating global CO_2 uptake, it's necessary to include P constraints more in global terrestrial C cycle models (Ellsworth et al., 2022). However, there are also tropical forests that face N limitation, such as those growing on the oldest and most infertile soil types in north-east and central Amazonia (Domingues et al., 2010). Furthermore, leaf N and P tend to co-vary in nature, so it is difficult to separate the roles of both nutrients in explaining variation in photosynthesis (Reich et al., 2009).

There is no global relationship between area-based A and SLA, only between A_{mass} and SLA (Wright et al., 2004). SLA reflects a trade-off between construction cost and longevity of leaves (Díaz et al., 2016). A leaf with a high SLA is easier to construct (less dense), but it has a shorter lifespan.

Having discussed all the relevant functional leaf traits, we can return to the leaf economics spectrum, in which all these traits are linked. The LES has two extreme ends with a continuous range in between (Table 2.1). Species can be placed somewhere on this spectrum. The spectrum runs from fast-growing species with quick returns on investments of nutrients and dry mass in leaves to slow-growing species with a slow return rate (Wright et al., 2004) (Table 2.1). Each end of the LES represents a different ecological strategy of plants. The LES reflects a trade-off between leaf construction costs and growth potential (Díaz et al., 2016) or between productivity and persistence (Reich, 2014). Species at the quick-return end have “acquisitive” leaves. They are “cheaply” constructed and have a high photosynthetic capacity, so the plant can quickly grow when conditions are favourable. Species at the slow-return end have “conservative” leaves. They are harder to build, but live longer, so they can perform photosynthesis for a longer time period (at a lower rate though). They can better survive abiotic and biotic hazards (e.g. herbivory) too. The LES suggests that leaf investment strategies that are not economically competitive in a certain environment are eventually eradicated through natural selection (Wright et al., 2004). Lastly, these trait relationships occur largely independently of growth form, plant functional type or biome, which indicates there is a single global spectrum of leaf economic variation (Wright et al., 2004).

Table 2.1: Overview of the two ends of the leaf economics spectrum (LES), as described by Wright et al. (2004).

Leaf functional trait	Quick return end (acquisitive strategy)	Slow return end (conservative strategy)
Photosynthetic capacity (A)	High	Low
Dark respiration rate (R_{dark})	High	Low
Leaf N content	High	Low
Leaf P content	High	Low
Specific leaf area (SLA)	High	Low
Leaf lifespan (LL)	Low	High

In this master's thesis, we want to check whether these relationships are similar for two sites in the Amazon Basin and one site in the Congo Basin.

2.4.2. Plant functional types (PFTs)

A more common (older) way to deal with variation in photosynthetic capacity between species in DGVM parametrisation is to divide the species into plant functional types (PFT). Each PFT gets assigned a unique parameter set (Yang et al., 2015). Plant functional types (PFTs) are defined as groups of plant species that are functionally similar (Box, 1996). Plants vary with environmental conditions, along gradients. They adapt to these conditions through certain functional modifications. But within an ecosystem (with similar external conditions) there are different plant groups too. PFTs can be differentiated based on structural-functional traits, such as overall size and seasonal (de)foliation pattern, or based on purely functional criteria, such as metabolism (including photosynthetic characteristics), resource requirements, allocation strategies and reproductive rate (Box, 1996). Wright et al. (2004) argue that a division in PFTs is unnecessary or not that important, since the PFTs can be explained by the leaf economics spectrum. Each PFT has a certain combination of leaf traits that fit somewhere in the LES. Functional types overlap substantially in their leaf characteristics. Yang et al. (2015) also argue that it is better to use functional traits in DGVMs instead of PFTs, e.g. due to great variation within PFTs. Nevertheless, categorisation in PFTs remains a convenient way to group species in hyperdiverse ecosystems. When studying ecosystem functioning of such diverse ecosystems, it is more convenient to use a functional classification framework than a taxonomic one. Below, the relevant PFTs for this study and their photosynthetic characteristics will be discussed.

In this master's thesis, two different classifications into PFTs are used. Firstly, tree species are divided into PFTs based on their light requirement and regeneration, as described by Hawthorne (1995). A species is assigned to one of the following regeneration guilds: pioneer (P), non-pioneer light-demanding (NPLD) or shade-bearing (SB) species. Pioneers are species whose seedlings require full sunlight to develop. NPLD species can tolerate some shade as seedlings, but they require openings in the canopy to grow into adult trees. SB species can survive in the shade during their entire lifespan (Biwole et al., 2015). Two more PFTs are

added, since they are unique life forms: lianas and understory shade-bearing (USB) species. The second division of species into PFTs is based on leaf phenology: evergreen vs. deciduous species.

2.4.2.1. Light requirement + regeneration

Light-demanding vs. shade-bearing species

Light is likely the most limiting resource in tropical forests (Chazdon et al., 1996). Shade tolerance reflects a trade-off in carbon investment. Shade-bearing (SB) species are more resistant to physical damage than light-demanding (LD) species, but they have lower carbon gain and relative growth rates (Kitajima, 1994). Leaves of SB species often have lower photosynthetic rates, a lower SLA and lower N content (Rijkers et al., 2000). SB species are thus more situated at the slow-return end of the LES and LD species at the quick-return end. Legner et al. (2014) describe that SB tree species have certain traits adapted to low-light conditions. They have a higher variation in SLA within the canopy, reflecting a higher plasticity to varying irradiance. This is partly because SB species have a canopy with greater vertical extension than LD species. The differentiation between shade leaves and sun leaves is more pronounced. These shade leaves have a high SLA but relatively low N_{area} , resulting in a lower A_{max} (see section 2.5). The study of Verbeeck et al. (2014) shows that shade tolerance is an important factor determining functional diversity in Congolese secondary tropical forests.

Pioneer vs. climax species

Swaine & Whitmore (1988) define two distinct groups of tree species in tropical rainforests: early-successional pioneer species and late-successional climax species. Pioneers are species that require gaps in the forest canopy, allowing direct sunlight to reach the ground for at least part of the day, for germination of seeds, establishment of seedlings and growth. They have a rapid growth and are often short-lived. Climax species, on the other hand, are defined by their ability to germinate in the shade of the forest, although exceptionally they may also germinate in full sunlight. By consequence, young plants are typically found under the forest canopy. However, climax species form a very heterogeneous group with different lifespans, light requirements, maximum heights, etc (Brzeziecki & Kienast, 1994). But in general, we can say that pioneers are located at the quick-return end of the LES and climax species at the slow-return end. The boundaries between these groups are not always sharp and there is a continuous range of species in between (Swaine & Whitmore, 1988).

Generally, species earlier in the succession exhibit higher values of SLA, N content, P content, V_{cmax} , J_{max} , and A_{max} , along with a lower N:P ratio and shorter-lived leaves (Raaimakers et al., 1995; Reich et al., 1994, 1995; Swaine & Whitmore, 1988; Zhang et al., 2018). These traits are useful for resource acquisition and rapid growth (Reich et al., 1994). But according to the LES, this comes at a price: the leaves of pioneers are more vulnerable to herbivory and mechanical damage (Raaimakers et al., 1995; Swaine & Whitmore, 1988). Zhang et al. (2018) only found a significant relationship between A_{max} and P in climax species, indicating that P has a stronger influence on photosynthetic capacity than N in late-successional species. They claim that P

limitation increases at later successional stage, since climax species have higher N:P ratios. Pioneers thus have a higher phosphorus use efficiency (PPUE).

The tree guilds described by Hawthorne (1995) can be roughly translated as follows: pioneers are light-demanding, early successional species; SB species are shade-bearing, late-successional species; and NPLD species are situated in between P and SB species. From quick-to slow-return end of the LES, they can be ranked as: P – NPLD – SB.

Understory

Woody plants of the understory remain their entire life under the forest canopy. We're not talking about saplings in this section. USB species are usually small and reproduce without ever exceeding a few centimetres in diameter (Lafrankie et al., 2006). Not much research has been done about photosynthesis of USB species in the tropics. Santiago & Wright (2007) studied photosynthetic and functional leaf traits in a lowland tropical forest in Panama on three life forms: trees, lianas and USB species. F. Zhu et al. (2014) and Mao et al. (2018) measured photosynthetic traits of some USB species in an old-growth tropical forest in southern China. All three studies concluded USB species have lower photosynthetic capacities than overstory tree species. Santiago & Wright (2007) found they also have lower leaf nutrient concentrations and higher SLAs. It is expected that understory species behave as shade-tolerant species, since they constantly live in the shade of the forest canopy. Despite their low photosynthetic capacities, Hubau et al. (2019) reveal the importance of understory trees in the carbon cycling of African tropical forests. Their analysis confirms that while the understory comprises a minor portion (11%) of the carbon stock, its contribution to the forest carbon sink is disproportionate, accounting for 20%. Despite being much smaller in size, USB species exhibit a higher mean carbon age (74 years) than sub-canopy (54 years) and canopy (57 years) trees (Hubau et al., 2019). Because of their slow and aperiodic growth, understory trees live longer. They're also less vulnerable to drought (Hubau et al., 2019).

Lianas

Verbeeck et al. (2016) propose to include lianas as a different PFT in vegetation models, considering their large impacts on the carbon cycle of tropical forests. Lianas (woody vines) are structural parasites that lack self-support and instead use the framework of trees to climb up to the forest canopy (Schnitzer & Bongers, 2011). Studies in a lowland tropical forest in Panama showed that lianas have lower photosynthetic capacities than trees (Santiago & Wright, 2007; Slot & Winter, 2017). In a seasonal tropical forest in Southwest China different observations were made: Han et al. (2010) found similar gas exchange rates between lianas and trees, while Y. Chen et al. (2015) found higher rates for lianas. Santiago & Wright (2007) found similar N_{area} and P_{area} values between lianas and trees. Several studies agree lianas have higher SLA values than trees (Han et al., 2010; Santiago & Wright, 2007; Tang et al., 2012), because of their faster growth and different resource allocation strategies (Tang et al., 2012). These contrasting results indicate that lianas do not form a homogeneous functional group. In the neotropical rainforests, liana abundance and biomass are increasing (Phillips et al., 2002; Schnitzer & Bongers, 2011), while this trend has not been witnessed in African tropical forests (Schnitzer & Bongers, 2011). Increasing liana abundance can have a huge negative impact on

tree growth and survival, since they compete with trees for light and nutrients (Phillips et al., 2002; Verbeeck et al., 2016). A possible explanation of this increase is that lianas are well adapted to droughts, which occur more due to climate change (Y. Chen et al., 2015). The different trend between the continents can be explained by differing external factors (climate or land-use changes) or by phylogenetic differences in liana communities between the continents (Schnitzer & Bongers, 2011). Indeed, Caballé (1993) found that neotropical liana species often have a different architecture than African liana species, making liana growth more favourable in the Amazon.

2.4.2.2. Leaf phenology

Deciduous tree species drop their leaves during a certain period of the year (e.g. the dry season), while evergreen species retain them for the entire year (Pringle et al., 2011). In the tropics, deciduousness is regarded as a drought-avoidance strategy: the tree minimizes water loss through evapotranspiration during the dry season (Pringle et al., 2011; Sobrado, 1991). Furthermore, deciduous species are more vulnerable to herbivory (Pringle et al., 2011; Silva et al., 2015). Deciduousness also reflects a trade-off between leaf construction costs and lifespans (Sobrado, 1991). Leaf construction and maintenance costs are higher in evergreen species, but their leaves are photosynthetically active for longer periods. All of this translates into certain leaf traits: evergreen species have a lower SLA and N content, higher toughness and often lower photosynthetic capacities (Pringle et al., 2011; Silva et al., 2015; Sobrado, 1991). Evergreens are thus more situated at the slow-return end of the LES and deciduous species at the quick-return end. Ouédraogo et al. (2016) examined the environmental determinants of forests deciduousness in the northern part of the Congo Basin and found the severity of the dry season and the geological substrate as main determinants. Deciduous species performed particularly well at drier, resource-rich soils. Fauset et al. (2012) analysed changes in plant functional composition in a variety of forest types in Ghana, which endured two decades of long-term drought, and they found a consistent increase of drought-tolerant deciduous species. This shows that rainforests may adapt to climate change through changes in species composition.

2.5. Photosynthetic variation within the crown

Photosynthetic traits do not only differ between tree species, but also within the crown of an individual tree. The amount of light decreases exponentially when it passes through the tree canopy (Lambers & Oliveira, 2019). The difference in light availability between the top and bottom can reach a factor of 30 – 100 in dense canopies (Niinemets, 2023). Next to higher light availability, air temperature increases and air humidity decreases as one ascends in the tree crown (Legner et al., 2014; Niinemets, 2023). These gradients in environmental conditions make it impossible for a single combination of leaf traits to optimize photosynthesis across all leaves of the crown (Niinemets, 2023). That's why leaves show light acclimation within the tree crown. Leaves at the top of the canopy are often sun adapted leaves and those at the bottom shade adapted leaves. They exhibit contrasting structural, biochemical and photosynthetic traits (Lambers & Oliveira, 2019).

Typically, sun leaves perform a higher photosynthetic rate at light saturation, compared to shade leaves. However, at low light intensity, shade leaves have a higher photosynthetic rate, because they are more efficient at capturing light (Lambers & Oliveira, 2019). $A_{\max}$, $V_{\max}$ and $J_{\max}$ are all higher for sun leaves, as shown by multiple studies (Carswell et al., 2000; X. Chen et al., 2020; Lambers & Oliveira, 2019; Legner et al., 2014; Niinemets, 2023).

The difference in photosynthetic parameters between sun and shade leaves results from their typical traits. Sun leaves are thicker, smaller and have a smaller SLA (Carswell et al., 2000; X. Chen et al., 2020; Lambers & Oliveira, 2019; Legner et al., 2014; Lichtenthaler et al., 1981; Lloyd et al., 2010; Niinemets, 2023). The increased thickness mainly comes from the elongation of the palisade cells within the mesophyll layer or from the development of multiple palisade layers (Lambers & Oliveira, 2019; Niinemets, 2023). These thicker leaves provide space for more chloroplasts per unit leaf area, increasing photosynthetic capacity (Lambers & Oliveira, 2019). But shade leaves have a more effective light absorption, which is linked to a higher chlorophyll concentration and longer pathlength of light (Lambers & Oliveira, 2019). This longer pathlength is due to the high amount of spongy mesophyll in shade leaves, causing greater internal light scattering. Furthermore, their higher area and SLA increases the light absorption surface. Another important explaining factor is the nutrient concentration, as N_{area} and P_{area} are typically higher for sun leaves (Carswell et al., 2000; Legner et al., 2014; Lloyd et al., 2010; Niinemets, 2023).

It is thus important to measure photosynthesis at different heights within the tree crown, because otherwise you won't get representative values for a species. That's why both top and bottom measurements are included in this thesis.

3. MATERIALS AND METHODS

3.1. Overview of data

This master's thesis wants to make an explorative comparison of leaf-level photosynthesis between the two biggest tropical forests. Field data for the Amazon Basin was already available, thanks to the works of Verryckt et al. (2022) and Pausenberger (2016). In the Congo Basin however, leaf-level photosynthesis was only measured for the first time during August – September 2022 in Yangambi. Extra data was collected there in the field for this thesis.

3.1.1. Amazon Basin

Verryckt et al. (2022) published a free accessible dataset of *ex-situ* measurements of photosynthesis in the tropical lowland forest sites of Paracou and Nouragues in French Guiana. They did a nutrient addition experiment, but for this study, we are only interested in the pre-treatment data. The measurements without nutrient addition were performed in both the wet (May – June) and dry season (October – November) of 2015 at both sites, in June 2016 at Paracou, in the dry season of 2017 at Nouragues, and in the wet season of 2019 at both sites. They measured leaf gas exchange of both shaded leaves at the lower canopy and sunlit leaves at the upper canopy. The dataset contains the following relevant parameters for this master's thesis: maximum carboxylation capacity (V_{cmax}), maximum rate of electron transport (J_{max}), leaf nitrogen content, leaf phosphorous content, specific leaf area (SLA), the height of the leaves on which photosynthesis was measured, and the stomatal conductance of the CO_2 response curves. In total, they gathered 571 CO_2 response curves on non-fertilised adult trees.

Verryckt et al. (2022) only measured photosynthesis on tree species and not on lianas. Therefore, data from the master's thesis of Nancy Pausenberger (2016) were also included in this thesis. The study includes *in-situ* leaf gas exchange measurements of 9 liana individuals from Paracou (French Guiana), taken from mid-September to the beginning of October 2015 (start of the long dry season). All measurements were carried out within the crown of the host tree, close to the trunk. V_{cmax} , J_{max} , leaf N content, leaf P content, SLA and the height of the leaves on which photosynthesis was measured were extracted for this study. Stomatal conductance data is not available.

3.1.2. Congo Basin

To get data for the Congo Basin, leaf gas exchange measurements were performed in the tropical rainforest near Yangambi (Democratic Republic of the Congo) in August 2023. These data were combined with data from a previous field campaign in Yangambi during August – September 2022. This dataset contains the first leaf-level photosynthetic measurements of the central Congo Basin so far.

All measurements in this study were conducted *ex-situ* on excised branches. Due to the height of the trees, *in-situ* measurements would be too dangerous and time-consuming. Besides,

according to Verryckt et al. (2020), branch excision does not have a significant effect on the measurement of leaf photosynthesis, provided that the branch is recut under water and given sufficient time to acclimate to its new environmental conditions. However, not all species are suited for measuring ex-situ. In some species, branch excision can significantly reduce photosynthetic rates (and by consequence V_{cmax} and J_{max}) due to stomatal closure (Santiago & Mulkey, 2003). That's why pre-screening of species is important.

3.2. Site descriptions



Figure 3.1: A) Map with indication of the research sites: red = Paracou, green = Nouragues, and yellow = Yangambi. B) French Guiana with indication of the research sites (same colour code).

3.2.1. Paracou (Amazon Basin)

A part of the data of Verryckt et al. (2022) and the data of Pausenberger (2016) were measured at the Paracou Research Station (5°16' N, 52°54' W). This old-growth, lowland tropical rainforest is located in northern French Guiana, South America (Figure 3.1).

French Guiana has a tropical wet climate, featuring a distinct wet and dry season (Figure 3.2) due to the north–south movement of the Intertropical Convergence Zone (ITCZ) (Bonal et al., 2008). The wet season runs from December to July, peaking in May with monthly rainfall typically exceeding 600 mm. The dry season, characterized by less than 100 mm of precipitation each month, lasts from August to November, with an additional brief, dry period in March. In Paracou, the average annual rainfall (2004–2015) counts 3100 mm and the average annual temperature (2004–2015) is $\pm 26^{\circ}\text{C}$ (Aguilos et al., 2018).

The soils at Paracou are mostly nutrient-poor acrisols, with parts of sandy ultisols (FAO-ISRIC-ISSS, 1998) (Bonal et al., 2008). They're old and highly weathered.

The site features an instrumentation tower, where since 2003 meteorological measurements and net ecosystem CO₂ exchange (NEE) have been continuously monitored using the eddy covariance technique (Bonal et al., 2008).

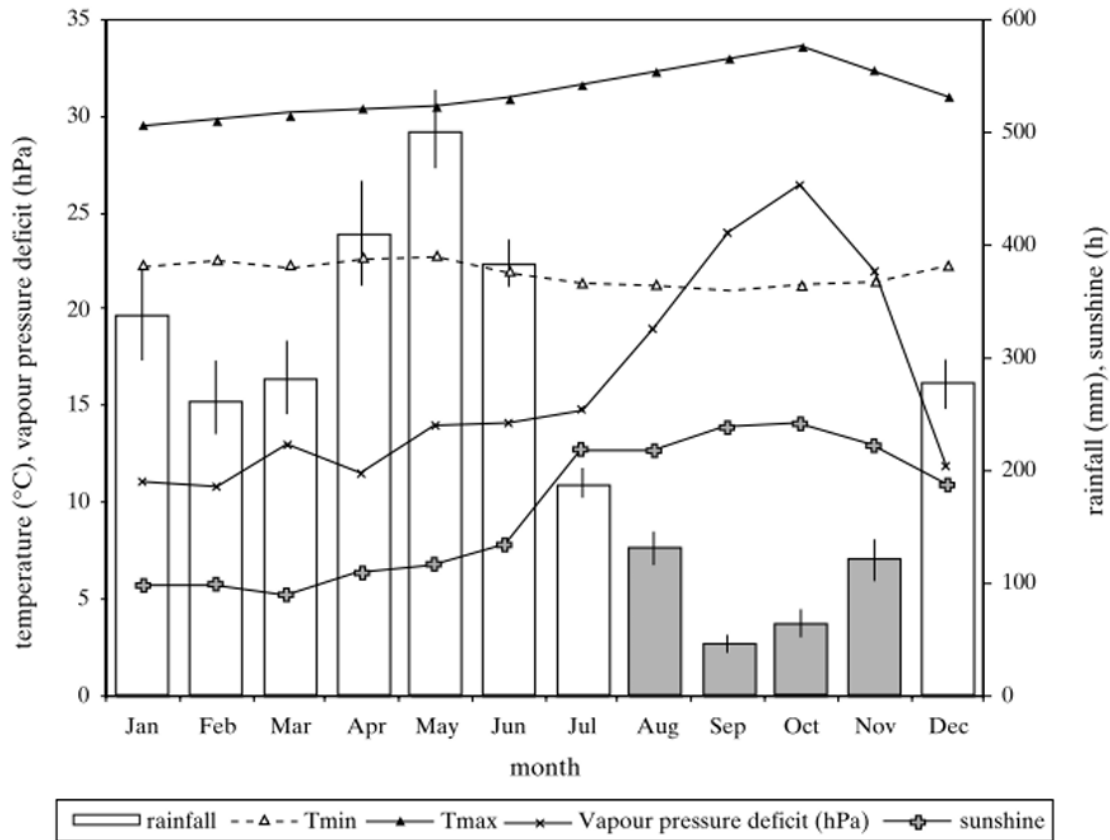


Figure 3.2: Climate diagram of Paracou (French Guiana). Bars represent the means of monthly precipitation levels recorded from 1979 to 2001, with the dry season indicated in grey. Average monthly hours of sunshine and temperatures were only recorded for 1989–1991 and 1995–2001, vapor pressure deficits for 1997–1998. Taken from Gourlet-Fleury et al. (2004).

3.2.2. Nouragues (Amazon Basin)

The Nouragues Research Station (4°02' N, 52°41' W) is located closer to the centre of French Guiana (Figure 3.1). The forest receives approximately 3000 mm rain yr⁻¹ and the average annual temperature is near 26°C (Bongers et al., 2001). The old and highly weathered soils are also characterized as nutrient-poor acrisols (FAO-ISRIC-ISSS, 1998). Since 2014, the Nouragues forest holds a flux tower as well.

3.2.3. Yangambi (Congo Basin)

For this thesis, field measurements and sample collection were conducted at the CongoFlux research site at the “Centre de Recherche de Yangambi”, the very heart of the Congo Basin (0°46' N, 24°26' E; Figure 3.1). Yangambi is situated 100 km northwest of Kisangani, the major

city of the province of Tshopo in the Democratic Republic of the Congo (DRC), along the Congo River (Figure 3.3). It's a representative location for studying the lowland tropical rainforests of the Congo Basin (Sibret et al., 2022).

Yangambi experiences a bimodal rainfall regime, featuring two distinct peaks in May and October and two distinct minima in June and January (Likoko et al., 2019). Over the period of 1931 to 2017, the Yangambi region experienced a mean annual rainfall of 1811.7 ± 214.8 mm, 172 ± 22 rainy days, 2040 ± 98 hours of sunshine per year, a relative air humidity of $87.2 \pm 7.0\%$, and a potential evapotranspiration of 1132.2 ± 54.4 mm (Likoko et al., 2019). The mean annual temperature was $24.9 \pm 0.3^\circ\text{C}$, the mean annual maximum and minimum temperature $29.8 \pm 0.4^\circ\text{C}$ and $19.8 \pm 0.3^\circ\text{C}$, respectively (Likoko et al., 2019). The climate of Yangambi is summarized in Figure 3.4.

The soils at the CongoFlux research site are highly weathered and mostly haplic ferralsols (FAO) (Sibret et al., 2022).

The CRY was founded in the 1930s and has since played an important role in scientific research on tropical forestry and agriculture in the DRC (Sibret et al., 2022). Long-term records of meteorological data and one of the richest herbariums in Africa remain valuable today. In 2019, the very first eddy-covariance flux tower in the Congo Basin rainforest was installed (Figure 3.3) (Sibret et al., 2022). The tower measures gas exchange fluxes, including CO_2 and H_2O , to quantify the NEE, greenhouse gas (GHG) balance, the impact of pollution on NEE, and water use efficiency (WUE) (Sibret et al., 2022). While the flux tower measures photosynthesis on an ecosystem level, this study wants to examine it on leaf level.

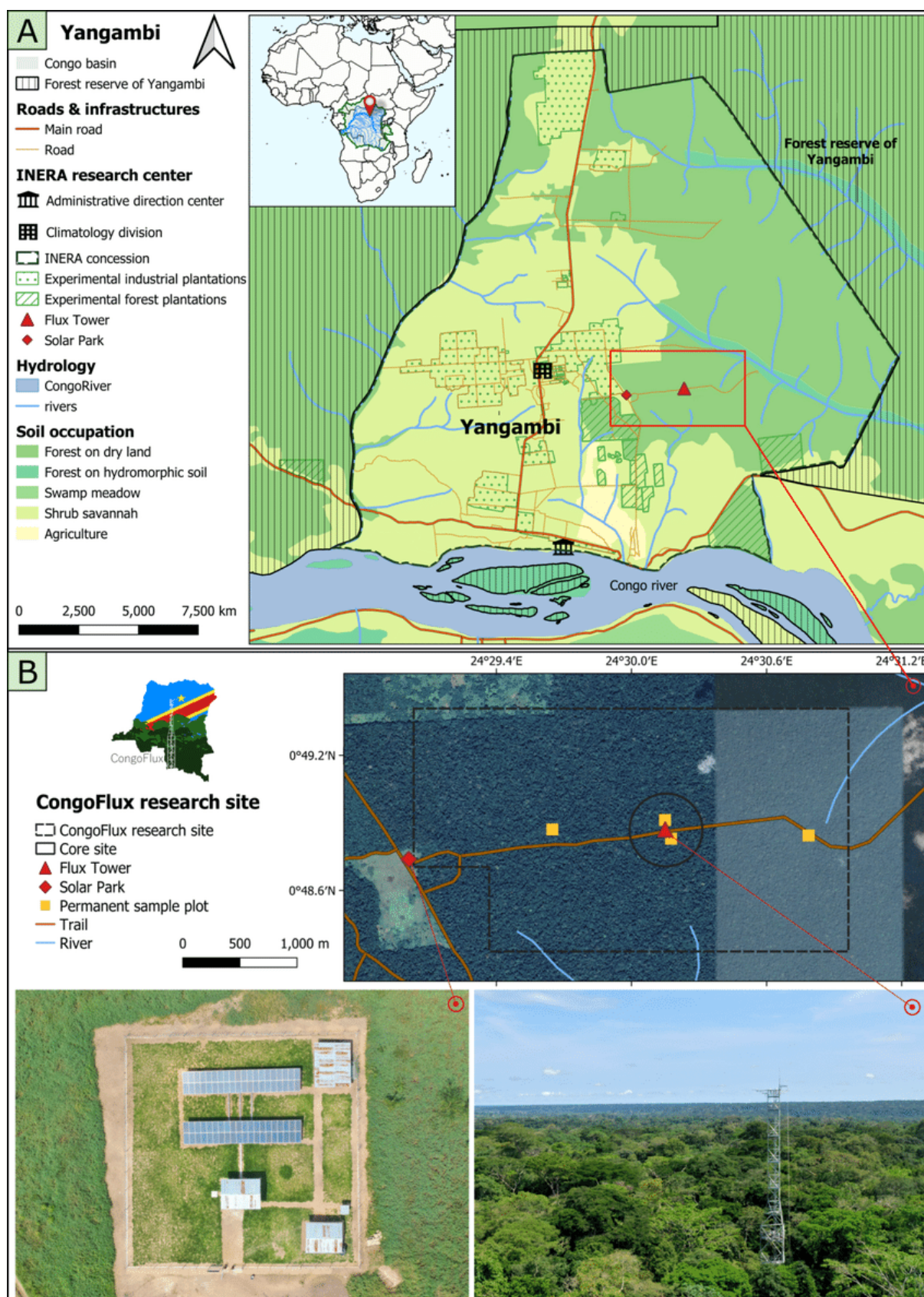


Figure 3.3: Map of the research centre of Yangambi in the Democratic Republic of the Congo (Panel A) and detailed map of the CongoFlux research site (Panel B) with illustration of the 55m-tall eddy covariance flux tower (bottom right). From Sibret et al. (2022).

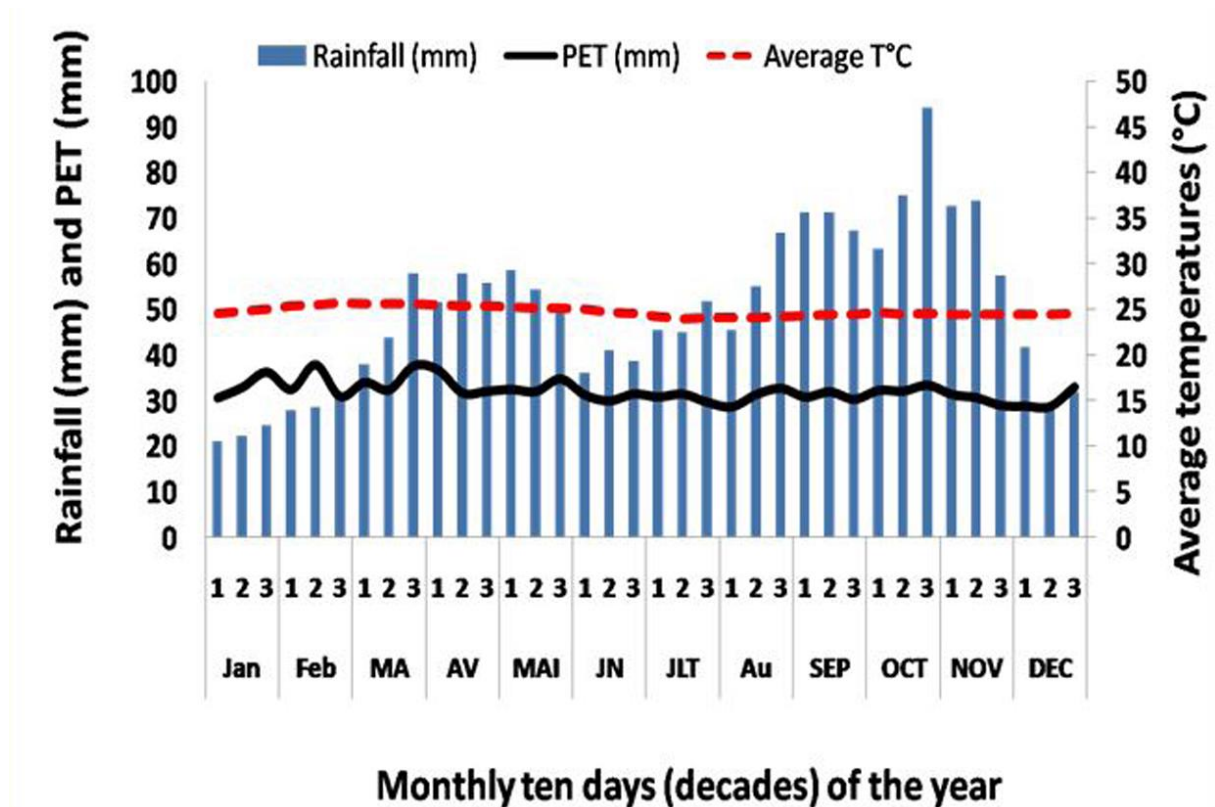


Figure 3.4: Climate diagram for the Yangambi region with monthly decadal means of rainfall (mm), potential evapotranspiration (mm) and average temperature (°C) from 1931 to 2017. Taken from Likoko et al. (2019).

3.3. Species selection

3.3.1. Amazonian sites

Verryckt et al. (2022) selected five mature trees in each 20 × 20 m plot at Paracou and Nouragues: three top-canopy trees likely dominating the plot's functioning, and two sub-canopy trees. The dataset used for this study contains 30 species (Table 3.1). The plant functional types were not mentioned. The plant guild as defined by Hawthorne (1995) and the leaf phenology of the measured species were derived from the appendix of the paper of Bonal et al. (2000). Pausenberger (2016) selected liana species based on how accessible the crown of the tree they grew on was, and on the condition of the liana itself. Not all 9 measured liana individuals were identified (Table 3.1).

The entire Amazon dataset contains 1 pioneer (P) species with 7 measurements, 5 non-pioneer light demanding (NPLD) species with 43 measurements, 14 shade bearing (SB) species with 119 measurements and 9 liana (L) measurements, of which 4 liana species were identified (Table 3.1). For the other 86 tree measurements, the PFT of the species could not be identified (Table 3.1).

Table 3.1: The species of the compiled data of Verryckt et al. (2022) and Pausenberger (2016) from Paracou and Nouragues, with indication of their PFT – based on light requirement and regeneration – (P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, L = liana), leaf phenology (E = evergreen, D = deciduous) and number of CO₂ response curves measured. NA = not available

Species	PFT	Leaf phenology	# curves
<i>Anacardium spruceanum</i>	NA	NA	2
<i>Brosimum rubescens</i>	SB	E	12
<i>Capirona decorticans</i>	NA	NA	7
<i>Chaetocarpus schomburgkianus</i>	SB	E	4
<i>Chrysophyllum sanguinolentum</i>	SB	E	3
<i>Couepia caryophylloides</i>	SB	E	3
<i>Dicorynia guianensis</i>	NPLD	D	7
<i>Drypetes variabilis</i>	SB	E	8
<i>Eperua falcata</i>	NPLD	D	14
<i>Eperua grandiflora</i>	NPLD	E	3
<i>Eschweilera coriacea</i>	SB	E	13
<i>Helicostylis pedunculata</i>	SB	E	3
<i>Lecythis persistens</i>	SB	E	2
<i>Lecythis zabucajo</i>	SB	D	8
<i>Licania alba</i>	SB	E	27
<i>Licania densiflora</i>	NA	NA	5
<i>Lueheopsis rugosa</i>	NPLD	D	10
<i>Micropholis</i>	SB	E	6
<i>Micropholis obscura</i>	SB	E	6
<i>Paloue guianensis</i>	NA	NA	11
<i>Pouteria eugeniifolia</i>	SB	E	17
<i>Pradosia cochlearia</i>	SB	D	7
<i>Pradosia ptychandra</i>	NA	NA	13
<i>Protium opacum</i>	NA	E	11
<i>Sextonia rubra</i>	NA	NA	4
<i>Sterculia multiovula</i>	P	NA	7
<i>Symphonia globulifera</i>	NPLD	E	9
<i>Talisia praealta</i>	NA	NA	2
<i>Tapura capitulifera</i>	NA	NA	24
<i>Tetragastris altissima</i>	NA	NA	7
<i>Lonchocarpus</i>	L	NA	1

<i>Stigmaphyllon sinuatum</i>	L	NA	1
<i>Strychnos bredemeyeri</i>	L	NA	1
<i>Coccoloba ascendens</i>	L	NA	1
Unidentified	L	NA	5

3.3.2. Yangambi

In Yangambi, species were chosen based on three selection criteria:

- First of all, the species had to be suitable for conducting ex-situ gas exchange measurements on excised branches. Some tested species immediately showed a decline in photosynthesis after excision, due to stomatal closure.
- The relative abundance of the species is of great importance as well, in order to create a representative view over the research area.
- At last, species were selected, so different PFTs were represented. Measurements were performed on different plant guilds described by Hawthorne (1995), divided based on light requirement and regeneration: pioneer (P), non-pioneer light-demanding (NPLD) and shade-bearing (SB) species. A species was assigned to one of these guilds, based on the data of Bénédet et al. (2019) and on the knowledge of the local botanist. Understorey shade-bearing (USB) species and lianas were examined too. Leaf phenology was also regarded: both evergreen and deciduous species were sampled.

A total of 103 CO₂ response curves were measured at Yangambi. Combined with the measurements of the previous field campaign, this creates a dataset with a total of 176 CO₂ response curves on 23 species. The dataset contains 4 pioneer species with 34 measurements, 3 NPLD species with 29 measurements, 9 SB species with 72 measurements, 4 USB species with 20 measurements and 3 liana species with 21 measurements (Table 3.2).

Table 3.2: The investigated species in Yangambi, with indication of their PFT – based on light requirement and regeneration (P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, USB = understory shade-bearing, L = liana), and leaf phenology (E = evergreen, D = deciduous, NA = not available). The species indicated with * were measured during the previous field campaign and the species indicated with ° were measured during both field campaigns.

Species	PFT	Leaf phenology
<i>Tridesmotermon omphalocarpoides</i> *	SB	E
<i>Strombasiopsis tetrandra</i> *	SB	E
<i>Pericopsis elata</i> °	NPLD	D
<i>Synsepalum subcordatum</i> *	SB	E
<i>Grossera multinervis</i> *	USB	E
<i>Staudtia kamerunensis</i> *	NPLD	E
<i>Triclisia gillettii</i> *	L	E

<i>Drypetes gossweileri</i> *	SB	E
<i>Panda oleosa</i>	SB	E
<i>Musanga cecropioides</i> *	P	E
<i>Macaranga spinosa</i>	P	E
<i>Petersianthus macrocarpus</i>	NPLD	D
<i>Tetrorchidium didymostemon</i>	P	E
<i>Macaranga barteri</i>	P	E
<i>Anonidium mannii</i>	SB	E
<i>Scorodophloeus zenkeri</i>	SB	E
<i>Millettia duchesnei</i>	L	NA
<i>Leplaea thompsonii</i>	SB	E
<i>Cola griseiflora</i>	SB	NA
<i>Scaphopetalum toneri</i>	USB	NA
<i>Landolphia klainei</i>	L	NA
<i>Cola bruneeli</i>	USB	NA
<i>Aidia micrata</i>	USB	NA

A local botanist from the “Institut national pour l’étude et la recherche agronomique” (INERA, Yangambi), called papa Bonyoma, helped identifying the targeted species in the forest. For each of the selected species, two mature individuals were randomly selected, leading to more representative and reliable results. The individuals were sampled within a range of 300 meters around the flux tower.

After a tree or liana was selected, branches needed to be collected for ex-situ measurement of photosynthesis. Two qualified local climbers, Papi and Bernard, climbed in the tree with the required safety equipment (Figure 3.5). For each individual, four branches were collected: two at the top of the crown, with fully sunlit leaves, and two at the bottom, with shaded leaves. This way, the difference in photosynthesis between sun leaves (“mouy” in Lingala, i.e. the local language) and shade leaves (“malili” in Lingala) could be examined. Furthermore, this excludes the effect of within-crown variation in photosynthesis for the other analyses (e.g. when comparing PFTs). However, this difference in sun and shade leaves is not always that apparent for all species, which will be discussed later. For understory species, only one branch was cut per individual, since there is no distinguishment between sun and shade leaves due to their limited height. Before cutting off a branch, its height was recorded (Appendix) with measuring tape (precision 0.1 cm). For understory species, the height of the entire individual was recorded (Appendix). After the climbers descended the tree, the branches were immediately put in a bucket of water and cut several times at the bottom (Figure 3.6). This is necessary to avoid cavitation (i.e. the entering of air bubbles in the xylem tubes and vessels, preventing water uptake) and ensure water supply to the leaves (Verryck et al., 2020).



Figure 3.5: The climbing procedure at the CongoFlux Research Site, performed by two local climbers and my tutor, Thomas Sibret.

3.4. Photosynthetic parameters

To get the photosynthetic parameters (V_{cmax} and J_{max}) of the investigated species in Yangambi, ex-situ leaf-level gas exchange measurements were performed, on which CO_2 response curves were fitted. On each branch, gas exchange measurements were taken on two different leaves. Looking at their colour and size, the leaves were selected based on their maturity, with neither young nor old leaves chosen. So, per species 8 CO_2 response curves were measured (4 for understory species), including 4 on leaves at the top of the crown and 4 on leaves at the bottom. This leads to a total of 176 CO_2 response curves measured. Due to circumstances (as mentioned in previous sections), not all species have exactly 8 measurements.

Each day, measurements started at $\pm 08:00$ h in the morning, when there was enough solar radiation in order for photosynthesis to start. On sunny days measurements could start earlier than on cloudy days. We stopped measuring when the midday depression in stomatal conductance was observed. The time at which this occurred depended on the weather conditions. At warmer, sunny days, the stomata closed faster and measurements ended around 13:00. At colder, cloudy days, measuring could sometimes continue up to 16:00. High rainfall could also affect the measurement timing.

Measurements were conducted using a portable photosynthetic system, the LI-6400XT (LI-COR, Lincoln, NE, United States) connected to a leaf chamber (REF) (Figure 3.6).



Figure 3.6: Ex-situ measurement on an excised branch, placed in a bucket of water, with the LI-6400XT.

3.4.1. Conditions in leaf chamber

In Yangambi, the conditions in the leaf chamber were chosen in order to emulate the natural conditions of the tropical rainforest as well as possible. The block temperature was set at 29°C. This is slightly higher than the average ambient temperature in Yangambi, to prevent condensation issues in the leaf chamber. The relative humidity was chosen as high as possible to emulate natural conditions, but below 85% to avoid condensation issues. In practice, it varied between 65 and 85%. The incoming light intensity (photosynthetic photon flux density) was held constant during measurements and at a level of light saturation. Based on literature, a light intensity of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for top leaves and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for bottom leaves was chosen. The ambient CO₂ concentration was considered 420 ppm.

Verryckt et al. (2022) also measured CO₂ response curves with the LI-6400XT. They used the following conditions in the leaf chamber: a block temperature of $30.1 \pm 0.9^\circ\text{C}$, a relative humidity of $67.9 \pm 0.06\%$, an ambient CO₂ concentration of 400 ppm and a light intensity of 1300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for top leaves and 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for bottom leaves. They found that 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is below light saturation and that 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ would have been optimal for bottom leaves. However, increasing the light intensity would only result in a slight increase in net photosynthesis.

Pausenberger (2016) did in-situ measurements with the portable photosynthetic system CIRAS-3 (PP-system, Amesbury, MA, USA). She used the following settings in the leaf chamber: a leaf temperature of $29.6 \pm 0.7^\circ\text{C}$, a relative humidity of $70 \pm 6\%$, an ambient CO₂ concentration of 400 ppm and a light intensity of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all liana leaves.

3.4.2. Measuring CO₂ response curves

CO₂ response curves were generated by measuring net photosynthetic rates (A) at various reference CO₂ concentrations, with a constant light intensity at light saturation. In Yangambi, the CO₂ concentration was altered between 50 and 2000 ppm, by taking a total of 12 measurements using the following sequence of CO₂ concentrations: 420, 300, 200, 100, 50, 420, 420, 800, 1200, 1500, 1800 and 2000 ppm.

Verryckt et al. (2022) used the following programme for measuring the CO₂ response curves: the CO₂ concentration was reduced stepwise to 50 ppm, then returned to 400 ppm, and thereafter increased to 2000 ppm to obtain a total of ± 19 measurements per leaf. Pausenberger (2016) used the following sequence of CO₂ concentrations to obtain a total of 14 measurements per leaf: 400, 300, 200, 100, 50, 400, 500, 600, 700, 900, 1300, 1500, 1800 and 2000 ppm.

3.4.3. Fitting CO₂ response curves

The CO₂ response curves were fitted using the *fitaci* function from the R package (version 1.4-6) “Plantecophys” (Duursma, 2015). This toolkit applies the Farquhar-von Caemmerer-Berry model, to estimate various photosynthetic parameters derived from the CO₂ response curve, including V_{cmax} and J_{max} .

3.5. Leaf trait analysis

From each measured branch in Yangambi, 10 leaves were collected: the leaf on which the CO₂ response curve was measured, and 9 other leaves in the close environment of that leaf. For species with very big leaves (e.g. *Anonidium mannii*), only 5 leaves were collected. The 10 (or 5) leaves were stored in an envelope. The leaf sampling is necessary for measuring leaf functional traits. The traits were all analysed averaged over the collected groups of leaves.

3.5.1. Specific leaf area

After the leaves were collected, their fresh weight was determined. The fresh leaves were scanned (Figure 3.7 A) and their area was calculated based on the scans using the ImageJ software (Schneider et al., 2012). After scanning, they were dried in an oven for 72h on 65°C. Afterwards, their dry weight was determined (Figure 3.7 B). The SLA was calculated with the following formula:

$$\text{SLA} = \frac{A_{\text{leaf}}}{m_{\text{dry}}} \quad (3.1)$$

where SLA [cm² g⁻¹] is the specific leaf area averaged over the collected group of leaves, A_{leaf} [cm²] is the total area of all the leaves together and m_{dry} [g] is the total dry mass of all the leaves together.

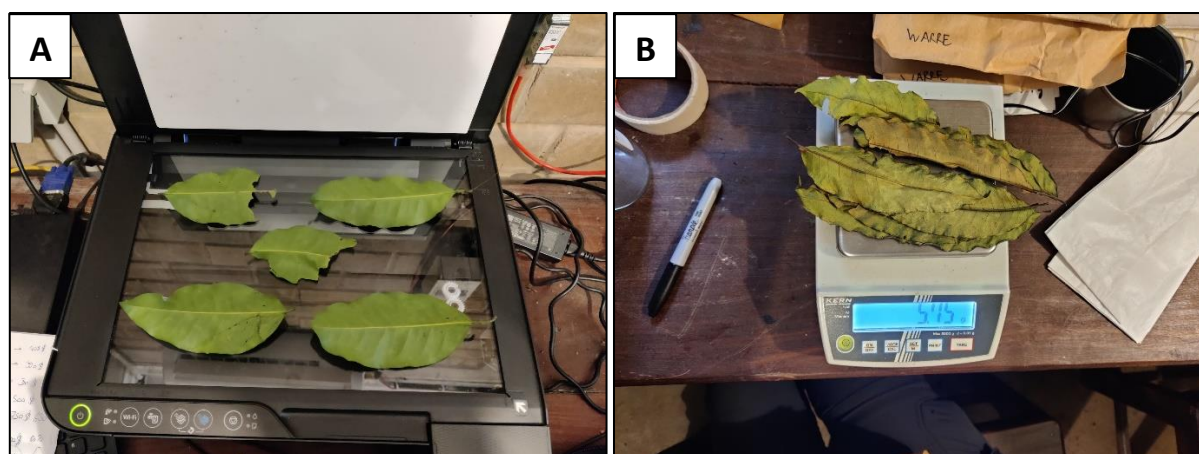


Figure 3.7: In field processing of the collected leaves: scanning (A) and weighing (B).

3.5.2. Leaf nutrient content

The average content of carbon (C), nitrogen (N) and phosphorus (P) were analysed for each group of leaves. The leaves were first ground and homogenized using a Retsch ZM-200 centrifugal mill with a mesh width of 25 μm and a speed of 14,000 rotations per minute (rpm) (Figure 3.8 A). To avoid contamination between different groups of leaves, the mill was carefully cleaned between each grinding session.

The leaf C and N content were analysed at the Isotope Bioscience Laboratory (ISOFYS) at Ghent University, using EA-IRMS (Elemental Analyser - Isotope Ratio Mass Spectrometer). This involves using a PDZ Europa ANCA-SL (Automated Nitrogen Carbon Analyser – Solids and Liquids) elemental analyser interfaced with a Sercon 20-22 IRMS with SysCon electronics (SerCon, Cheshire, UK). Samples were prepared by weighing 2 ± 0.2 mg into tin (Sn) foil capsules (Sercon Ltd, Standard Weight 8 x 5 mm) on a microbalance (Figure 3.8 B). Contamination is avoided by cleaning with ethanol between each weighing and no direct handling of samples. The prepared samples were then analysed with EA-IRMS, using wheat flour (IA-R001-2019) as a reference.

The leaf P content was analysed at the Laboratory for Chemical Analyses (LCA) at Ghent University. Samples were heated at 500°C for four hours. The resulting ashes were dissolved in diluted hydrochloric acid (HCl), and the elemental composition was determined using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES).

The nutrient content calculated in the laboratory was expressed on a mass basis (in %). Since photosynthetic parameters are mostly expressed on an area basis, the mass-based nutrient contents were converted to area-based nutrient contents (in g m^{-2}), using the SLA. This conversion was also done for the data of Verryck et al. (2022).

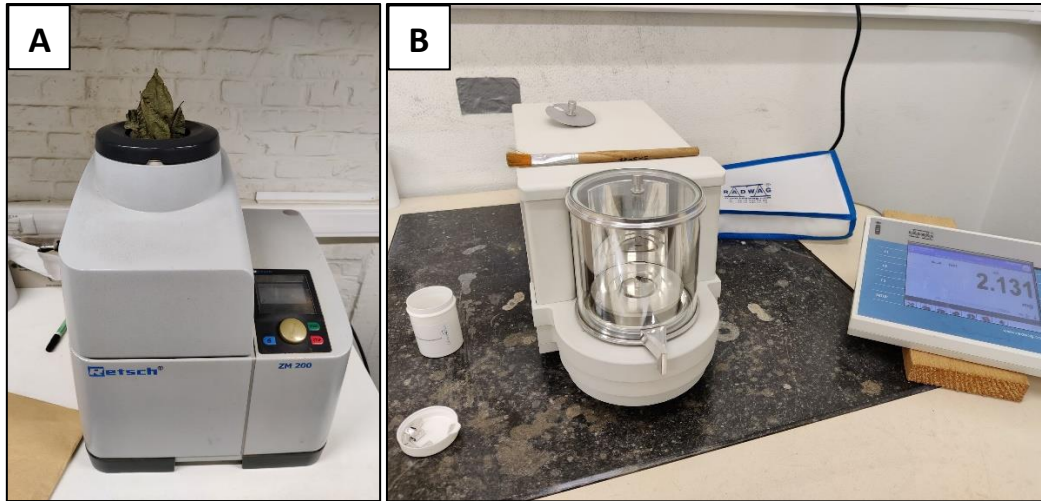


Figure 3.8: The Retsch ZM-200 centrifugal mill (A) and the microbalance (B) at the ISOFYS laboratory.

3.6. Data analysis

3.6.1. Processing Amazonian data

For the Amazonian data of Verryckt et al. (2022), a pre-selection was done based on the stomatal conductance (g_s) of the CO_2 response curves, to exclude stressed measurements potentially leading to underestimation of the calculated V_{cmax} and J_{max} parameters. A threshold value of $0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ for g_s was chosen. All those curves in which the g_s (at ambient CO_2 concentration) was smaller than the threshold were removed from the dataset. Initially the dataset contained 470 CO_2 response curves and after the selection 255 curves. All 30 species of the original data are still present.

Furthermore, in the data of Pausenberger (2016) and Verryckt et al. (2022) V_{cmax} and J_{max} were rescaled to a temperature of 25°C . For the Yangambi data both parameters were calculated at ambient temperature (29°C). In order to be able to compare these parameters between both locations, they were recalculated for the Amazonian data at their respective ambient leaf temperatures (section 3.4.1), using the Farquhar-von Caemmerer-Berry model. Rescaling the Yangambi data to 25°C would not be appropriate, since there are no temperature response curves available yet for the Congo Basin.

3.6.2. Statistical analysis

All statistical analyses were performed with Rstudio (R version 4.1.2 (2021-11-01)).

To analyse the effect of PFT – based on light requirement and regeneration – on measured parameters, being two photosynthetic parameters (V_{cmax} and J_{max}) and three leaf functional traits (N_{area} , P_{area} and SLA), all site data were pooled (Paracou, Nouragues and Yangambi) and the different PFTs were compared using a Kruskal-Wallis test (Hollander et al., 1973). Thereafter, Dunn's test (Dunn, 1964) was used (method of Holm) to check which groups differed significantly from each other. Deciduous and evergreen species were compared using the Wilcoxon signed rank test (Bauer, 1972) or the Student's t-test (Kim, 2015) on

logarithmically transformed data, to ensure normality and to minimize the heterogeneity of the residuals.

Using the Student's t-test on logarithmically transformed data or the Wilcoxon signed rank test, the same five parameters were compared between leaves at the top and the bottom of the crown across all three sites.

To check for potential differences between the continents, firstly a general comparison was made for the two photosynthetic parameters (V_{cmax} and J_{max}), three leaf functional traits (N_{area} , P_{area} and SLA) and the g_s of the CO_2 response curves, between all the examined species of the Amazonian sites and all the examined species of Yangambi. This analysis was performed with the Wilcoxon signed rank test or the Student's t-test on logarithmically transformed data. Thereafter, four important parameters (V_{cmax} , J_{max} , N_{area} and P_{area}) were compared between the tropical forests per PFT – based on light requirement and regeneration – with the Wilcoxon signed rank test and t-test (sometimes on logarithmically transformed data).

To examine the bivariate relationships between the photosynthetic parameter V_{cmax} and three leaf functional traits (N_{area} , P_{area} and SLA), as well as a potential relationship of V_{cmax} with g_s , Standardized Major Axis (SMA) (Warton et al., 2006) regressions were performed for both tropical forests. These relationships were all assumed to be linear, except V_{cmax} and g_s were assumed to have a linear squared roots association (Farquhar & Sharkey, 1982). Robust regressions were used each time to minimise the effect of outliers.

At last, two mixed-effect models (Kuznetsova et al., 2017) were established, one for V_{cmax} and one for J_{max} , with fixed effects of PFT (P, NPLD, SB, USB or L), leaf phenology (deciduous or evergreen), canopy position (top, bottom or middle of the crown) and location (Amazonian sites of Paracou and Nouragues or Yangambi site in the Congo Basin), and with random effect of species. An ANOVA-test (Chambers & Hastie, 1992) was performed on these mixed-effect models, to determine which fixed effects had the biggest influence on photosynthesis.

All statistical tests were performed on the 5% significance level. Significance is indicated by a p-value, with corresponding significance code:

- *** when $p < 0.001$, indicating a strong statistical difference;
- ** when $p < 0.01$, indicating a moderate statistical difference;
- * when $p < 0.05$, indicating a weaker statistical difference;
- “ns” when there is no statistical difference ($p > 0.05$).

3.7. Use of ChatGPT

The language model ChatGPT (developed by OpenAI) was used during this master's thesis to rewrite (limited) parts of text from the original sources and to finetune R scripts (e.g. for the layout of graphs). It was never used to gather information for the literature review, to analyse data, or to interpret results. ChatGPT was never used to generate new content. All content is derived from scientific authors and referred to correctly.

4. RESULTS

4.1. Comparison between PFTs

4.1.1. Light requirement + regeneration

For the three sites together, the average V_{cmax} significantly differed between all PFTs, except between USB species and L (Figure 4.1 A; $p < 0.05^*$ for SB – L; $p < 0.01^{**}$ for P – NPLD, NPLD-SB and SB-USB; $p < 0.001^{***}$ for P – SB, P – USB, P – L, NPLD – USB and NPLD – L; Dunn's test). The average V_{cmax} values were 76.96 ± 4.29 (SE) $\mu\text{mol m}^{-2} \text{s}^{-1}$ for P, 56.19 ± 2.24 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for NPLD, 46.80 ± 1.19 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for SB, 33.34 ± 2.37 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for USB and 37.57 ± 2.34 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for L.

The average J_{max} significantly differed between all PFTs, except between SB species and L and between USB species and L (Figure 4.1 B; $p < 0.05^*$ for NPLD – SB; $p < 0.01^{**}$ for P – NPLD, NPLD – L and SB – USB; $p < 0.001^{***}$ for P – SB, P – USB, P – L and NPLD – USB; Dunn's test). The average J_{max} values were 115.82 ± 6.78 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for P, 83.38 ± 3.30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for NPLD, 72.5 ± 1.87 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for SB, 50.84 ± 3.06 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for USB and 62.48 ± 3.79 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for L.

Average N_{area} was similar across most PFTs, except between USB species and all other PFTs (Figure 4.1 C; $p < 0.05^*$ for P – USB; $p < 0.01^{**}$ for NPLD – USB, SB – USB and L – USB; Dunn's test). The average N_{area} values were 1.89 ± 0.11 g m^{-2} for P, 2.01 ± 0.098 g m^{-2} for NPLD, 1.97 ± 0.057 g m^{-2} for SB, 1.38 ± 0.033 g m^{-2} for USB and 2.03 ± 0.11 g m^{-2} for L.

Significant differences in P_{area} were found between all PFTs, except between NPLD and SB, NPLD and L and SB and L (Figure 4.1 D; $p < 0.05^*$ for NPLD – USB and USB – L, $p < 0.01^{**}$ for P – L and SB – USB; $p < 0.001^{***}$ for P – NPLD, P – SB and P – USB; Dunn's test). The average P_{area} values were 0.12 ± 0.0049 g m^{-2} for P, 0.083 ± 0.0040 g m^{-2} for NPLD, 0.086 ± 0.0028 g m^{-2} for SB, 0.057 ± 0.0027 g m^{-2} for USB and 0.082 ± 0.0048 g m^{-2} for L.

SLA was significantly different between all PFTs, except between P and L, and between NPLD and SB (Figure 4.1 E; $p < 0.05^*$ for USB – L; $p < 0.01^{**}$ for P – NPLD, P – USB and NPLD – L; $p < 0.001^{***}$ for P – SB, NPLD – USB, SB – L and SB – USB; Dunn's test). The average SLA values were 132.55 ± 6.41 $\text{cm}^2 \text{g}^{-1}$ for P, 102.73 ± 3.91 $\text{cm}^2 \text{g}^{-1}$ for NPLD, 97.25 ± 2.14 $\text{cm}^2 \text{g}^{-1}$ for SB, 181.77 ± 7.42 $\text{cm}^2 \text{g}^{-1}$ for USB and 140.98 ± 10.64 $\text{cm}^2 \text{g}^{-1}$ for L.

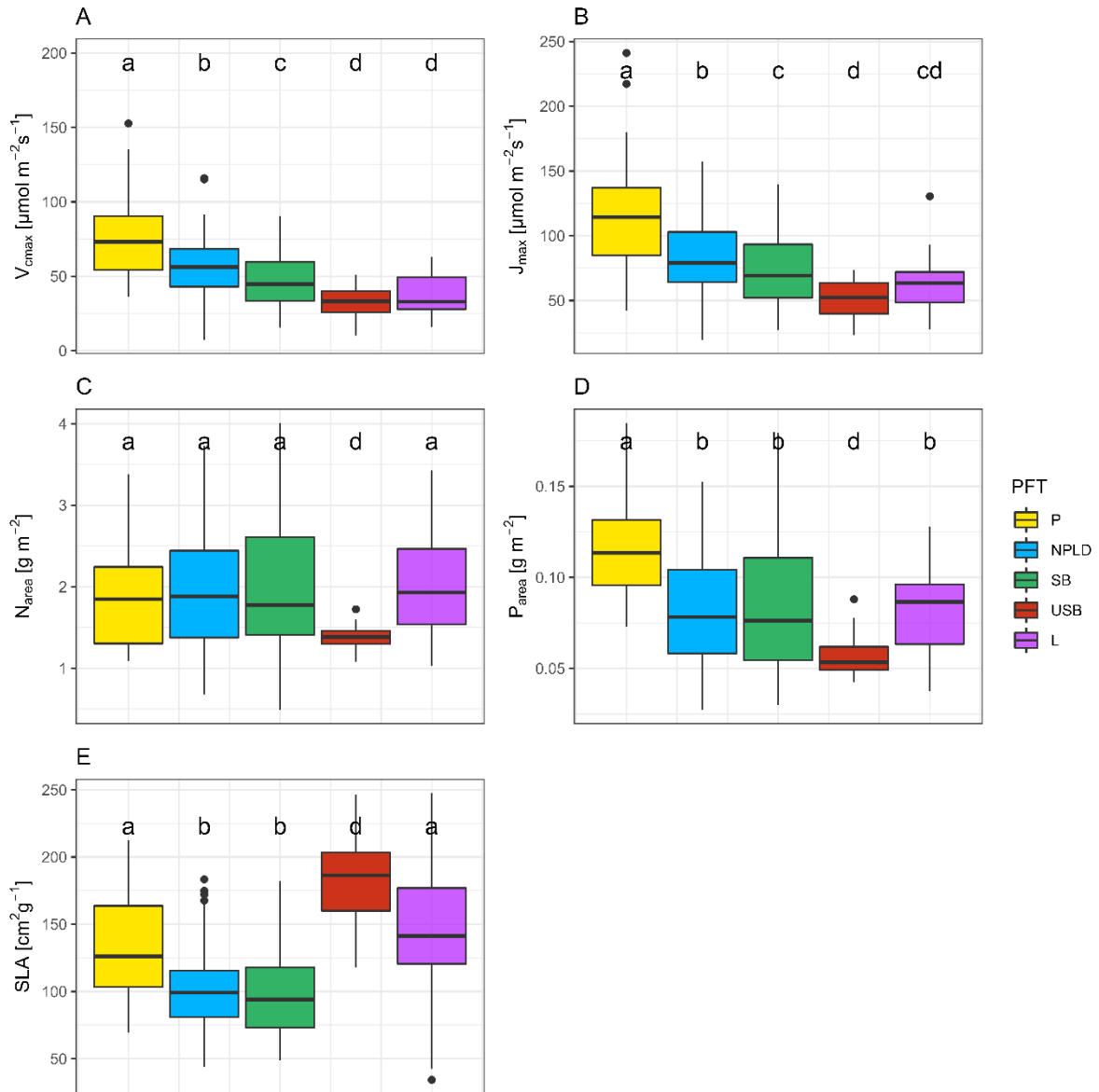


Figure 4.1: Five parameters of 47 species, compared between five PFTs – based on light requirement and regeneration – for the Paracou (Amazon Basin), Nouragues (Amazon Basin) and Yangambi (Congo Basin) sites together. If the same superscript letter occurs, there is no significant difference between the PFTs (Dunn’s test – Holm method). P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, USB = understory shade bearing and L = liana. A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

4.1.2. Leaf phenology

A significant difference was witnessed between deciduous and evergreen species only for the V_{cmax} ($p = 0.016^*$), J_{max} ($p = 0.041^*$) and N_{area} ($p = 0.039^*$) parameters, where the average was higher for deciduous species (Figure 4.2; Wilcoxon signed rank test). Deciduous species had an average V_{cmax} of $56.05 \pm 2.39 \mu\text{mol m}^{-2} \text{s}^{-1}$ and evergreen species an average of $51.04 \pm 1.39 \mu\text{mol m}^{-2} \text{s}^{-1}$. J_{max} was on average $84.10 \pm 3.58 \mu\text{mol m}^{-2} \text{s}^{-1}$ for deciduous species and $77.98 \pm 2.10 \mu\text{mol m}^{-2} \text{s}^{-1}$ for evergreen species. The average N_{area} counted $2.10 \pm 0.10 \text{ g m}^{-2}$ for deciduous species and $1.89 \pm 0.048 \text{ g m}^{-2}$ for evergreen species. Deciduous species had an

average P_{area} of $0.084 \pm 0.0040 \text{ g m}^{-2}$ and evergreen species an average of $0.086 \pm 0.0025 \text{ g m}^{-2}$. The average SLA counted $104.32 \pm 3.75 \text{ cm}^2 \text{ g}^{-1}$ for deciduous species and $106.67 \pm 2.48 \text{ cm}^2 \text{ g}^{-1}$ for evergreen species.

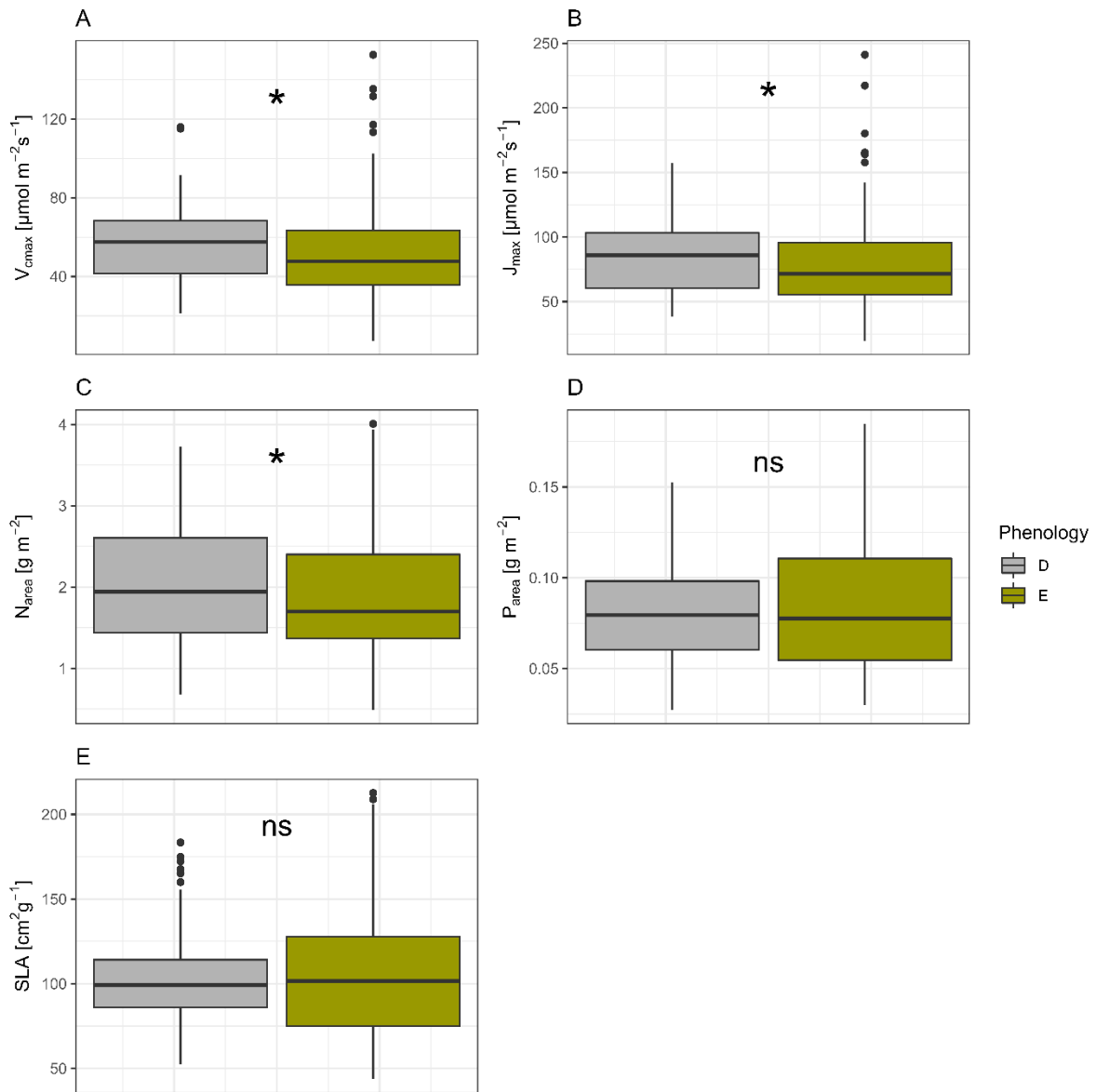


Figure 4.2: Five parameters compared between 7 deciduous (D) and 30 evergreen (E) species for the Paracou (Amazon Basin), Nouragues (Amazon Basin) and Yangambi (Congo Basin) sites together, with indication of the significant difference level (Wilcoxon signed rank test and Student's t-test on logarithmically transformed data). A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

4.2. Within-crown variation

All considered parameters significantly differed between leaves at the top of the crown and leaves at the bottom of the crown (Figure 4.3). V_{cmax} ($p = 4.81\text{e-}13^{***}$), J_{max} ($p = 6.88\text{e-}19^{***}$), N_{area} ($p = 2.95\text{e-}05^{***}$) and P_{area} ($p = 0.0031^{**}$) were significantly higher for leaves at the top, while SLA ($p = 2.25\text{e-}11^{***}$) was significantly higher for leaves at the bottom (Wilcoxon signed

rank test and Student's t-test on logarithmically transformed data). The average V_{cmax} was $55.77 \pm 1.54 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the top and $41.41 \pm 1.11 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the bottom. J_{max} was on average $85.24 \pm 2.29 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the top and $61.85 \pm 1.65 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the bottom. The average N_{area} was $2.02 \pm 0.056 \text{ g m}^{-2}$ at the top and $1.70 \pm 0.046 \text{ g m}^{-2}$ at the bottom. The average P_{area} was $0.087 \pm 0.0028 \text{ g m}^{-2}$ for top leaves and $0.075 \pm 0.0023 \text{ g m}^{-2}$ for bottom leaves. SLA was on average $96.83 \pm 2.32 \text{ cm}^2 \text{g}^{-1}$ at the top and $122.97 \pm 3.11 \text{ cm}^2 \text{g}^{-1}$ at the bottom.

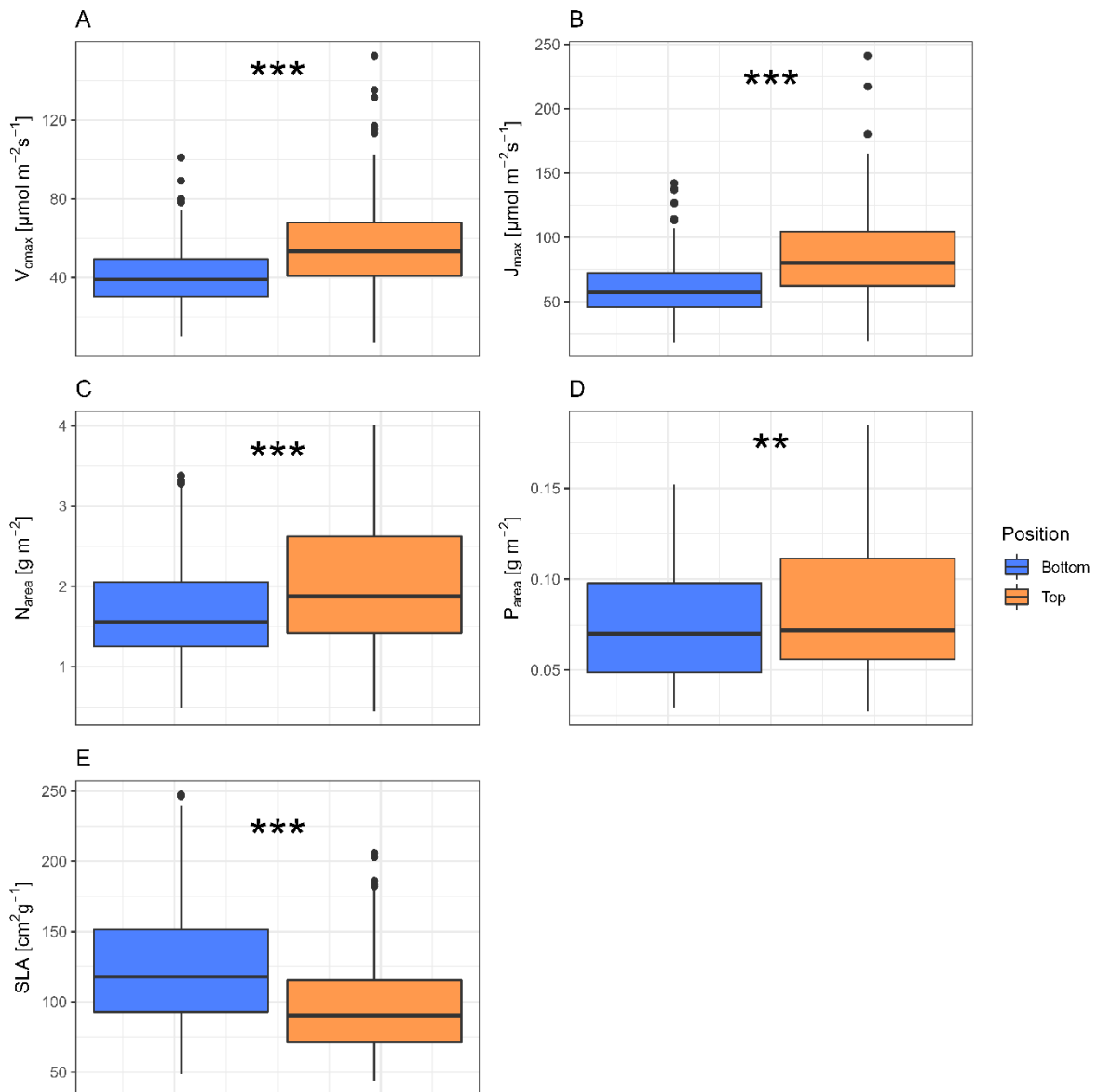


Figure 4.3: Five parameters compared between the top and the bottom of the crown for 57 species of the Paracou (Amazon Basin), Nouragues (Amazon Basin) and Yangambi (Congo Basin) sites together, with indication of the significant difference level (Wilcoxon signed rank test and Student's t-test on logarithmically transformed data). A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

4.3. Comparison between sites in the Amazon and Congo Basin

4.3.1. General comparison

V_{cmax} ($p = 7.79\text{e-}10^{***}$), J_{max} ($p = 6.01\text{e-}16^{***}$), N_{area} ($p < 2.2\text{e-}16^{***}$), P_{area} ($p < 2.2\text{e-}16^{***}$), SLA ($p < 2.2\text{e-}16^{***}$) and g_s ($p = 5.21\text{e-}13^{***}$) were all significantly higher for the examined species of the Yangambi site in the Congo Basin, when compared with the examined species of the Paracou and Nouragues sites in the Amazon Basin (Figure 4.4; Wilcoxon signed rank test and Student's t-test on logarithmically transformed data). The species in the Amazonian sites had an average V_{cmax} of $43.77 \pm 1.66 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the species in Yangambi an average of $55.59 \pm 1.66 \mu\text{mol m}^{-2} \text{s}^{-1}$. J_{max} was on average $63.47 \pm 1.40 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the Amazonian sites and $88.38 \pm 2.64 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Yangambi. The average N_{area} counted $1.55 \pm 0.033 \text{ g m}^{-2}$ in the Amazonian sites and $2.29 \pm 0.058 \text{ g m}^{-2}$ in Yangambi. The species in Paracou and Nouragues had an average P_{area} of $0.062 \pm 0.0013 \text{ g m}^{-2}$ and the species in Yangambi an average of $0.11 \pm 0.0027 \text{ g m}^{-2}$. The average SLA counted $95.66 \pm 1.92 \text{ cm}^2 \text{ g}^{-1}$ for the Amazonian species and $130.05 \pm 3.34 \text{ cm}^2 \text{ g}^{-1}$ for the species in Yangambi. In Paracou and Nouragues, g_s had a mean value of $0.10 \pm 0.0034 \mu\text{mol m}^{-2} \text{s}^{-1}$, and in Yangambi $0.15 \pm 0.0082 \mu\text{mol m}^{-2} \text{s}^{-1}$.

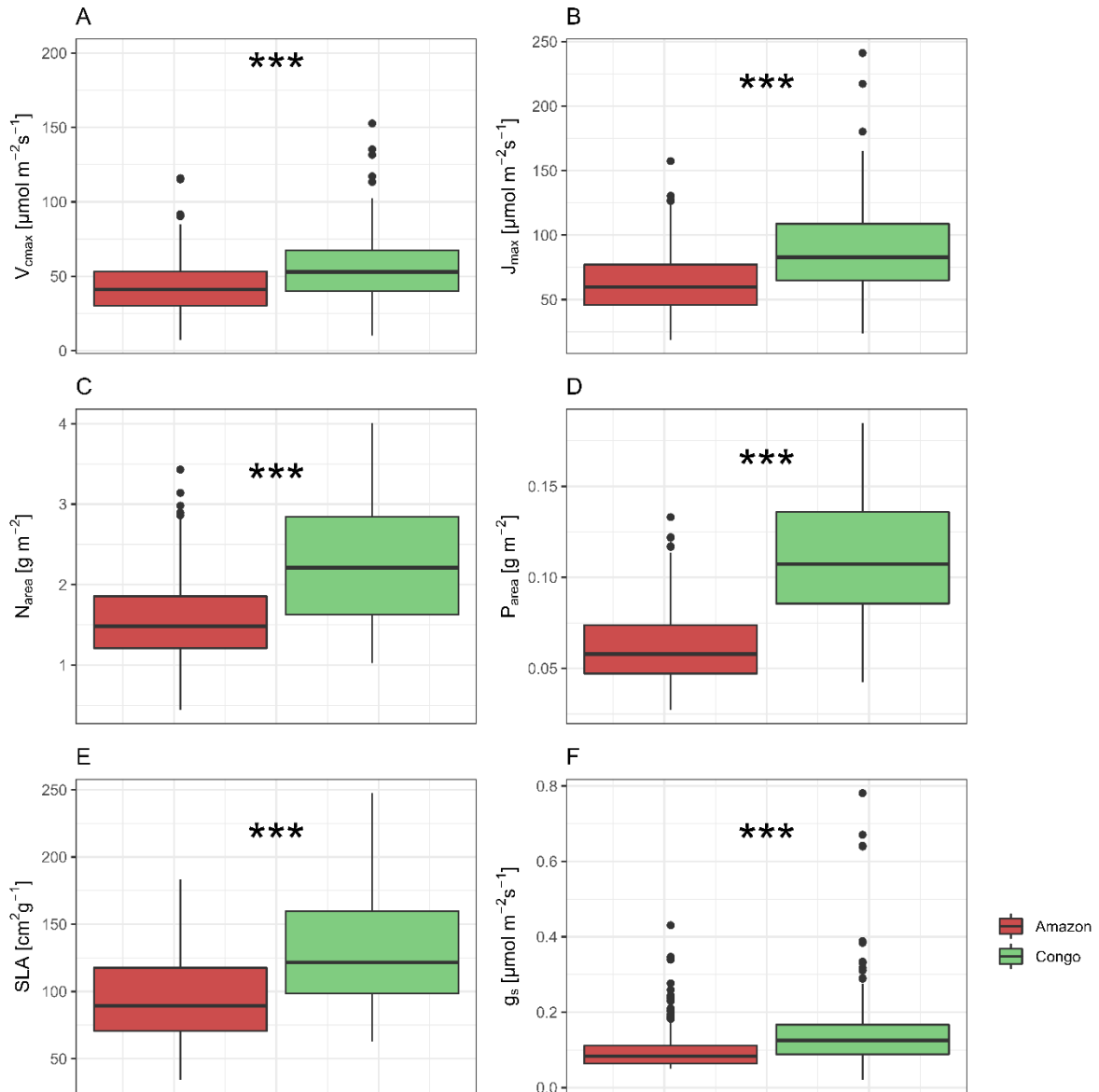


Figure 4.4: Comparison of six parameters between 34 species of the Paracou and Nouragues sites in the Amazon Basin and 23 species of the Yangambi site in the Congo Basin, with indication of the significant difference level (Wilcoxon signed rank test and Student's *t*-test on logarithmically transformed data). A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area, F) Stomatal conductance at ambient CO_2 concentration

4.3.2. Comparison of PFTs

For all considered parameters, values were systematically higher ($p < 0.05$; Wilcoxon signed rank test and *t*-test – sometimes on logarithmically transformed data) in Yangambi than in the Amazonian sites (Figure 4.5), when comparing tree PFTs. Lianas showed similar values for J_{max} and N_{area} , but not for V_{cmax} and P_{area} , which were higher in Yangambi than in the Amazonian sites (Figure 4.5).

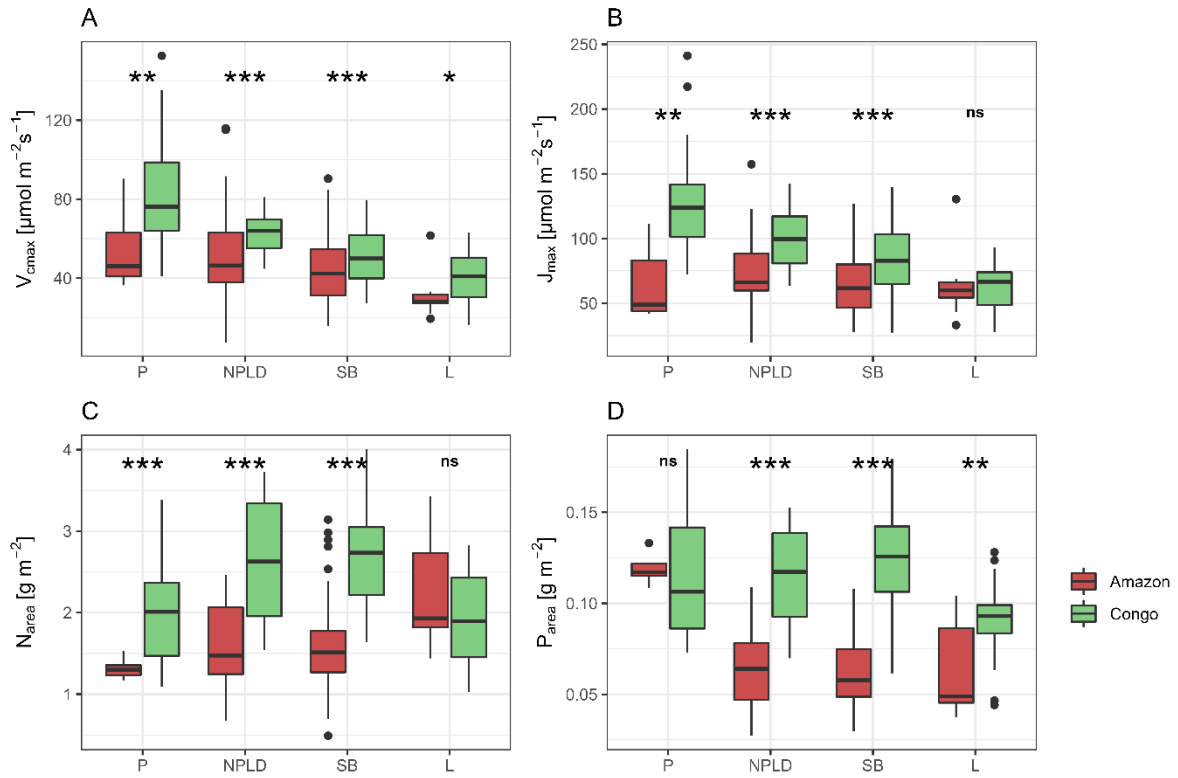


Figure 4.5: Comparison of four parameters of four PFTs – based on light requirement and regeneration – between 34 species of the Paracou and Nouragues sites in the Amazon Basin and 19 species of the Yangambi site in the Congo Basin, with indication of the significant difference level (Wilcoxon signed rank test and t-test – sometimes on logarithmically transformed data). P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, and L = liana. A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content

4.3.3. Bivariate relationships

Figure 4.6 displays the result of the Standardized Major Axis (SMA) regressions between V_{cmax} and the considered parameters. For the Amazonian sites, all relationships were significant, except the one between V_{cmax} and SLA ($p = 0.0030^{**}$ for N_{area} , $p = 9.23\text{e-}09^{***}$ for P_{area} , and $p = 1.23\text{e-}06^{***}$ for g_s). For Yangambi, all relationships were significant ($p = 1.46\text{e-}06^{***}$ for N_{area} , $p = 5.53\text{e-}12^{***}$ for P_{area} , $p = 1.37\text{e-}09^{***}$ for SLA, and $p < 2.22\text{e-}16^{***}$ for g_s).

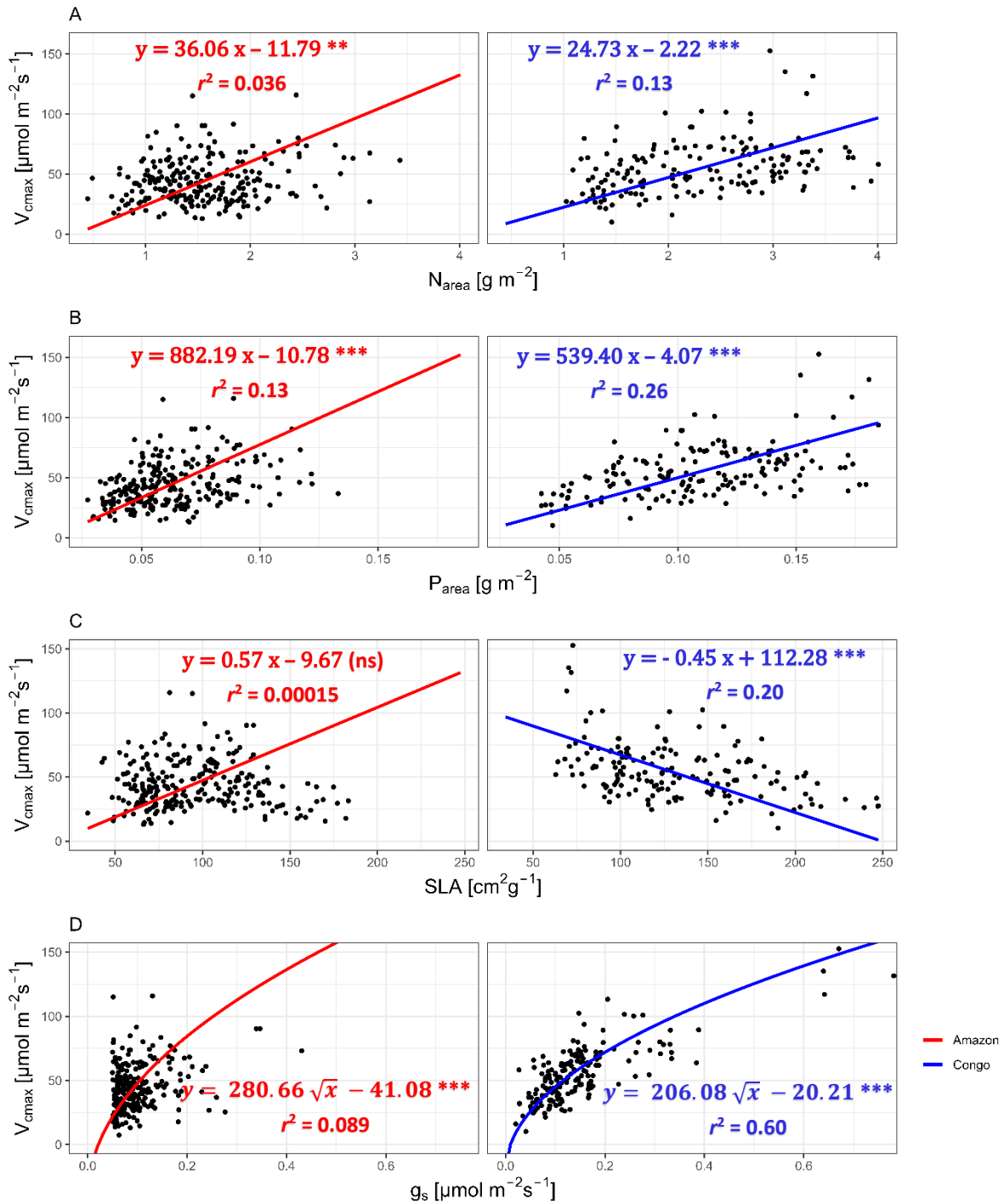


Figure 4.6 Standardized Major Axis (SMA) regression between V_{cmax} and A) area-based leaf N content, B) area-based leaf P content, C) specific leaf area, and D) the stomatal conductance at ambient CO_2 concentration, for 34 species of the Paracou and Nouragues sites in the Amazon Basin and 23 species of the Yangambi site in the Congo Basin. The fitted curves are indicated on the plot together with their significance level. The fit of the model is represented by the coefficient of determination (r^2).

4.4. Mixed-effect models

The result of the mixed-effect models is displayed in Table 4.1 (ANOVA). The mixed-effect models indicate that only the crown position and the PFT – based on light requirement +

regeneration – had a significant effect on both V_{cmax} and J_{max} . The location (site) only had a significant effect on J_{max} . Leaf phenology had no significant effect on photosynthetic capacity (V_{cmax} and J_{max}). Crown position had the strongest impact, followed by PFT.

Table 4.1: Summarized results of the mixed-effect models of V_{cmax} and J_{max} , with fixed effects of PFT (P, NPLD, SB, USB or L), leaf phenology (deciduous or evergreen), canopy position (top, bottom or middle of the crown) and location (Amazonian sites of Paracou and Nouragues or Yangambi site in the Congo Basin), and with random effect of species. The sum of squares (Sum Sq) indicates the size of the fixed effect on V_{cmax} and J_{max} , and the p-value indicates the significance of the fixed effect (ANOVA). The proportion of the model's random variance accounted for by the species-effect is shown as well.

FIXED EFFECTS	V_{cmax}		J_{max}	
	Sum Sq	p	Sum Sq	p
PFT	4834	0.00086 ***	7106	0.0017 **
Leaf phenology	236	0.27	544	0.20
Crown position	17045	< 2.2e-16 ***	46994	< 2.2e-16 ***
Location	696	0.063	2539	0.0078 **
RANDOM EFFECT (%)	Species	Residual	Species	Residual
	37.66	62.34	47.85	52.15

5. DISCUSSION

5.1. Comparison between PFTs

5.1.1. Light requirement + regeneration

The most limiting resource in tropical forests is most likely light (Chazdon et al., 1996), which makes a categorization in PFTs based on light requirement and regeneration very relevant. When comparing the photosynthetic parameters V_{cmax} and J_{max} across the PFTs, for both the Amazonian sites and Yangambi together, a clear distinction was visible between them (Figure 4.1 A and B). V_{cmax} and J_{max} were highest for pioneer (P, light-demanding) species, followed by NPLD, SB and USB species, in respective order. This trend is in agreement with literature, stating that light demanding species have higher photosynthetic rates than shade tolerant species (Rijkers et al., 2000), and that early successional species have higher photosynthetic rates than late successional species (Raaimakers et al., 1995; Reich et al., 1994, 1995; Zhang et al., 2018). This aligns with the ecological strategies these PFTs apply. Rapid growth (through high photosynthetic capacities) gives pioneers a competitive advantage to quickly colonize gaps in the forest canopy and effectively exploit resources (Reich, 2014; Swaine & Whitmore, 1988; Wright et al., 2004). SB species have lower photosynthetic capacities due to lower light availability, but they show a higher persistence, since they can survive better under these low-light conditions (Reich, 2014). NPLD species are situated in between P and SB species. USB species receive even less light than SB species. Hence, it makes sense their photosynthetic capacity was lowest, as confirmed by other studies (Mao et al., 2018; Santiago & Wright, 2007; F. Zhu et al., 2014). The shade tolerance and successional status gradients reflect a trade-off between growth/productivity and survival (Reich, 2014).

The liana species in this study exhibited values of V_{cmax} and J_{max} close to those of the SB and USB species (Figure 4.1 A and B). The data show that lianas had a lower photosynthetic capacity than top canopy trees. The studies of Slot & Winter (2017) and Santiago & Wright (2007) in a lowland tropical forest in Panama concluded that lianas have lower gas exchange rates than trees. Santiago & Wright (2007) give a possible explanation for this difference, stating that lianas have a higher leaf area per stem area than trees, so water needs to be transported to more leaves, leading to lower water supply to individual leaves and lower gas-exchange rates. In a seasonal tropical forest in Southwest China, Y. Chen et al. (2015) found the opposite trend, while Han et al. (2010) found similar photosynthetic capacities (A_{max}) between lianas and trees. The data from China however might not be that comparable with the data of this thesis, since the examined forest types are quite different. It seems lianas are, just like trees, a heterogeneous life form (Ek-Rodríguez et al., 2024). Liana abundance and biomass are increasing, and relatively more so in the Amazon Basin than in the Congo Basin (Schnitzer & Bongers, 2011). Aligning with previous results (Santiago & Wright, 2007; Slot & Winter, 2017), the presented results highlight these increases are not to be linked to extraordinary photosynthetic capacities of lianas, which on the contrary are rather low

compared to other woody plants. The cause must be found elsewhere. A possible explanation is that lianas are better adapted to droughts, e.g. due to strong stomatal control (Y. Chen et al., 2015). Another hypothesis is that increasing tree turnover (including mortality) in the Amazon favours liana growth, since they are forest gap specialists (Phillips et al., 2002).

The leaf chemical traits didn't follow the same trend. N_{area} was similar across all PFTs, except for USB species, which had a lower N_{area} (Figure 4.1 C). P_{area} was similar across NPLD, SB and liana species, higher for pioneer species and lower for USB species (Figure 4.1 D). Reich et al. (1995) didn't find a difference in N_{area} between early, mid- and late-successional species. Some other studies disagree, and found that pioneers have a higher N_{area} (Raaimakers et al., 1995; Rijkers et al., 2000) and P_{area} (Raaimakers et al., 1995; Zhang et al., 2018). The data in this thesis suggest that P_{area} is a better explanation for the higher V_{cmax} and J_{max} values of pioneers, than N_{area} . N:P ratios are indeed lower for pioneer species (Wright et al., 2004; Zhang et al., 2018), indicating they are less P limited. This links to their efficient resource acquisition and rapid growth, since P is an important compound in the energetic molecules ATP and NADP, required for photosynthesis (Ellsworth et al., 2022). The USB species (only measured in Yangambi) stood out with lower N_{area} and P_{area} , as Santiago & Wright (2007) found as well. They found similar N_{mass} and P_{mass} values between USB species and overstory trees, but due to their higher SLA, the area-based nutrient concentrations were lower in USB species. This can be linked to their low gas exchange rates, since N and P are essential elements in the photosynthetic process (Wright et al., 2004). USB species have more shallow roots than overstory trees, but since most nutrients in tropical forests are located at the upper part of the soil, this doesn't reduce their nutrient uptake (Becker & Castillo, 1990). Santiago & Wright (2007) found similar N_{area} and P_{area} values between lianas and trees as well. Since they found lower gas exchange rates in lianas than in trees, but similar leaf N and P concentrations, they concluded both life forms have a different way of allocating resources to photosynthesis.

The SLA was highest for USB species, followed by pioneer and liana species, and SB and NPLD species had the lowest SLA (Figure 4.1 E). The spread was high within each PFT. Wright et al. (2004) indeed found a big range in SLA for trees. Other studies in the tropics (Raaimakers et al., 1995; Reich et al., 1994, 1995; Rijkers et al., 2000) found higher SLA values for light demanding, early successional species too. This is typical for species situated at the quick return end of the leaf economics spectrum, such as pioneers (Wright et al., 2004). USB species clearly stood out with higher SLA values than all other PFTs, as Santiago & Wright (2007) found as well. Their SLA values closely matched those of Hatangi et al. (2023) (with average values around $180 \text{ cm}^2 \text{ g}^{-1}$), who also measured SLA of several USB species in Yangambi. Due to strong light limitation in the understory, these species tend to have large SLAs to optimize light capture at the expense of V_{cmax} (Hatangi et al., 2023; Santiago & Wright, 2007). Liana species showed SLA values higher than tree species (not significantly higher though than pioneers), which is in agreement with other studies (Han et al., 2010; Santiago & Wright, 2007; Tang et al., 2012). This is due to their faster growth and different resource allocation strategies (Tang et al., 2012).

Some general trends could be witnessed in the PFT data. Zhang et al. (2018) mention that the link between photosynthetic rates and leaf functional traits is not uniform across succession,

which was also visible in the data of this research. For example, higher V_{cmax} and J_{max} values of pioneers were associated with higher SLA values, but not with higher N_{area} values. Furthermore, there was a considerable spread on the examined parameters within each PFT, with a few outliers, as Yang et al. (2015) mentioned as a critique on using PFTs. This is due to differences between the sites (Appendix), between species (Appendix) and even between individuals of the same species. When looking at the pioneer class of Yangambi for example, *Musanga cecropioides* had way higher V_{cmax} , J_{max} , N_{area} and P_{area} values and way lower SLA values than *Tetrorchidium didymostemon* (Appendix). The latter species had values that leaned closer to NPLD species.

The old PFT categorization based on light requirement and regeneration (Hawthorne, 1995) proved to be useful in explaining the huge variability in traits between tree species, since considerable differences in the examined traits were witnessed between P, NPLD and SB species. The categorization cannot explain all the variability between species, but it simplifies the complex species pool in tropical forests. It is also best to include USB species and lianas as separate PFTs. Using different parameters in DGVMs for each PFT is thus very important, so carbon fluxes in tropical forests can be modelled more accurately.

5.1.2. Leaf phenology

The photosynthetic parameters V_{cmax} and J_{max} were higher for the deciduous species than for the evergreen species (Figure 4.2 A and B), as expected (Sobrado, 1991). N_{area} was higher for deciduous species as well (Figure 4.2 C). Pringle et al. (2011) and Silva et al. (2015) found higher N_{mass} values in deciduous species, while Sobrado (1991) found higher N_{mass} values in evergreen species, but neither of them examined N_{area} . Leaf phenology had no effect on P_{area} and SLA (Figure 4.2 D and E). Several studies (Pringle et al., 2011; Silva et al., 2015; Sobrado, 1991) did however find higher SLA values for deciduous species. Takashima et al. (2004) found a possible explanation for the higher photosynthetic capacity of deciduous species. They found that in deciduous species a bigger fraction of nitrogen was allocated to photosynthetic proteins, and a smaller fraction to structural proteins, when compared to evergreen species. This aligns with the trade-off present in the LES: deciduous species are more focused on productivity, while evergreen species are more focused on persistence (Pringle et al., 2011; Reich, 2014; Takashima et al., 2004). Deciduous species are more situated at the fast-return-on-investment side of the spectrum, with shorter leaf life-spans.

Most deciduous species included were NPLD species, so perhaps light requirement indirectly influenced this comparison too. Important to note is that only 7 deciduous species were included in the comparison, and 30 evergreen species. The skewed ratio can make the results less reliable (e.g. for SLA). There was also a big spread on the data with some high outliers, due to inter- and intra-species variability.

The differences between leaf phenology were smaller than those between light requirement categories, suggesting that a division into PFTs based on light requirement explains more interspecific variability in wet tropical forests than a division based on leaf phenology. Nonetheless, leaf phenology can be an extra categorization to use in DGVMs.

5.2. Within-crown variation

Leaves at the top of the crown are more exposed: they experience higher light intensities, higher air temperatures and lower air humidity (Legner et al., 2014; Niinemets, 2023). Leaves at the bottom are more shaded. Top leaves are often sun leaves and bottom leaves are often shade leaves, which both have specific traits adapted to their respective environments (Lambers & Oliveira, 2019), some of which are witnessed in this dataset. One of them is that top leaves have a higher photosynthetic capacity (Niinemets, 2023), which was also the case in this study. Crown position clearly affected photosynthetic capacity. Leaves at the top of the crown showed higher V_{cmax} and J_{max} values than leaves at the bottom (Figure 4.3 A and B), which is in agreement with other studies (Carswell et al., 2000; Lambers & Oliveira, 2019; Legner et al., 2013, 2014; Niinemets, 2023). Moreover, N_{area} and P_{area} were both higher for leaves at the top (Figure 4.3 C and D), as found in other studies (Carswell et al., 2000; Legner et al., 2014; Lloyd et al., 2010; Niinemets, 2023). Another acclimation is the lower SLA of top leaves (thicker leaves) to increase their photosynthetic capacity and protect them against extremer conditions (Niinemets, 2023). Bottom leaves have high SLAs to increase their light capture capacity (Lambers & Oliveira, 2019). This phenomenon was also present in the data, showing clearly higher SLA values at the bottom of the crown (Figure 4.3 E). All these adaptations lead to a maximisation of photosynthesis across the entire canopy (Niinemets, 2023).

However, some remarks have to be made. First of all, the comparison was made across all species, so the effect of crown position per species (or PFT) was not examined. This effect was not similar across all species. Generally, the SB species (e.g. *Panda oleosa* in Yangambi) showed clearly higher differences in the examined parameters between top and bottom measurements than NPLD species (e.g. *Pericopsis elata* in Yangambi), because their crown has a greater vertical extension (Legner et al., 2014). One *P. elata* tree had a very short crown of only 3.8m. Hence, *P. elata* might not have a differentiation between sun and shade leaves, since all leaves are heavily exposed to sunlight. A *P. elata* tree is also generally higher than a *P. oleosa* tree. Thus, top or bottom says nothing about the height of the measurement (Appendix) or the strategy of the species. Some bottom measurements were even higher than top ones (Appendix). This inter- and intra-specific variability explains the big spread in the data (with some outliers). A way to deal with this problem would be to look at the correlation between height and photosynthetic capacity instead of using crown positions. Furthermore, USB species were considered as bottom measurements, but they don't have sun-exposed top leaves to compare with. Since USB species had the lowest photosynthetic capacity, this could have influenced the results.

Nevertheless, the data confirm it is important to measure photosynthetic capacity at different positions in the crown, in order to get representative values of species for carbon flux modelling.

5.3. Comparison between sites in the Amazon and Congo Basin

5.3.1. General comparison

The photosynthetic parameters V_{cmax} and J_{max} were significantly higher in Yangambi than in the sites of Paracou and Nouragues (Figure 4.4 A and B). The important question that now arises is whether there are real (a)biotical difference between the sites or whether this difference is due to methodological issues.

N_{area} and P_{area} were a lot higher in Yangambi (Figure 4.4 C and D), which could explain this difference in photosynthetic capacity. Verryckt et al. (2022) found average total N concentrations in the surface soils of Paracou and Nouragues ranging from 0.13 to 0.22% across the seasons. The soil Bray P (plant available) counted 1.7 – 3.3 ppm across the seasons. Mapenzi et al. (2024) measured soil properties in the Lobilo catchment near Yangambi, and found N ranges of 0.14 – 0.25%, and P ranges of 16.24 – 17.83 ppm. Soil N values are similar between the sites, but plant available P is a lot higher in Yangambi. However, this comparison isn't very appropriate, since the study of Mapenzi et al. (2024) is an agroforestry experiment, and not conducted inside the rainforest. More appropriate soil data in the Yangambi rainforest are required to check whether the N and P bio-availability are indeed higher in Yangambi than in the Amazonian sites, explaining the observed higher productivity. An increased nitrogen and phosphorus deposition is witnessed in the central Congo Basin and not (or only minorly) in the Amazon Basin, mainly caused by the natural and anthropogenic fires in nearby grasslands and savannas (Bauters et al., 2018, 2021; Goll et al., 2023), which might explain possible higher N and P concentrations in the Congo Basin. Goll et al. (2023) claim that the increased nutrient deposition since the 1980s could have contributed to the Central African carbon sink over the past 40 years, potentially to a degree comparable to the combined impact of rising atmospheric $[\text{CO}_2]$ and climate change. Especially P deposition would have a large impact, since tropical forests are more P limited (Goll et al., 2023). The difference in P_{area} (Figure 4.4 D) indeed seems more pronounced than the difference in N_{area} (Figure 4.4 C). In French Guiana (where the sites of Paracou and Nouragues are located), there is nutrient (importantly P) deposition too from Sahara dust (Prospero et al., 2020), but the deposition rates are considerably lower than those Bauters et al. (2021) reported over Central Africa.

The SLA was also higher in Yangambi (Figure 4.4 E), which indicates generally thinner leaves (Wright et al., 2004). Furthermore, the stomatal conductance of the CO_2 response curves was higher in Yangambi as well (even after the filtering of the Amazonian data; Figure 4.4 F) and a higher g_s is generally associated with higher photosynthetic rates (Domingues et al., 2014; Farquhar & Sharkey, 1982; Santiago & Wright, 2007). It is uncertain whether this difference is linked to structurally different characteristics of the species (e.g. different stomatal density or stomatal size) in Yangambi. Other studies in the Amazon (Domingues et al., 2014; Santiago & Wright, 2007) reported generally higher g_s values than those of Verryckt et al. (2022). Besides, the values found in Yangambi are quite similar to those found by Bahar et al. (2017) and Carswell et al. (2000) in Amazonia, hinting at no structurally different g_s between the continents.

It would be interesting to compare leaf lifespans between the sites as well. Since the Congo Basin is drier than the Amazon Basin and has relatively more deciduous species (Luambua et al., 2021), it might be expected that the leaf lifespan is lower in the Congo Basin. A lower leaf lifespan is associated with a higher photosynthetic capacity (Wright et al., 2004). Sadly, leaf lifespan data is not available yet for the Congo Basin.

Important to note is that the distribution of the PFTs was not equal for the research sites. In the Amazon, only one pioneer species was included, compared to four in Yangambi. One species is not representative for an entire PFT. Maybe the results would be different if more pioneer species were included in the Amazonian dataset, since they have the highest photosynthetic capacity. The Amazonian data also contained relatively more measurements on SB species (which have lower gas exchange rates), and relatively less on light-demanding species, which is another explanation for the lower values in the Amazonian sites reported in this study. But the fact that fewer pioneer species were detected in the Amazonian sites might be a bigger, more general pattern. In most central African rainforests a remarkable abundance of light-demanding canopy species (including NPLD species) is observed (Biwolé et al., 2015; Luambua et al., 2021). A popular hypothesis is that these forests are still recovering from extensive past slash-and-burn agricultural practices, although this cannot be unambiguously proven (Luambua et al., 2021). Claeys et al. (2019) project a compositional shift towards long-lived pioneer species, at the cost of SB species, in central African forests under climate change. Furthermore, the Yangambi data contains USB species and the Amazonian data does not. The difference in V_{cmax} between the sites for example would have even been bigger if the USB species wouldn't be included in the comparison.

Lastly, differences in the leaf chamber conditions could be regarded as well. Verryck et al. (2022) used a light intensity for bottom leaves that is only half the amount of the intensity used in Yangambi. They however found that increasing the light intensity wouldn't make a big difference. Besides, there were no remarkable differences in how leaf nutrients were measured (e.g. leaf sampling, used equipment, etc.) between the Amazonian and Yangambi data.

Although there are some methodological issues in the comparison (being an unequal PFT distribution across the sites and minor differences in leaf chamber conditions), the differences in the examined parameters between the sites are striking. A comparison per PFT – based on light requirement and regeneration – could help clarify this interesting difference.

5.3.2. Comparison of PFTs

V_{cmax} and J_{max} were higher in Yangambi than in the Amazonian sites for each PFT, except J_{max} for lianas (Figure 4.5 A and B). This was associated with higher N_{area} and P_{area} in Yangambi, with some exceptions (Figure 4.5 C and D). By consequence, the different PFT distribution between the sites (as mentioned before) is likely not the cause of the observed differences.

Remarkable is that there was no significant difference in J_{max} for the lianas (Figure 4.5 B). This could indicate that ex-situ measurements in Yangambi were systematically lower than in-situ measurements performed by Pausenberger (2016). Santiago & Mulkey (2003) indeed found

that branch excision reduced photosynthetic rates for several species. S.-D. Zhu & Cao (2009) state that lianas are more vulnerable to cavitation than trees, since they have longer and wider vessels, potentially leading to an underestimation of the photosynthetic capacities of lianas in Yangambi. This similarity in $J_{\max}$ could also be an indication that the relative success of lianas in the Amazon compared to the Congo Basin (Schnitzer & Bongers, 2011) is not due to higher photosynthetic capacities.

Another observation is that the distinction between the PFTs was clearer in Yangambi (see Appendix too). Photosynthetic capacities and leaf nutrient concentrations didn't really seem to differ between the PFTs in the Amazonian sites, which is not in agreement with literature. The single pioneer species, *Sterculia multiovula*, didn't have typically higher values (except for P_{area}). Perhaps the used classification by Bonal et al. (2000) is not entirely correct and this species is not a pioneer. The division in PFTs remains something arbitrary. The fact that there is no clear difference in the examined parameters in the Amazonian sites also affects the general PFT comparison for the Amazon and Congo Basin together (section 5.1.1; Figure 4.1), making the overall trends less clear and increasing the spread on the data. A last detail that should be mentioned is that for the Amazonian data 91 measurements were not included in the PFT comparison, because their PFT could not be identified.

The PFT comparison indicates that there are real (a)biotic differences between the sites, because values were systematically higher in Yangambi for all PFTs, despite an unequal distribution of the PFTs. A last important addition is to compare the Amazonian values used in this thesis and the Yangambi values with other studies.

5.3.3. Comparison with literature

When the average V_{cmax}^{25} and J_{max}^{25} of the Amazonian dataset of Verryckt et al. (2022) are compared with literature (Table 5.1), they seem rather low. V_{cmax}^{25} and J_{max}^{25} are the V_{cmax} and J_{max} values rescaled at 25°C (as originally reported in the dataset of Verryckt et al. (2022)), because in literature mostly V_{cmax}^{25} and J_{max}^{25} are reported instead of V_{cmax} and J_{max} at ambient temperature. Coupled to that, the average leaf nutrient content found by Verryckt et al. (2022) is also lower than values found in literature (Table 5.1). There are several possible hypotheses to explain this trend. Perhaps the forests in Paracou and Nouragues are more nutrient poor and hence less productive, as the N_{area} values indicate. Besides, the examined species pool differs between the studies, and big differences in photosynthetic parameters between species (and individuals of the same species) have been detected. The data of Verryckt et al. (2022) also contains mostly SB species, which have lower photosynthetic capacities.

Table 5.1: Comparison of the examined parameters from the data of Verryckt et al. (2022) in the sites of Paracou and Nouragues (French Guiana), used in this thesis, with other studies conducted in lowland Amazonian rainforests. The reported mean value of each parameter is mentioned, together with the standard error (SE). Important to note is that Bahar et al. (2017) only measured at the top of the canopy, which affects all examined leaf parameters.

Study	Location	Parameter: mean $\pm$ SE
Verryckt et al. (2022)	French Guiana	V_{cmax}^{25} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: 25.4 ± 1.3 J_{max}^{25} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: 56.2 ± 1.4 N_{area} [g m^{-2}]: 1.52 ± 0.03 P_{area} [g m^{-2}]: 0.062 ± 0.001 SLA [$\text{cm}^2 \text{g}^{-1}$]: 93.62 ± 2.1
Kattge et al. (2009)	Tropical trees on oxisol soils	V_{cmax}^{25} : 29.0 ± 0.4 N_{area} : 2.17 ± 0.04
Bahar et al. (2017)	Peru	V_{cmax}^{25} : 35.9 ± 1.1 J_{max}^{25} : 66.7 ± 1.4 N_{area} : 1.96 ± 0.52 P_{area} : 0.09 ± 0.004 SLA : 75.6 ± 1.21
Carswell et al. (2000)	Brazil	V_{cmax}^{25} : 33.3 ± 4.1 J_{max}^{25} : 84.7 ± 10.5 N_{area} : 2.87 ± 0.18 SLA : 101.7 ± 6.0
Rowland et al. (2015)	Brazil	V_{cmax}^{25} : 29.1 ± 1.8 J_{max}^{25} : 51.1 ± 2.8

The V_{cmax}^{25} (as was originally reported) data of the lianas in Paracou from Pausenberger (2016) range from 28.56 to $78.05 \mu\text{mol m}^{-2} \text{s}^{-1}$. Domingues et al. (2014) measured V_{cmax}^{25} in a tropical rainforest in Brazil on 6 liana species at the top of canopy (in situ), and found average values of 29.7 ± 4.4 to $55.2 \pm 5.2 \mu\text{mol m}^{-2} \text{s}^{-1}$. Slot & Winter (2017) found an average V_{cmax} of 79 (SD = 30) $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 5 liana species in a lowland wet tropical forest in Panama, at their optimal temperature of 29.6°C (in situ). This is a lot higher than the average V_{cmax} at ambient temperature of Pausenberger (2016), being $30.96 \pm 4.08 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Photosynthetic capacity has never been measured in the Congo Basin before, so the values of this study can't be compared to literature properly. However, measurements have been done in drier tropical forests in Africa (e.g. Domingues et al., 2010; Gvozdevaite et al., 2018). But

these values cannot be easily compared with those from Yangambi, since the latter were not rescaled to 25°C, because no temperature response curves are available yet for the Congo Basin. In a dry forest in Ghana, Gvozdevaite et al. (2018) found average N_{area} and P_{area} values of 2.21 ± 0.06 and $0.19 \pm 0.01 \text{ g m}^{-2}$ respectively, which are similar to those found in Yangambi. Verbeeck et al. (2014) measured functional leaf traits on 10 tree species in secondary lowland tropical forests in the Congo Basin (including Yangambi), and found average values of N_{area} , P_{area} and SLA of $1.37 \pm 0.07 \text{ g m}^{-2}$, $0.0781 \pm 0.004 \text{ g m}^{-2}$ and $220 \pm 9.6 \text{ cm}^2 \text{ g}^{-1}$, respectively. These values differ substantially from this study, which is surprising, given the close proximity of these studies. P_{area} and especially N_{area} are higher in this study, and SLA a lot lower. This difference might be explained by the fact that the examined species pool differs between the studies, given the big differences in leaf functional traits between species (and even between individual trees), witnessed in the Yangambi data. Lastly, the values found in Yangambi are close to or higher than the Amazonian values mentioned in Table 5.1, which could indicate that the values found by Verryckt et al. (2022) are underestimated.

The Amazonian data used in this study showed generally lower values than those found in literature and the Yangambi values leaned closer to other studies in the Amazon than to the study of Verryckt et al. (2022). Nevertheless, the differences between the sites in French Guiana and Yangambi are striking, despite some small methodological issues. These results are very interesting, but still only explorative, since only one location in the Congo Basin was studied and two in the Amazon Basin. Upscaling will be needed, if we want to know whether the photosynthetic capacity is generally higher in the Congo Basin than in the Amazon Basin. Hence, more data will need to be collected in the Congo Basin (on different locations) to be able to make a representative comparison. Hubau et al. (2020) modelled a higher increase in carbon gains in the Congo Basin relative to the Amazon Basin. They mention some plausible reasons: slower warming, overall lower temperatures, fewer or less extreme droughts and lower sensitivity to droughts in the African tropical forests. The higher N and P deposition, as explained by Gollet et al. (2023), could be another influencing factor.

5.3.4. Bivariate relationships

A significant positive relationship was observed between V_{cmax} and N_{area} and P_{area} (Figure 4.6 A and B), which is in agreement with the global dataset of Wright et al. (2004) (which involves A_{max} instead of V_{cmax} though). Positive relationships were observed in the tropics as well (e.g. Bahar et al., 2017; Kattge et al., 2009). Kattge et al. (2009) found a regression of $V_{cmax}^{25} = 10.71 N_{area} + 1.99$ for tropical trees growing on oxisols. These coefficients are a lot smaller than those found in Paracou and Nouragues (Figure 4.6 A). However, in this thesis V_{cmax} at ambient temperature was used instead of V_{cmax}^{25} (to avoid inaccurate rescaling), making the comparison less straightforward. In both the Amazonian sites and Yangambi there was a stronger correlation between V_{cmax} and P_{area} than between V_{cmax} and N_{area} (higher r^2), hinting at a stronger P limitation of photosynthesis than N limitation (Domingues et al., 2010). This trend is witnessed in other studies on tropical forests (e.g. Domingues et al., 2010), with the explanation that tropical soils are highly weathered, reducing plant available P (Domingues et al., 2010; Reich et al., 2009). However, data on bio-availability of nutrients in the Yangambi

rainforest would be needed to confirm this (see section 5.3.1). The correlation was better in Yangambi for both nutrients, but the slopes were steeper in the Amazonian sites. This could mean N_{area} and P_{area} were better predictors of V_{cmax} in Yangambi, but the dependency of V_{cmax} on these leaf nutrients was higher in Amazonia. The Amazonian sites could be more nutrient poor (see section 5.3.1). Another interesting analysis would be to examine the relationship between photosynthetic capacities and leaf N and P allocated to photosynthesis (instead of the entire leaf N or P). This could be examined by measuring photosynthetic proteins (Takashima et al., 2004). Perhaps the correlations would be stronger then.

In Paracou and Nouragues there was no significant correlation between V_{cmax} and SLA, while in Yangambi there was a significant negative relationship (Figure 4.6 C). Globally there is no relationship observed between A_{max} (on an area basis) and SLA (Wright et al., 2004). In a lowland tropical rainforest on the contrary, Santiago & Wright (2007) found an overall negative relationship between A_{max} and SLA. However, within each growth form (being trees, USB species and lianas) they did not find a significant relationship. They conclude that the overall negative trend is largely caused by the unique characteristics of USB species, having a low photosynthetic capacity and a high SLA. This likely explains the different trend witnessed between the forests as well, since no USB species were measured at the Amazonian sites.

In all sites a steep positive relationship could be observed between V_{cmax} and g_s (Figure 4.6 D). Other studies (Domingues et al., 2014; Santiago & Wright, 2007) found a strong correlation between A_{max} and g_s as well. A higher g_s means the stomata are opened more widely, allowing more CO_2 to enter the leaf (Farquhar & Sharkey, 1982). The fit was much better for the Yangambi data. It is uncertain whether this is a systematic difference between the Amazon and the Congo Basin or whether this difference is data-driven (meaning there are some issues in the data of Verryckt et al. (2022)). It would be interesting to do a different regression for each PFT (plus directly compare g_s values between PFTs), to examine whether g_s is linked to PFT.

In general, the correlations were all stronger in Yangambi. In the Amazonian sites, P_{area} was the best predictor of V_{cmax} ($r^2 = 0.13$), followed by g_s ($r^2 = 0.089$). In Yangambi, g_s is by far the best predictor of V_{cmax} ($r^2 = 0.60$), followed by P_{area} ($r^2 = 0.26$). An interesting addition would be to perform a regression for each PFT separately. Domingues et al. (2010) found a different scaling of photosynthesis with leaf traits for different vegetation types. The same regressions could also be repeated with J_{max} , to increase the evidence of the correlations between photosynthetic capacity and leaf functional traits. These correlations with the leaf functional traits are useful to parametrise DGVMs for the Amazon and Congo Basin. The results indicate the need for a different parameterisation on both continents.

5.4. Mixed-effect models

The mixed-effect model (Table 4.1) says only the PFT (P, NPLD, SB, USB, and L) and the crown position had a significant effect on V_{cmax} , and the location and the leaf phenology didn't. This expresses the importance of distinguishing between PFTs and of measuring at different crown positions when parametrizing carbon flux models. That way, the tropical C cycle can be

simulated more accurately. When looking at each factor separately, the effects on photosynthetic parameters were always significant. It thus remains interesting to keep studying effects of leaf phenology and especially location in the future, considering the striking differences between the sites. However, the differences in average V_{cmax} (and J_{max}) values were indeed higher for crown position and for PFT than for location and for leaf phenology. V_{cmax} differed on average $14.36 \mu\text{mol m}^{-2} \text{s}^{-1}$ between the top and bottom of the crown, $30.16 \mu\text{mol m}^{-2} \text{s}^{-1}$ between P and SB species, $11.82 \mu\text{mol m}^{-2} \text{s}^{-1}$ between Yangambi and the Amazonian sites, and $5.01 \mu\text{mol m}^{-2} \text{s}^{-1}$ between deciduous and evergreen species. The differences in leaf phenology were less significant as well.

The random effect of species explained a lot of variance in both models. Indeed, a big variation in photosynthetic parameters was observed between species, also within the same PFT and between top – bottom differences. The big species-effect highlights the complexity of tropical rainforests, making classification into PFTs not so straightforward (Swaine & Whitmore, 1988), but nonetheless very important to simplify the plant realm. The species-effect also means that in tropical forests a lot of different species need to be measured for accurate DGVM parametrisation. Since this is not always possible, it is best to focus on dominant species (e.g. productivity hyperdominants, section 2.2.3).

It would also be interesting to perform a mixed-effect model on V_{cmax} and J_{max} with the leaf functional traits N_{area} , P_{area} , SLA and g_s . Combined with the SMA regression (Figure 4.6), this would give a more complete image on the combined effects of these parameters on photosynthetic capacity.

6. CONCLUSION

This master's thesis provides a first, explorative comparison of leaf-level photosynthesis between the two biggest tropical forests on the planet. It helps closing the existing data gap in the Congo Basin tropical forests (Central Africa), through the collection of important photosynthetic parameters and leaf functional traits of 23 species at the CongoFlux research site in Yangambi (Democratic Republic of the Congo). These data were compared with existing data on 34 species at the Paracou and Nouragues sites (French Guiana) in the Amazon Basin.

The mixed-effect models conclude that the position in the crown had the biggest effect on the photosynthetic parameters V_{cmax} (the maximum carboxylation capacity) and J_{max} (the maximum rate of electron transport), followed by the plant functional type (PFT) – based on light requirement and regeneration. Both the location and the leaf phenology had no significant effect on V_{cmax} . Location did have an effect on J_{max} though. However, when the effects of each of these four factors on the photosynthetic capacity (V_{cmax} and J_{max}) were examined separately, significant results were found each time. It is especially surprising that the mixed-effect model indicates that location did not have a significant impact on V_{cmax} , since the differences between the locations (Yangambi vs. Amazonian sites) were striking. Furthermore, the random effect of species was considerably high, indicating that big differences in photosynthesis exist between species (even within species of the same PFT), which highlights the complexity of tropical forests.

When the site data were pooled (Paracou, Nouragues and Yangambi), the photosynthetic capacity was highest for pioneers, followed by non-pioneer light demanding (NPLD), shade-bearing (SB) and understory shade-bearing (USB) species, in respective order. This agrees with the more acquisitive strategy (aimed at rapid growth) of early-successional, light-demanding species and the more conservative strategy (aimed at survival) of late-successional, shade-tolerant species. Lianas showed generally lower values than trees. The recent success of lianas in tropical forests, and their relatively better performance in the Amazon Basin, remain unclear. The results of this study highlight that this success is not to be linked to extraordinary photosynthetic capacities of lianas. Further research needs to be done to find an explanation for this interesting phenomenon. Leaf functional traits varied less among PFTs, with the exception of USB species, having low leaf nitrogen (N_{area}) and phosphorus (P_{area}) contents and high specific leaf areas (SLAs), as an adaptation to resource limitation. Furthermore, deciduous species showed higher photosynthetic capacities than evergreen species.

Leaves at the top of the crown had higher photosynthetic capacities, higher N_{area} and P_{area} , and lower SLA than leaves at the bottom of the crown. These are adaptations to their respective environmental conditions.

Photosynthetic capacity, leaf nutrient content, SLA and g_s were all higher in Yangambi than in the Amazonian sites of Paracou and Nouragues. These differences could be partly attributed to methodological issues, being an unequal PFT distribution across the sites and minor differences in instrument settings. However, there seem to be real (a)biotic differences present

between the sites as well, since for each PFT the measured parameters were systematically higher in Yangambi (except $J_{\max}$ and N_{area} for the lianas). The higher N_{area} and P_{area} could indicate that the site of Yangambi is more nutrient rich and productive than the sites of Paracou and Nouragues.

There were considerable differences in the bivariate relationships with V_{cmax} between the sites. All correlations were stronger in Yangambi. A stronger correlation was observed with P_{area} than with N_{area} at all sites, indicating a stronger P limitation, which has been observed in other tropical studies as well. P plays an important role in photosynthesis, since it is a component of the energetic molecules ATP and NADP. The better regressions with the leaf nutrients in Yangambi could be another indication that the forests in Paracou and Nouragues are more nutrient poor. This should be checked by gathering more data on bio-availability of nutrients in Yangambi. Furthermore, V_{cmax} showed a strong positive correlation with g_s , as expected.

The data presented in this study have some important implications for the parametrisation of Dynamic Global Vegetation Models (DGVMs) in tropical forests. First of all, distinguishing between PFTs proved to be very useful in representing and simplifying the high variability in photosynthetic capacity between species. Lianas and understory species should be included as separate PFTs. Furthermore, the data confirmed it is important to measure photosynthesis at different heights in the crown, to get more accurate values for species. Lastly, given the striking differences in photosynthetic capacity between Yangambi and the Amazonian sites, it would be better to use different parameters for the Amazon and Congo Basin rainforests. Different bivariate relationships should be used between both tropical forests as well. All of this would allow for more accurate simulations of global carbon fluxes and climate change.

In conclusion, photosynthetic capacity was strikingly higher in Yangambi, highlighting there could be important differences between the tropical forests of both continents. Doing further research on the Congo Basin will be necessary, because the African tropical forests will undoubtedly play a crucial role in the future of our planet.

7. FURTHER RESEARCH

Since this was only an explorative study, research on this topic is far from finished. This study revealed several interesting options for further research.

First of all, there are several opportunities to examine the differences between the PFTs more deeply. USB species were not measured in the Amazonian sites. It would be interesting to examine whether photosynthesis also differs between USB species of both tropical forests. The stomatal conductance (g_s) could be compared between PFTs as well. Top-bottom differences clearly varied between species, so a better, more detailed understanding would be gained when these differences would be examined per PFT. Another option would be to look at the correlation between photosynthetic capacity and height in the crown. Another interesting addition would be to examine the bivariate relationships per PFT, which could give extra valuable information for DGVMs.

It would be interesting to perform a mixed-effect model on V_{cmax} and J_{max} with the leaf functional traits N_{area} , P_{area} , SLA and g_s . Combined with the SMA regression, this would help to identify which of these parameters are predictors of the photosynthetic capacity. Potential differences between the sites could be examined as well.

During the same field campaign (August 2023), temperature response curves were measured at Yangambi. Using this temperature response, V_{cmax} and J_{max} could be properly rescaled to 25°C. This would enable us to compare the data from Yangambi globally with standardised values.

Most importantly, more photosynthetic data on tropical forests (especially in the Congo Basin) are needed to find out whether there is a general difference in leaf-level photosynthetic capacity between both continents, and what could explain this potential difference. Possible drivers could be a different vegetation composition (e.g. more light-demanding, dry-tolerant species in the Congo Basin; Luambua et al., 2021), different climatic trends (Hubau et al., 2020), and higher atmospheric N and P depositions in the Congo Basin (Goll et al., 2023). Comparing bio-available soil nutrients might offer an explanation. It would also be interesting to further examine the potentially different impacts of climate change on both tropical forests (including vegetation shifts and shifts in carbon dynamics).

Furthermore, the data on leaf-level photosynthesis could be compared with the net ecosystem exchange (NEE), measured by the flux tower at the CongoFlux research site. Leaf-level photosynthesis, dark respiration, temperature response curves of species, forest inventories (including tree mortality), NEE ... could all be combined so the entire ecosystem is covered at Yangambi. This way, the carbon fluxes of the entire ecosystem (with all its facets) could be compared across sites on both continents.

Summarized, more measurements are needed, especially in the Congo Basin (on different locations than Yangambi as well), to further examine the differences between the two largest

tropical rainforests. The upscaling should not only be done in terms of the number of measurements and sampled locations, but also in terms of the studied level (e.g. from leaf-level to ecosystem-level).

Gathering more data on the two biggest tropical forests in the world is very important and urgent. We would be able to more accurately assess the impact of these biomes on future climate change, and the impacts of climate change on their functioning. Eventually, this would allow for a better management, more adapted to the conditions of each forest, which would help securing the future of our tropical rainforests. Tropical forests are the lungs of our planet and they are crucial in the battle against climate change.

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APPENDIX

Table A.1: The heights of the top and bottom measurements from each individual tree or liana (Ind) of the 23 species measured in Yangambi. The year of the field mission in which the individual was measured is mentioned as well. For understory shade-bearing (USB) species only the height of the entire individual was measured.

Species	Year	Ind	Top height [m]	Bottom height [m]
<i>Tridesmostemon o.</i>	2022	1	31	13
	2022	2	21	10
<i>Strombosiopsis t.</i>	2022	1	24	14
	2022	2	21	12
<i>Pericopsis e.</i>	2022	1	30	25
	2022	2	26	22
	2023	3	31.2	27.4
<i>Synsepalum s.</i>	2022	1	27	17
	2022	2	22	12
<i>Grossera m. (USB)</i>	2022	1	13	6
	2022	2	14	8
<i>Staudtia g.</i>	2022	1	26	20
	2022	2	33	27
<i>Triclisia g.</i>	2022	1	20	9
	2022	2	19	9
<i>Drypetes g.</i>	2022	1	23	17
	2022	2	20	16
<i>Panda o.</i>	2023	1	24.4	11.1
	2023	2	28.5	18.7
<i>Musanga c.</i>	2022	1	20	12
	2022	2	2022	12
<i>Macaranga s.</i>	2023	1	13.2	13.5
	2023	2	12.2	12.6
<i>Petersianthus m.</i>	2023	1	31.1	20.9
	2023	2	27.8	21.8
	2023	3	NA	18.4
<i>Tetrorchidium d.</i>	2023	1	11.3	6.4

	2023	2	18.5	11.7
<i>Macaranga b.</i>	2023	1	17.4	13.2
	2023	2	16.2	10.1
<i>Anonidium m.</i>	2023	1	24.1	15.8
	2023	2	17.1	14.7
<i>Scorodophloeus z.</i>	2023	1	26.3	21.7
	2023	2	23.4	15.1
	2023	3	26.6	13.8
<i>Millettia d.</i>	2023	1	17.2	12
	2023	2	14.5	8.4
<i>Lepiae t.</i>	2023	1	25	19.4
	2023	2	26.5	13.5
<i>Cola g.</i>	2023	1	17.2	13.1
	2023	2	20.3	14.4
<i>Scaphopetalum t. (USB)</i>	2023	1	4.9	/
	2023	2	4.6	/
<i>Landolphia k.</i>	2023	1	25	8.1
	2023	2	25	19
<i>Cola b. (USB)</i>	2023	1	3.8	/
	2023	2	6.4	/
<i>Aidia m. (USB)</i>	2023	1	4.6	/
	2023	2	8.3	/

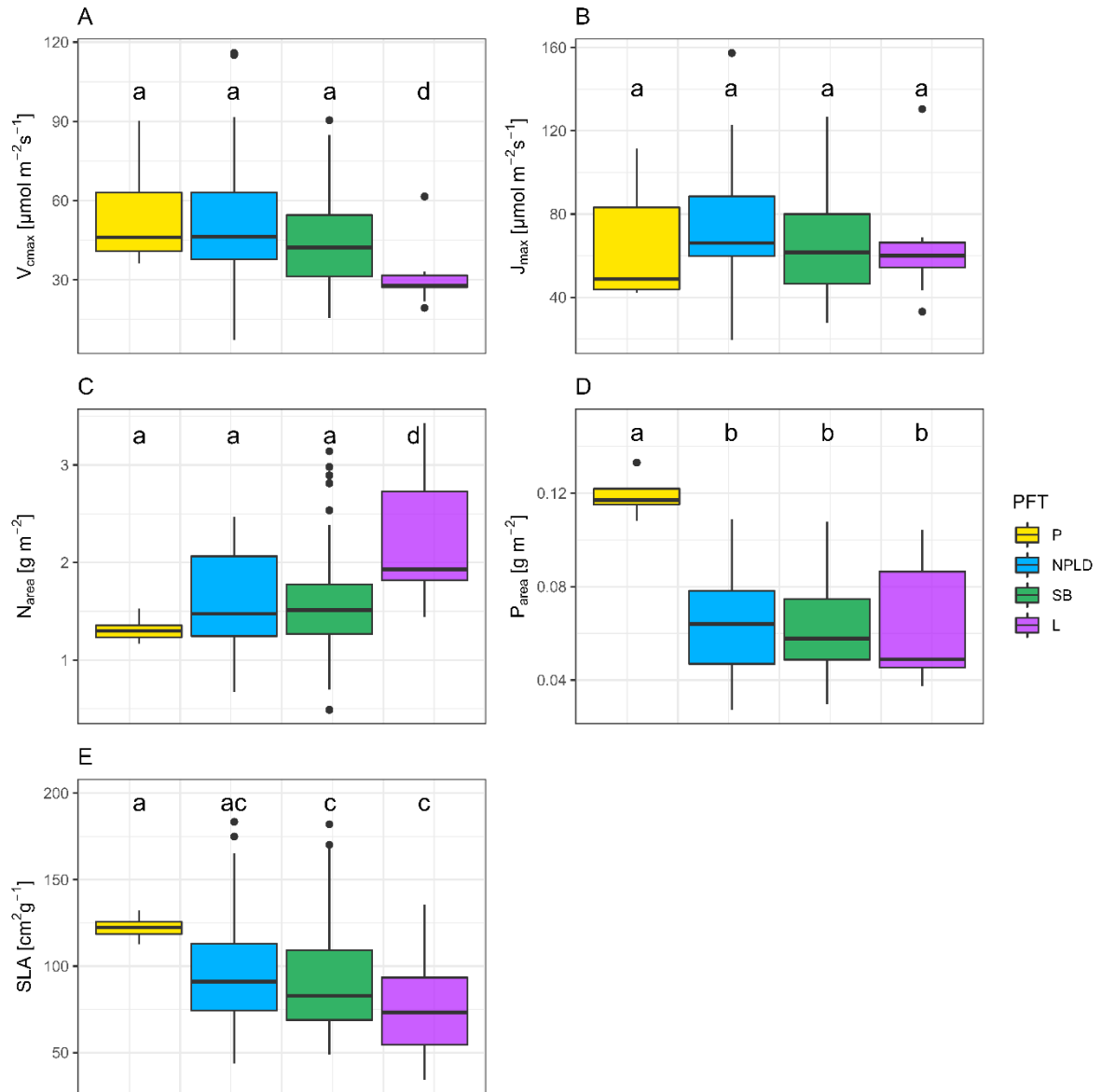


Figure A.1: Five parameters of 25 species, compared between four PFTs – based on light requirement and regeneration – of the sites of Paracou and Nouragues in the Amazon Basin. If the same superscript letter occurs, there is no significant difference between the PFTs (Dunn's test – Holm method). P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, and L = liana. A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

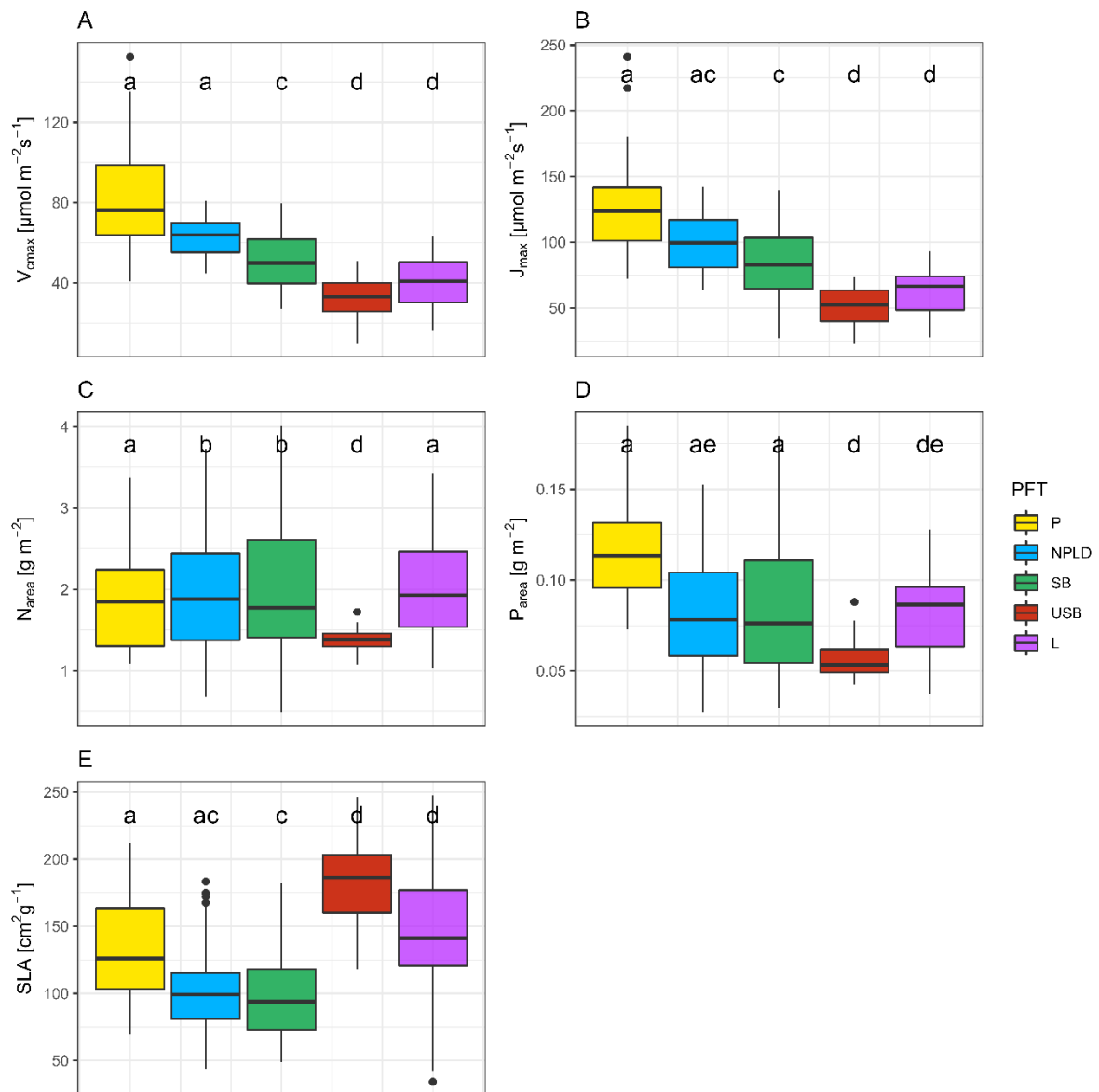


Figure A.2: Five parameters of 23 species, compared between five PFTs – based on light requirement and regeneration – of the Yangambi site in the Congo Basin. If the same superscript letter occurs, there is no significant difference between the PFTs (Dunn's test – Holm method). P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, USB = understory shade-bearing, and L = liana. A) V_{max} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

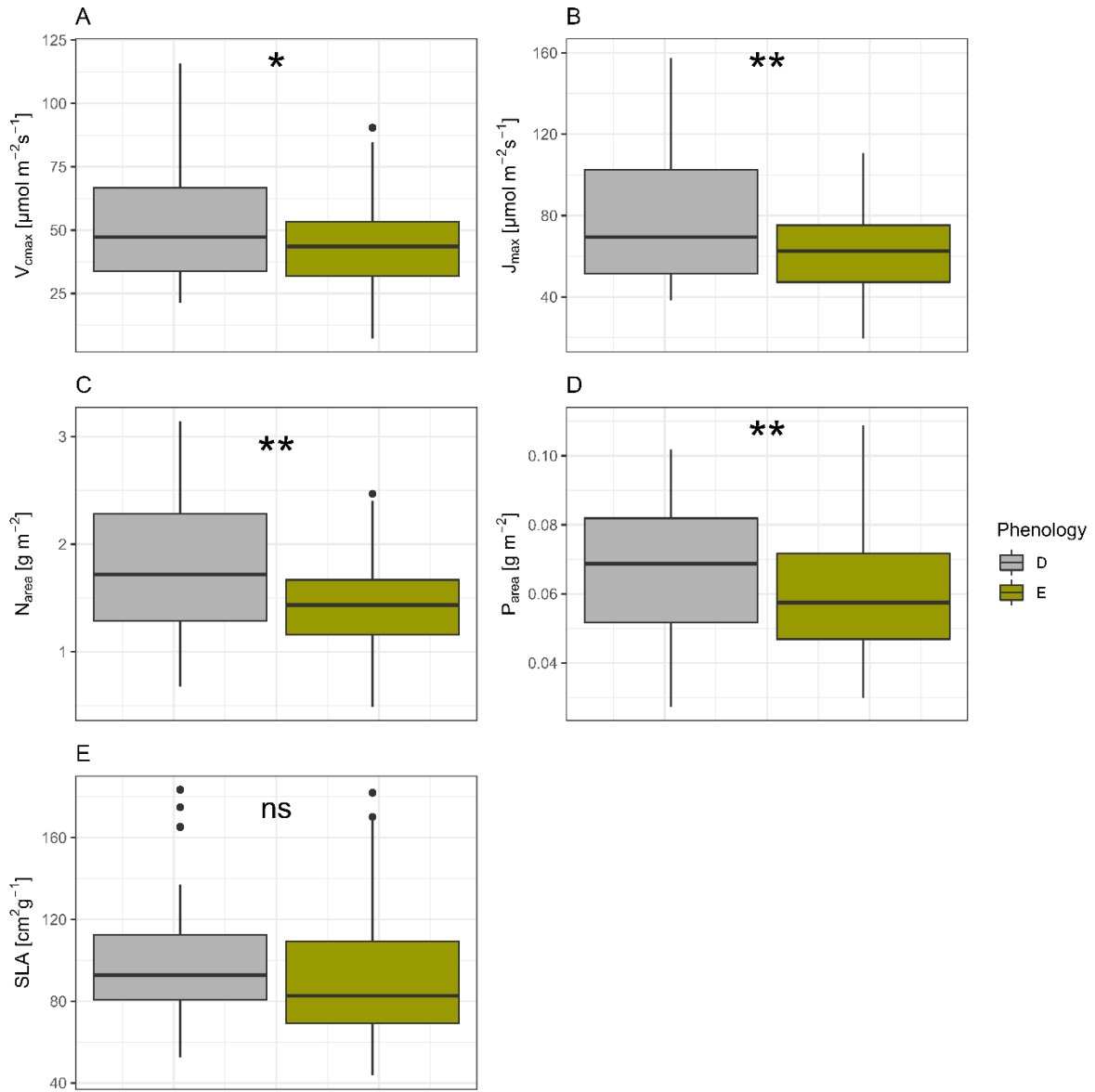


Figure A.3: Five parameters compared between 5 deciduous (D) and 15 evergreen (E) species of the sites of Paracou and Nouragues in the Amazon Basin, with indication of the significant difference level (Wilcoxon signed rank test). A) V_{max} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

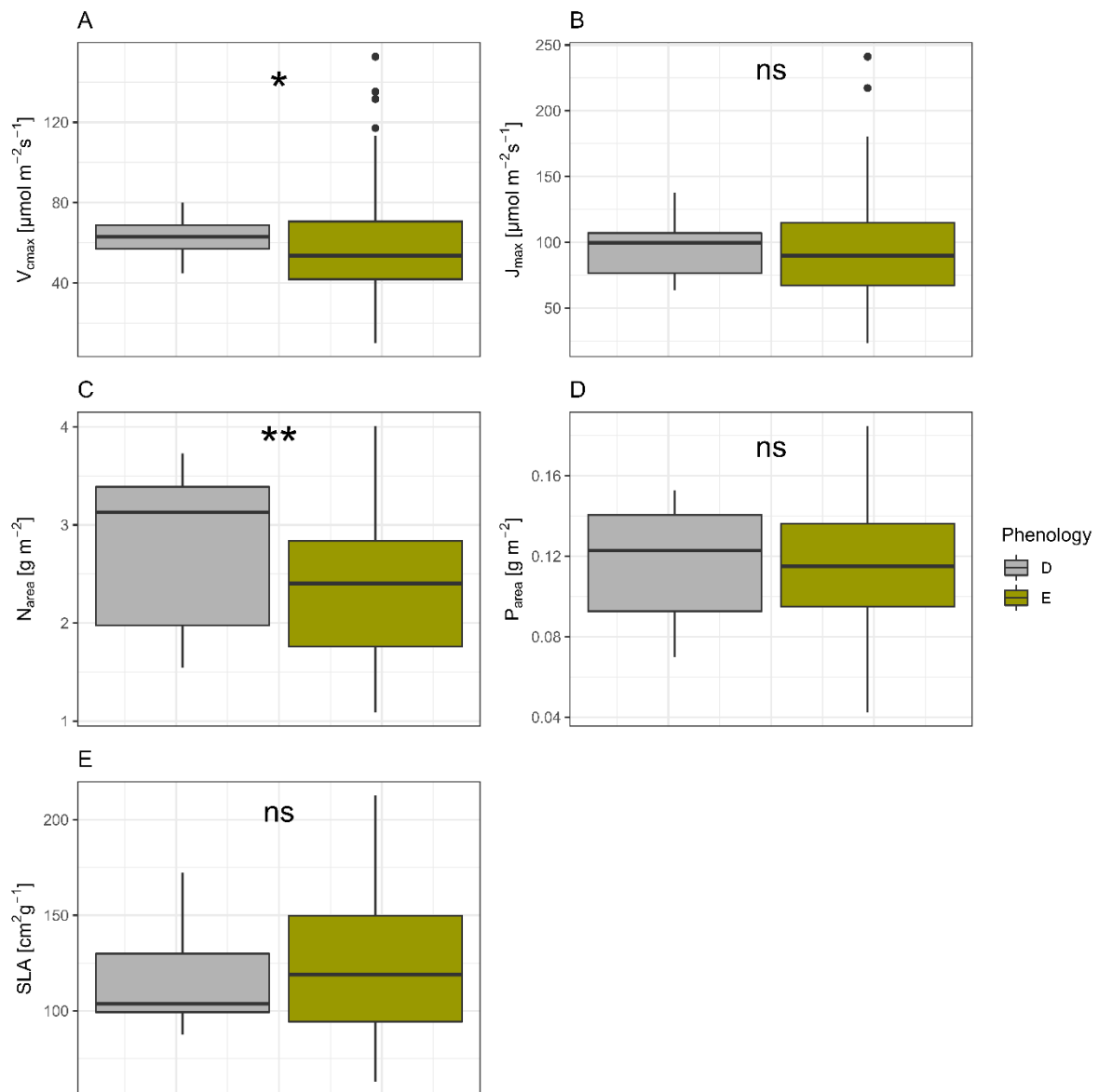


Figure A.4: Five parameters compared between 2 deciduous (D) and 15 evergreen (E) species of the Yangambi site in the Congo Basin, with indication of the significant difference level (Wilcoxon signed rank test). A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

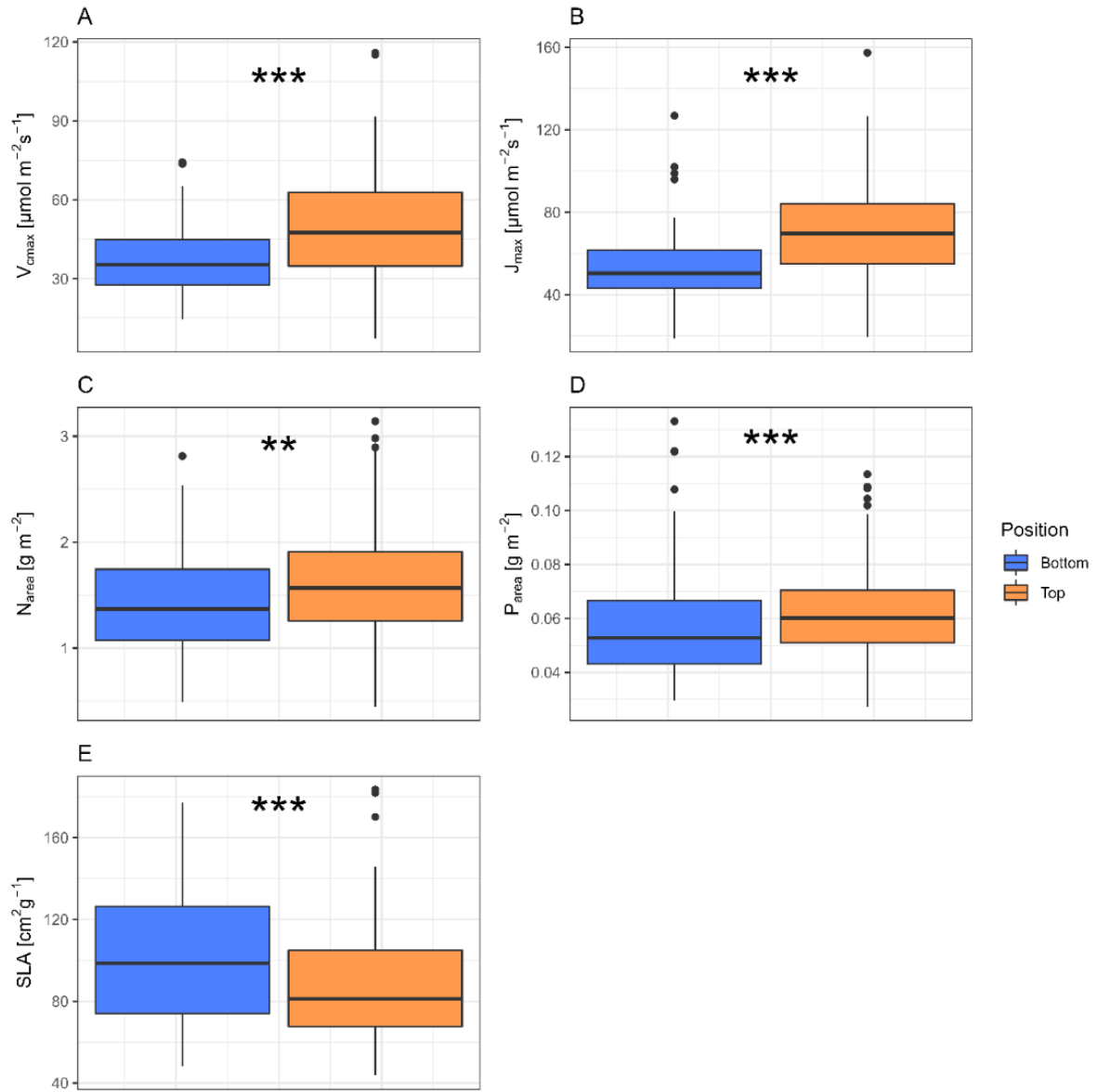


Figure A.5: Five parameters compared between the top and the bottom of the crown for 30 tree species of the sites of Paracou and Nouragues in the Amazon Basin, with indication of the significant difference level (Wilcoxon signed rank). A) V_{max} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

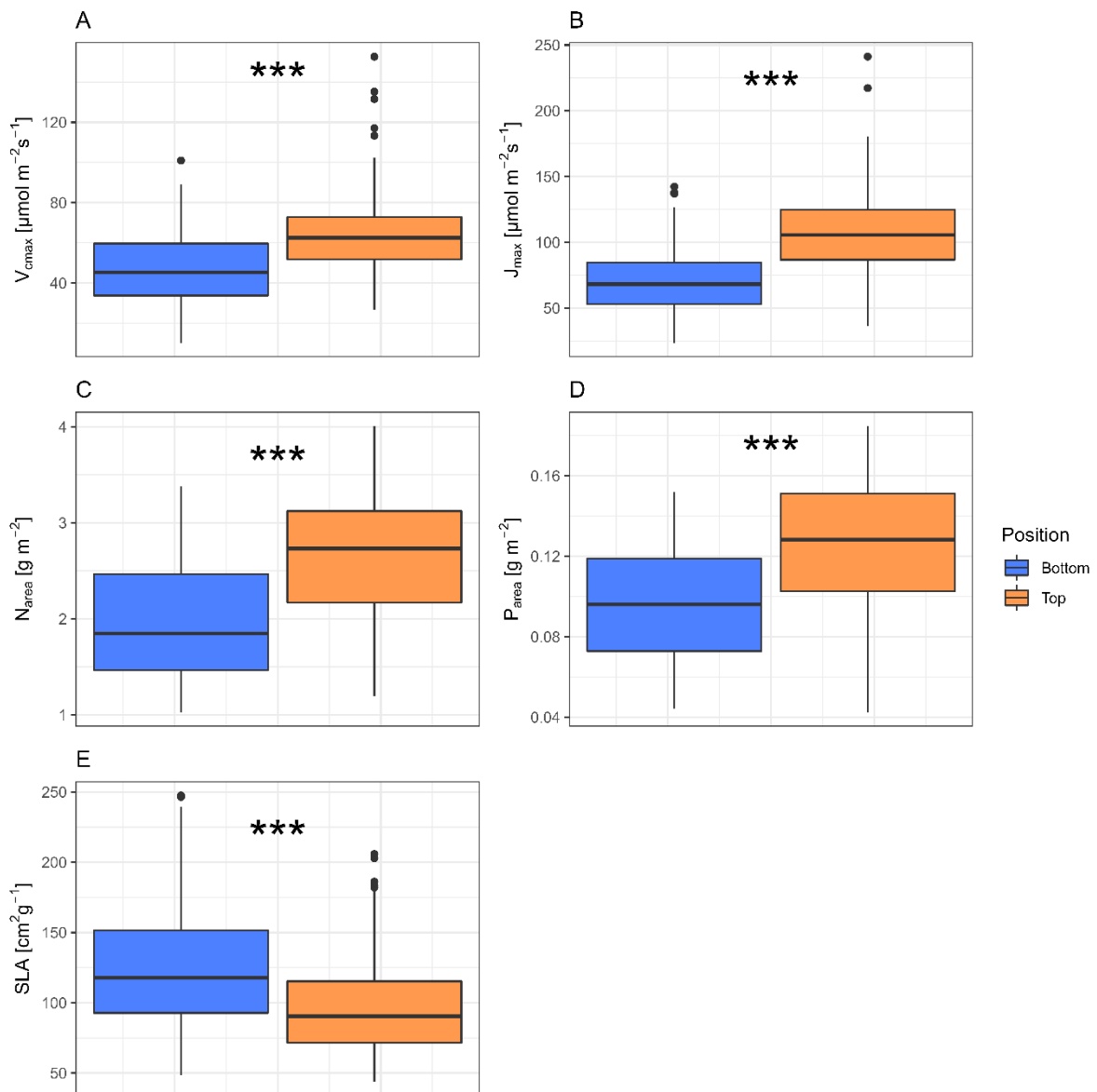


Figure A.6: Five parameters compared between the top and the bottom of the crown for 23 species of the Yangambi site in the Congo Basin, with indication of the significant difference level (Wilcoxon signed rank). A) V_{cmax} , B) J_{max} , C) Area-based leaf N content, D) Area-based leaf P content, E) Specific leaf area

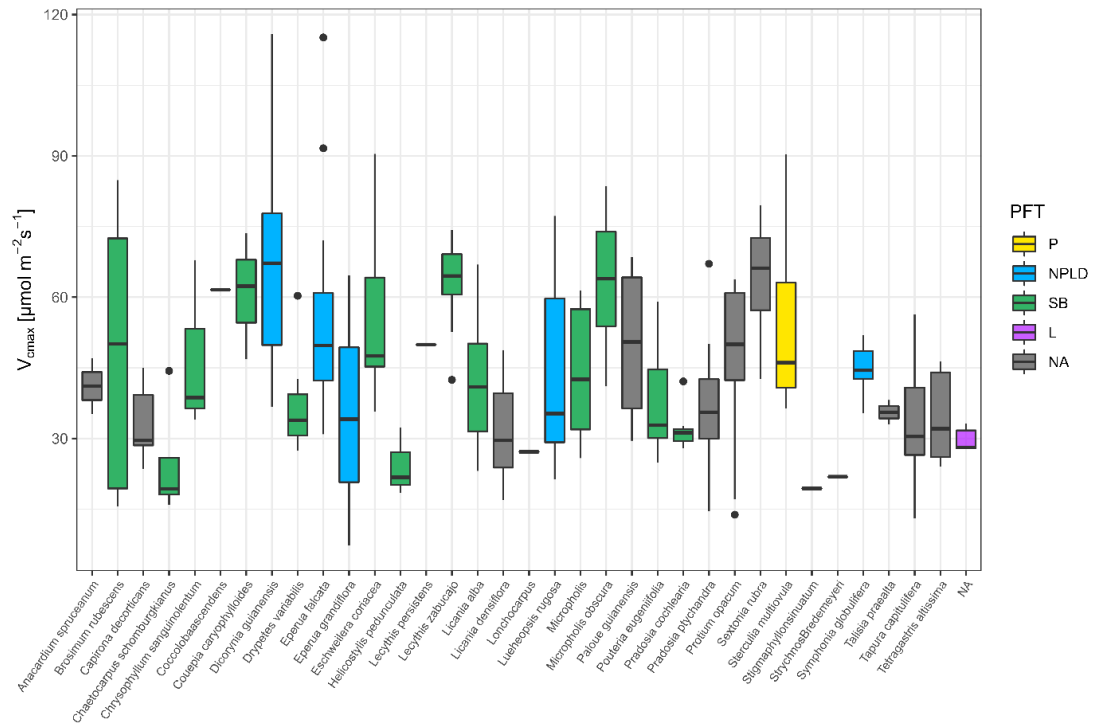


Figure A.7: The maximum carboxylation capacity (V_{max}) of 34 species from the sites of Paracou and Nouragues in the Amazon Basin, with indication of their plant functional type (PFT) – based on light requirement and regeneration. For some species, the PFT could not be identified (NA). For several lianas, the species was not identified (NA). P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, and L = liana

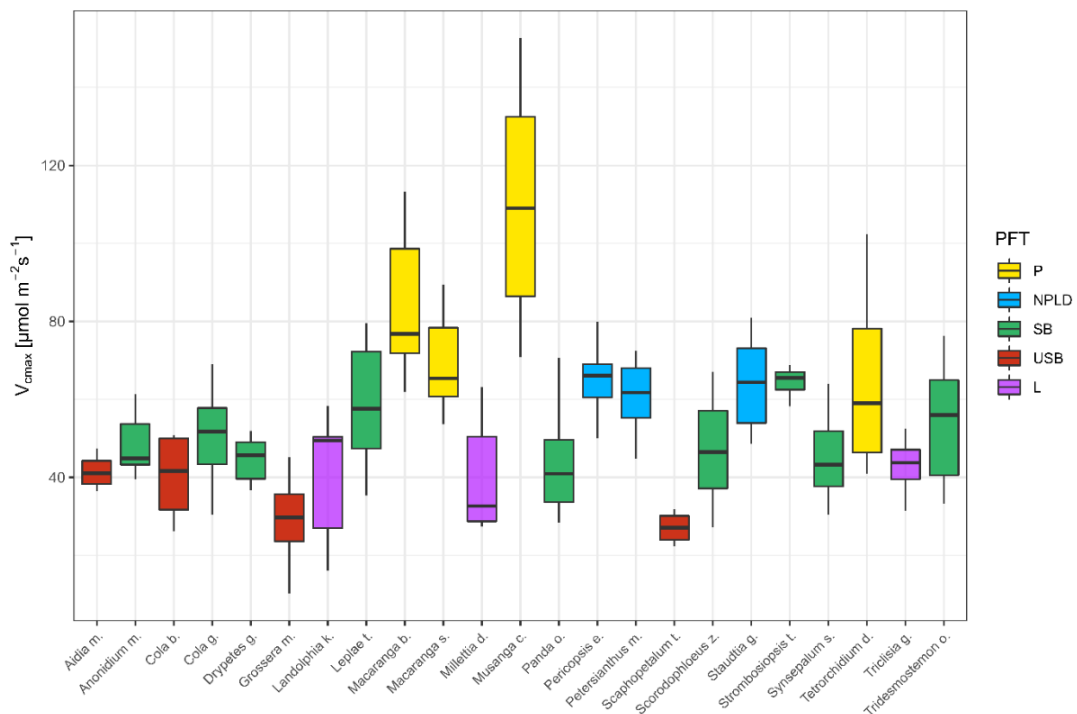


Figure A.8: The maximum carboxylation capacity (V_{max}) of 23 species from the Yangambi site in the Congo Basin, with indication of their plant functional type (PFT) – based on light requirement and regeneration. P = pioneer, NPLD = non-pioneer light demanding, SB = shade bearing, USB = understory shade-bearing and L = liana