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1. ABSTRACT

1.1 Abstract (English)

Climate change is increasingly threatening ecosystems globally, including tropical forests in the Amazonian region. One consequence of the anthropogenic greenhouse effect is the change in the global water cycle, with a growing frequency and intensity of droughts in the tropics. As water availability is a major driver of tree growth in the tropics, the foreseen changes in precipitation are anticipated to provoke substantial declines in tree growth and extensive forest diebacks throughout tropical forests.

Functional characteristics that are involved in the regulation of the plant water budget, specifically water transport, are referred to as hydraulic traits, or more general water relations traits. They are known to play a crucial role in plant stress responses to water scarcity and can thus offer a useful tool to explore the drought resilience of tree species in tropical forest communities. These include leaf hydraulic traits such as minimum leaf conductance (g_{\min}), leaf water potential at full hydration (π_o), relative water content (RWC), and leaf saturated water content (LSWC). Recent research has focused on associations between plant hydraulic traits and commonly measured leaf or stem functional traits in trees. Leaf and wood traits, respectively, are assumed to vary on the axes of traits syndromes, referred to as the leaf economics spectrum (LES) and the stem economics spectrum (SES). Those functional traits can be ranged in a fast-slow continuum, being substantiated by the trade-off between short-term gains and longevity.

In the present study, we therefore measured leaf hydraulic traits and other functional traits in 103 abundant tree species in an old-growth rainforest in French Guiana. The coordination of leaf water relations characteristics with traits representing the LES and SES was investigated by regression analyses and principal component analysis. Additionally, by fitting linear models we tested whether leaf hydraulics have significant explanatory power to predict tree diameter growth and drought-induced mortality. The phylogenetic signal was assessed with Pagel's λ as the quantitative measure of resemblance in closely related species.

The results of this investigation illustrate the tight structural and functional coupling between LSWC and π_o , which shows the inherent dependence of saturated water content to the concentration of solutes (ergo a low π_o). Accordingly, a high π_o implies a high LSWC, which

both represent drought-avoiding strategies in fast-growing species. We further found a strong negative association of RWC and g_{\min} , indicating that this might be driven a simple mechanistic link: if less water is lost after stomatal closure, the mean momentary water content will be generally higher.

The hypothesis that leaf hydraulics are largely decoupled from stem and leaf functional traits could not be verified. As expected, WSG represented an exception to this, being coupled to LSWC, which is due to their functional integration in the fast-slow continuum. Also, laminar thickness (L_{thick}) was positively related to RWC, LSWC and g_{\min} , clearly impacting the capacity of a leaf to hold and retain water.

As suggested, leaf hydraulic characteristics were not significantly related to stem diameter growth rates or mean annual mortality rates. The major finding of this thesis was, that the leaf oxygen isotopic composition ($\delta^{18}\text{O}$) is the main predictor for both, tree species growth and mortality. This likely is due to $\delta^{18}\text{O}$ being an indicator for stomatal conductance, which drives leaf transpiration, plant nutrient uptake, and therefore indirectly influences plant productivity. Hydraulic efficiency stands in conflict with embolism resistance which might explain the role of $\delta^{18}\text{O}$ in mortality. Finally, leaf hydraulics, as well as most nutrient-sourcing traits, exhibited moderate to high levels of phylogenetic conservatism. This indicates that adaptations to water and nutrient availability evolve comparably slowly, and that these traits are subject to stabilizing selection.

1.2 Abstract (Deutsch)

Ökosysteme auf der ganzen Welt werden zunehmend von den Folgen des Klimawandels bedroht, darunter auch die Regenwälder der Amazonasregion. Eine Folge des anthropogenen Treibhauseffekts die Veränderung des globalen Wasserkreislaufs mit einer zunehmenden Häufigkeit und Intensität von Dürreperioden. Da die Wasserverfügbarkeit eine wesentliche Triebkraft für Baumwachstum in den Tropen ist, wird erwartet, dass die prognostizierten Niederschlagsveränderungen das Baumwachstums erheblich beeinträchtigen und so zu einem weitreichenden Waldsterben im gesamten Biom des Amazonas führen.

Funktionelle Traits, die an der Regulierung des pflanzlichen Wassertransportes beteiligt sind, spielen bekanntermaßen eine entscheidende Rolle bei ökologischen Stressreaktionen auf Wasserknappheit und können daher ein nützliches Instrument zur Erforschung der Trockenheitsresistenz von Waldgemeinschaften darstellen. Diese Traits werde allgemein als Wasserverhältnis-Traits bezeichnet, falls sie spezifisch beim Wassertransport involviert sind, werden sie hydraulische Traits genannt. Zu den viel diskutierten Wasserverhältnis-Traits von Blättern gehören unter anderem die minimale Blattleitfähigkeit (g_{min}), das Wasserpotenzial der Blätter bei voller Hydratation (π_0), der relative Wassergehalt (RWC) und der gesättigte Wassergehalt von Blättern (LSWC). Die Forschung konzentriert sich nun zunehmend darauf, Zusammenhänge zwischen der Hydraulik und konventionell gemessenen funktionellen Merkmalen des Holzes und von Blättern zu finden. Es wird davon ausgegangen, dass die Blatt- beziehungsweise Stammmerkmale auf einer Achse konstanter Korrelationen variieren, welche als Blattökonomiespektrum („leaf economic spectrum“, LES) beziehungsweise als Stammökonomiespektrum („stem economic spectrum“, SES) bezeichnet werden.

In der vorliegenden Studie habe ich daher die hydraulischen Eigenschaften der Blätter und andere funktionelle Merkmale von 103 häufig vorkommenden Baumarten in einem, im atlantischen Tiefland gelegenen, Regenwald in Französisch-Guayana gemessen. Die Koordination der blatthydraulischen Eigenschaften untereinander und mit den Merkmalen, welche das LES und SES repräsentieren, wurde mittels PCA und Regressionsanalysen untersucht. Darüber hinaus habe ich mithilfe von linearen Modellen getestet, ob die Blatthydraulik eine signifikante Erklärungskraft für die Vorhersage von Wachstum des

Baumdurchmessers oder die Sterblichkeitsrate hat. Das phylogenetische Signal wurde mit Pagels λ als quantitativem Maß der Ähnlichkeit eng verwandter Arten bewertet.

Die Ergebnisse dieser Untersuchung verdeutlichen den engen strukturellen, aber auch funktionellen Zusammenhang zwischen LSWC und π_o , der die inhärente Abhängigkeit des Wassergehalts von Blättern von einer hohen Konzentration gelöster Stoffe (ergo ein niedriges π_o) zeigt. Eine hohe LSWC impliziert also ein hohes π_o und dies sind beides trockenheits-ausweichende Strategien, die von schnellwachsenden Bäumen angewandt werden. Darüber hinaus fanden wir einen starken negativen Zusammenhang zwischen RWC und g_{min} . Das könnte von dieser simplen mechanistischen Verknüpfung herrühren: wenn bei Trockenheit weniger Wasser verdunstet, führt das auch im Allgemeinen zu einem höheren Wassergehalt im Blatt.

Die Hypothese, dass die Blatthydraulik weitgehend von den nicht-physiologischen funktionellen Merkmalen von Stamm und Blatt entkoppelt ist, konnte nicht bestätigt werden. Erwartungsgemäß ist WSG stark mit LSWC gekoppelt, was erneut auf funktionelle Konvergenz von konservativen Strategien zurückzuführen ist. Auch die Blattdicke (L_{thick}) stand in positiver Beziehung zu RWC, LSWC und g_{min} , denn diese wirkt sich eindeutig auf die Fähigkeit eines Blattes aus, Wasser zu speichern.

Wie vermutet, standen die hydraulischen Eigenschaften der Blätter in keinem signifikanten Zusammenhang mit der Wachstumsrate des Stammdurchmessers oder der mittleren jährlichen Mortalitätsrate. Die wesentlichste Erkenntnis dieser Arbeit war, dass die Sauerstoff-Isotopenzusammensetzung des Blattes ($\delta^{18}O$) sowohl für das Baumwachstum als auch für die Mortalität den wichtigsten und einzig signifikanten Prädiktor darstellt. Dies ist wahrscheinlich darauf zurückzuführen, dass $\delta^{18}O$ ein Indikator für die stomatäre Leitfähigkeit ist, die die Transpiration der Blätter und die Nährstoffaufnahme der Pflanzen steuert und somit indirekt die Pflanzenproduktivität beeinflusst. Dass hydraulische Effizienz im Widerspruch mit hydraulischer Sicherheit, bzw. Embolieresistenz steht, könnte die Beziehung zwischen $\delta^{18}O$ und der Mortalitätsrate erklären. Schließlich wiesen die Blatthydraulik sowie die meisten Merkmale der Nährstoffversorgung ein mäßiges bis hohes Maß an phylogenetischem Konservatismus auf. Dies deutet darauf hin, dass sich die Anpassungen an die Wasser- und Nährstoffverfügbarkeit vergleichsweise langsam entwickeln und dass diese Merkmale einer stabilisierenden Selektion unterworfen sind.

2. GENERAL INTRODUCTION

Ecosystems across the globe are progressively challenged by the destructive impacts of climate change. Alarming, biodiversity loss, that is caused by global warming, is omnipresent and incremental. One major issue is the increase in the frequency and intensity of drought events. Intensified dry periods are a ubiquitous threat that particularly affect forest ecosystems, as drought events have been shown to reduce tree growth and are linked to an increased tree mortality in forests across biomes (Allen et al., 2010; McDowell et al., 2011). By intuition, tropical ecosystems might not seem to be affected acutely by drought events. However, as water availability is one of the primary drivers of tree productivity in the tropics, decreases in annual precipitation and temperature increases are expected to induce fundamental changes in the composition, structure, and biogeography of tropical forests. Various Earth system models foresee substantial declines in the productivity and an incremental dieback of rainforests across the globe (Allen et al., 2010; Wagner et al., 2012).

Amazonian rainforests are the most biodiverse on Earth, hosting about 25 % of all currently existing plant species (Malhi et al., 2008, 2009). The Amazon biome is home to one in ten of all globally known species. Its plant biodiversity has been depicted as the highest on Earth, with an average of approximately 300 tree species (with at least 10 cm diameter) per ha (Gentry, 1988; Silva et al. 2008). Amazonia is an indispensable contributor to the biogeochemical functioning of the Earth. Forests in this region account for about 15 % of global terrestrial photosynthesis, absorbing vast amounts of CO₂, and thus having a crucial impact on the atmospheric carbon cycle. The Amazonian rainforests store about 120 Pg of carbon in their biomass (Field et al., 1998). Through photosynthesis and respiration 18 Pg of carbon per year are processed in this biome, which equals more than twice the annual rate of anthropogenic fossil fuel emissions (Malhi & Grace, 2000 & Malhi et al., 2008). In addition, evaporation and condensation processes in Amazonia are elementary drivers of atmospheric circulation, affecting precipitation not only in South America, but also across the Northern hemisphere (Werth & Avissar, 2002; Malhi et al., 2008). As a consequence, relatively small changes in forest community composition and ecosystem dynamics in the Amazon biome can have substantial effects on the global concentration of atmospheric CO₂ and can thus reinforce the rate of climate change (Malhi & Grace, 2000).

Precipitation changes, especially in the dry season, are assumed to be the most crucial determinant for the fate of Amazonian forests. With decreased rainfall, which is predicted by global climate models (GCMs), the tropical biome is unsustainable and will essentially dry out over the course of the 21st century. Since deforestation intervenes with a forest's air humidity and microclimate, this can exacerbate the effects of aridity and even cause droughts. The Amazon biome has been predicted to reach a tipping point, which will, alongside with deforestation and forest fires, initiate the loss of rainforest cover in the Amazon basin by the year 2100 (Malhi et al., 2009; Staal et al., 2020). If Amazonia dries, as anticipated, the resulting CO₂ emissions and reduced carbon sink strength are likely to accelerate global warming even further (Phillips et al., 2009).

Various studies have revealed that biodiversity in plant communities can be beneficial for ecosystem functioning (Díaz & Cabido, 2001; Tilman et al., 2014). Biodiversity offers several advantages for plant productivity, but also stabilizes the community when environmental disturbances occur. Particularly functional characteristics, which directly impact species' fitness (Violle et al., 2007) are eminently responsible for stabilizing community persistence through various mechanisms. These traits allow insights into functions of different tissues, species strategies and trade-offs, and are thus used to explain variations in species' responses to different environmental stressors. If plant trait diversity is high, at least some species are likely able to withstand a given disturbance, even if others might not survive. More biodiverse communities are also more likely to contain competitors that can compensate each other's functions. In addition, higher biodiversity results in a considerably lower susceptibility to herbivory, disease and pathogens (Mori et al., 2013; Tilman et al., 2014). Taking these findings into account, this principle can also be applied to drought tolerance of tropical rainforest communities.

Functional plant traits related either to water transport, water storage or use contribute to the physiological response that prevent or delay plant desiccation (Blackman et al., 2019; Brodribb, 2009; Choat et al., 2012). These eco-physiological traits are generally referred to as water relations traits, which determine the different drought response strategies and vary strongly across tree species (Blackman et al., 2019). Exclusively, those traits that are involved in plant water transport are referred to as hydraulic traits. A recent global study indeed revealed that a forest's sensitivity to drought decreases with a higher hydraulic trait variation

in trees, but not with that of commonly measured leaf or wood traits (Anderegg et al., 2018). Further investigations revealed that drought survivorship of tree species is closely associated with hydraulic traits (Anderegg et al., 2018; Sapes et al., 2019). This points towards the ability to cope with water scarcity, at tree and community-level, which cannot be inferred from measurements of conventional, soft functional traits. Hydraulic leaf traits, however, have been shown to be tightly associated with tree survival during drought events (Choat et al., 2018), and are assumed to be a potent tool to disentangle questions about the hydraulic functional diversity and the drought susceptibility of tropical tree communities (Blackman et al., 2019; Maréchaux et al., 2015).

During drought, when photosynthesis is reduced, it is advantageous for plants to close their stomata to prevent leaf water loss. However, small amounts of water are still lost through incompletely closed stomata and the cuticle. This loss is called minimum leaf conductance (g_{\min} ; Kerstiens, 1996; Duursma et al., 2019). There is a general consensus that leaf minimum conductance plays an essential role in tree canopy water fluxes and eco-physiological drought responses (Blackman et al., 2016). A higher g_{\min} , meaning that there is more water loss after stomatal closure, is believed to be negatively linked to drought tolerance (Choat et al., 2018; Duursma et al., 2019).

Leaf relative water content (RWC), as well as leaf saturated water content (LSWC), are useful indicators for the water budget of a plant. LSWC represents the maximum potential to store water in a leaf, whereas RWC describes its momentary water status. RWC reflects the balance between leaf water supply and transpiration rate (Lugojan & Ciuca, 2011). A close linkage between LSWC and leaf capacitance has been suggested by various researchers (Blackman et al., 2019; Borchert & Pockman, 2005). Higher leaf capacitance is coupled with longer times before desiccation of a plants tissue, which points towards the significance of LSWC in physiological drought sensitivity (Blackman et al., 2016).

One widely discussed and highly indicative hydraulic trait is leaf osmotic potential at full turgor, i.e., π_0 (Bartlett, Scoffoni & Sack, 2012). Water potential, in principle, represents the tendency of water to move from one place to another. Water generally moves from a site with a more positive water potential (e.g. pure water) to a site with a more negative water potential (e.g. salt solution). π_0 describes the osmotic adjustment in plant cells, which is a crucial mechanism for water conservation under hydraulic stress (Powell et al., 2017).

Essentially, π_o has been shown to be tightly linked to the water potential at turgor loss point (π_{tlp}), which is defined as the accumulation of solutes. π_{tlp} has been used as an indicator for the drought response of plants for decades now (Delzon, 2015), and has proven to be indicative for long-term plant adaptation to water scarcity (Binks et al., 2016). By impacting plant functioning on a molecular and cellular level, π_o is negatively linked to drought tolerance; meaning the lower the π_o the better a tree can deal with water scarcity (Zhu et al., 2018).

Since the measurement of hydraulic traits can be cumbersome and time consuming, researchers have attempted to find short-cuts for estimating the resistance against water stress in trees. Many studies tried to link hydraulic traits with other functional traits, which are more prevalent in previous research and easier to measure (soft plant traits).

The leaf economics spectrum (LES) describes consistent relations between a variety of leaf functional traits. These traits represent a gradient from conservative to resource-acquisitive plant strategies (Reich et al. 2014; Wright et al., 2004). One prevalent representative of the LES is specific leaf area (SLA), indicating how much leaf area a plant builds per biomass. SLA plays an important role in light capture and resource acquisition. Lamina thickness (L_{thick}) is a crucial factor that impacts mechanical strength and resistance to herbivory or disease, while the leaf carbon-nitrogen ratio (C:N) is an indicator for the nutrient use efficiency of a plant and is negatively linked to photosynthetic capacity. Another informative leaf functional trait is the carbon isotope composition ($\delta^{13}C$), which depends on the ratio of intercellular to ambient CO_2 concentrations. Both stomatal conductance and the rate of CO_2 fixation by RuBisCO influence $\delta^{13}C$ substantially (Prieto et al., 2018; Scheidegger et al., 2000; Cherubini et al., 2021). Hence, the leaf carbon isotope ratio serves as a proxy for leaf-level intrinsic water-use efficiency (WUE_i; Seibt et al., 2008). By contrast, the oxygen isotopic composition ($\delta^{18}O$) of leaf material is inversely related to the ratio between the intercellular and ambient water vapour and is thus strongly impacted by stomatal conductance. This makes the leaf oxygen isotopic ratio a useful proxy measure of stomatal conductance and transpiration (Barbour & Farquhar, 2000; Barbour, 2007, 2017). To our knowledge, the relationship of $\delta^{18}O$ with plant water relations and drought resilience strategies has not been investigated thoroughly. Hence, the role of $\delta^{18}O$ in plant dry-down as well as its contribution to the fast-slow continuum still require further elucidation.

Wood traits have been shown to co-vary in a comparable manner along one single axis of trait variation, that has been termed the stem economics spectrum (SES; Baraloto et al., 2010a). Wood specific gravity (WSG), i.e. the ratio of wood density to that of water at 4 °C, relates to biomechanical strength and resistance. In a comparable way bark thickness, B_{thick} , is decisive for mechanical stability and defence against predators and pathogens. The SES has been shown to be orthogonal to the axis of the LES, suggesting that trade-offs operate independently on stem and leaf levels (Baraloto et al., 2010; Fortunel et al., 2012). The previous findings of researchers point towards the fact that hydraulic traits are equally decoupled from leaf and wood economics (Blackman et al., 2016; Li et al., 2015; Maréchaux et al., 2019). One exception for this is wood density, which has been proven to relate to several hydraulic characteristics, such as LSWC and π_0 (Ishida et al., 2008), by regulating whole-plant water transport and consequently interfering with leaf hydraulic status.

In principle, trait coordination is assumed to arise from two distinct mechanisms. If traits have a genetic basis in common, they are structurally coordinated. Traits are functionally coordinated if they were co-selected in a certain habitat, however, they can be structurally unrelated (Sack et al., 2003). This pattern, where an environmental filter selects for specific traits independently, is also referred to as concerted convergence (Bartlett et al., 2016). Although correlations between leaf hydraulic traits and with other functional trait dimensions have been investigated (Ishida et al., 2008; Li et al., 2015; Blackman et al., 2016; Santiago et al., 2018), a more precise elucidation of how leaf hydraulic traits are coordinated in tropical forest communities and whether they interact with other functional trait spectra, is lacking and hence imperatively required.

There is an apparent trade-off between survival and growth, as plants have been shown to either maximize productivity or prioritize to invest in longevity and persistence (Rüger et al., 2018). If trees invest in the construction of costly and long-lived tissue, which comes with greater C and time investments, these slow strategists are more susceptible to rapid environmental changes (Brodribb et al., 2020). This underpins the existence of a fast-slow continuum that has been postulated previously (Rosas et al., 2021): Accordingly, as fast-growing species should have a high water-transport capacity they can acquire nutrients quicker, which results in higher leaf nutrient concentration (Chave et al., 2009; Li et al., 2018; Reich, 2014; Sack et al., 2013). However, since these species grow rapidly, they tend to

produce more short-lived leaves with a higher leaf area per dry mass. Fast strategists are thus assumed to be less tolerant to environmental stressors such as resource scarcity, shade or herbivory (Reich, 2014; Sack et al., 2013). Slow-growing species, in contrast, are resource-conservative, develop thicker leaves, which are more durable and resistant, but also have a lower nutrient concentration (Wright, 2004).

This concept was taken one step further by incorporating hydraulic traits into the fast-slow continuum (Sterck et al., 2011; Zhu et al., 2018), coming to the conclusion that fast-growing species exhibit traits that make them less drought tolerant. A rather weak relation between leaf functional traits, such as SLA, and growth rates was shown by R uger et al. (2012), who thus claimed that leaf traits are not suitable for modelling tropical tree growth. Wood traits, on the other hand, exhibit an inextricable link to growth, which holds true across taxa (Reich, 2014). Since WSG represents a trade-off between volumetric growth and mechanical strength, it is not surprising that the trait has been shown to be strongly inversely related to relative and absolute growth rates (Chao et al., 2008; R uger et al., 2012; Kleinschmidt et al., 2020; Rosas et al., 2021). A similar approach was used by Oliveira et al. (2021), who found a trade-off between growth rates and hydraulic safety. They justified this functional compromise with the fact that acquisitive (fast-risky) species need to maintain high photosynthetic rates that require high stomatal conductance and high hydraulic conductivity within the stem, which on the other hand makes them more vulnerable to hydraulic failure. Furthermore, Qi et al. (2021) found that stomatal conductance (g_s) was tightly linked to stem diameter growth, which is explained by the interrelation of g_s with the overall plant water potential. Thus, water transport rates in the xylem and consequently plant productivity and growth depend on g_s . By investigating trait-growth relationships across species for $\delta^{13}C$ and π_{tip} , among other traits, Rosas et al. (2021) did not detect any significant correlations. This was attributed to the fact that growth is a process regulated at the whole-plant level, governed by the interplay of various organs and the trade-off of several functional traits differing between organs. These findings highlight that single water relations traits are not predictive for tree growth across species and environments, and that explanatory approaches combining the effects of multiple functional traits are required to advance this field.

The elaboration of predictive models for climate-induced tree mortality was the subject of numerous papers (McDowell et al., 2011; Anderegg et al., 2016; Hartmann et al., 2018).

Functional traits, such as wood density or maximum tree height, have a strong explanatory power in predicting tree survival (Aubry-Kientz et al., 2013). By revealing a strong negative correlation between whole-plant volumetric water content and drought-induced tree mortality Sapes et al. (2019) proved that hydraulic traits play an essential role in tree survivorship. This was attributed to the inherent link between leaf water content and the irreversible turgor loss, which causes wilting and cellular damage, as a higher water content offers more time before leaf desiccation. Nevertheless, the elucidation of how other plant hydraulic traits, and generally the leaf hydraulic dimension, affect tree death is still needed.

Hydraulic traits are key for plants to adapt to contrasting environmental conditions, which is why they are subject to strong selective pressure (H. Liu et al., 2015; Sanchez-Martinez et al., 2020). A significant phylogenetic signal implies that closely related species have more similar trait values than would be expected by chance (Losos, 2008). One relatively simple method to assess the phylogenetic signal of species traits is to calculate Pagel's λ (Pagel, 1997). Under Brownian motion, phylogenetic relationships predict the covariance among taxa for trait values perfectly. In such a case the expected value of λ is one. If a trait is not phylogenetically dependent, demonstrating phylogenetic relationships between taxa do not predict the trait covariance, λ of this trait is expected to be zero (Freckleton et al., 2002). Phylogenetic niche conservatism means that related species are more similar than would be expected under Brownian motion evolution (Losos, 2008; Münkemüller et al., 2012; Pavoine & Ricotta, 2013). However, most ecologically relevant traits have a phylogenetic signal below this threshold (Molina-Venegas & Rodríguez, 2017). Previous analyses on drought-related eco-physiological traits, namely π_{tip} and g_s , and other leaf and stem traits demonstrated the phylogenetic signal in functional traits (Liu et al., 2015). In fact, high levels of phylogenetic dependence were revealed in stem and leaf traits of sub-tropical tribes of Magnoliaceae, including SLA, leaf nitrogen content and wood density. Hydraulic traits turned out to be moderately dependent on phylogeny, as opposed to photosynthetic traits or plant water use efficiency, which seem to be phylogenetically independent. These findings were attributed to the fact that photosynthetic traits represent quick responses to environmental cues, whereas traits related to nutrient and water use are shaped by stabilizing selection in contrasting habitats and gradual co-adaptation among multiple functional traits. However, questions about phylogenetic dependencies in hydraulic traits have remained largely unexplored.

3. MANUSCRIPT

*"Leaf hydraulic traits and eco-physiological drought responses of trees
in a hyper-diverse tropical rainforest in French Guiana"*

3.1 List of abbreviations

B_{thick}	(trunk) bark thickness
C_o	equilibrium solute concentration
CIRAD	centre de coopération internationale en recherche agronomique pour le développement (fr., international research centre for agronomic development)
cg	centigram
C_{leaf}	leaf capacitance
DGR	(annual) diameter growth rate
DT	drought tolerance
DW	(leaf) dry weight
$\delta^{13}\text{C}$	(leaf) carbon isotope ratio
$\delta^{18}\text{O}$	(leaf) oxygen isotope ratio
e.g.	exempli gratia (lat., for example)
EcoFog	Écologie des Forêts de Guyane (fr., ecology of French Guianese forests)
et al.	et alia (lat., among others)
FW	(leaf) fresh weight
GCM	global climate model
g_{min}	minimum leaf conductance
g_s	(leaf) stomatal conductance
i.e.	id est (lat., that is)
IRMS	isotope ratio mass spectrometer
kPa	kilo Pascal
LMA	leaf mass per area
LSWC	leaf saturated water content
L_{thick}	laminar thickness
λ	Pagel's Lambda
m	(annual) mortality
MPa	mega pascal
n	number of observations
π_o	(leaf) osmotic potential at full hydration
π_{tlp}	(leaf) osmotic potential at turgor loss point
PCA	principal component analysis
Pg	petagram = 10^{15} g
RWC	(leaf) relative water content
SLA	specific leaf area
SW	(leaf) saturated weight
t	time, measurement interval
TC-EA-IRMS	thermal conversion - elemental analyser - isotope ratio mass spectrometer
VPD	vapour pressure deficit
VP_{sat}	saturated water vapour pressure
WSG	wood specific gravity
WUEi	intrinsic water use efficiency

3.2 Introduction

The negative impacts of climate change are increasingly threatening terrestrial ecosystems across the globe. One negative consequence of the anthropogenic greenhouse effect is the increasing frequency and intensity of droughts. As water availability is one of the main drivers of tree productivity in tropical rainforests, the changes in precipitation foreseen by global climate models (GCMs) are anticipated to provoke substantial declines in tree growth and extensive forest diebacks throughout the tropics (Allen et al., 2010; McDowell et al., 2011). Even though Amazonian rainforests might not intuitively seem to be threatened by the decrease of precipitation, they have been predicted to reach a tipping point. This will eventually initiate large losses of rainforest cover in the Amazon basin over the course of the 21st century (Malhi et al., 2009; Staal et al., 2020). This would have major consequences for the global carbon cycle, accelerating global warming even further.

Functional traits that are related to plant water budget contribute to the eco-physiological response to drought and help with the prevention of plant desiccation (Brodribb, 2009; Choat et al., 2012; Rosas et al. 2021). These traits are generally referred to as water relations traits, which define different drought response strategies and vary strongly across species (Blackman et al., 2019). Exclusively those traits being involved in water transport, are so-called hydraulic traits. A recent global study revealed that a forest's sensitivity to drought decreases with a higher hydraulic trait variation in trees, but not with that of commonly measured leaf or wood traits (Anderegg et al., 2018). This highlights that hydraulic leaf traits are associated with tree survival during drought events (Choat et al., 2018; Sapes et al., 2019) and that they are potent measures to disentangle functional diversity responses to drought in tropical tree communities (Blackman et al., 2019; Maréchaux et al., 2015).

During drought, plants close their stomata to prevent water loss which causes a decline in photosynthesis. However, small amounts of water are still lost through incompletely closed stomata and through the cuticle. This loss is referred to as minimum leaf conductance (g_{min} ; Kerstiens, 1996; Duursma et al., 2019). A lower g_{min} , indicates that there is less water loss after stomatal closure, hence it was suggested to be negatively linked to drought tolerance (Choat et al., 2018; Duursma et al., 2019).

Leaf relative water content (RWC) as well as leaf saturated water content (LSWC) are useful indicators for the water budget of a plant. LSWC represents the maximum capacity to store water in a leaf, defined by the ratio of saturated leaf water to dry weight, whereas RWC depicts the momentary water status of a leaf (Lugojan & Ciulca, 2011). Higher LSWC values are frequently associated with increased drought tolerance (Binks et al., 2016).

Another widely discussed hydraulic trait is leaf osmotic potential at full turgor π_0 (Bartlett, Scoffoni, & Sack, 2012). As water potential, in principle, stands for the tendency of water to move from one place to another, it represents a crucial mechanism for water conservation under hydraulic stress (Powell et al., 2017). It has been used as a negative correlate for drought response for decades (Delzon, 2015), meaning the lower the π_0 the better a tree can deal with water scarcity (Zhu et al., 2018).

The leaf economics spectrum (LES) describes consistent relationships between leaf functional traits. These traits represent a gradient from conservative to resource-acquisitive plant strategies (Reich et al. 2014; Wright et al., 2004). Prevalent representatives of the LES are the specific leaf area (SLA), laminar thickness (L_{thick}) and the leaf C:N, which are strongly dependent on leaf longevity and photosynthetic as well as respiratory rates. Another informative leaf functional trait is the carbon isotope signature ($\delta^{13}\text{C}$), an indicator for leaf-level intrinsic water-use efficiency (iWUE; Seibt et al., 2008), which we therefore considered as a water relations trait. By contrast, the leaf oxygen isotopic composition ($\delta^{18}\text{O}$) has been used as a proxy for stomatal conductance and transpiration (Barbour & Farquhar, 2000; Barbour, 2007, 2017), which are potentially indicative for the hydraulic performance of plants. To our knowledge, the relationship of $\delta^{18}\text{O}$ with plant water relations and drought tolerance strategies has not been investigated thoroughly.

Wood traits have been shown to covary in a comparable manner along one single axis of variation, which has been described as the stem economics spectrum (SES; Baraloto et al., 2010a). Wood specific gravity (WSG) and bark thickness (B_{thick}) are decisive for mechanical stability and defence against predators and pathogens. The SES has been shown to be orthogonal to the axis of the LES, suggesting that trade-offs operate independently on stem and leaf levels (Baraloto et al., 2010; Fortunel et al., 2012). Some previous findings pointed towards plant hydraulics being equally decoupled from the leaf and wood economics spectrum (Blackman et al., 2016; Li et al., 2015; Maréchaux et al., 2019). However, there is a

general disagreement on this matter. Wood density, for instance, has been demonstrated to be strongly linked to several plant hydraulic characteristics (Ishida et al., 2008) by regulating whole-plant water budget by interfering with water capacitance (Chave et al., 2009; Christoffersen et al., 2016) and consequently being linked to leaf hydraulic status.

There is an apparent trade-off between plant survival and growth, as plants have been shown to either maximize short-term gains or invest in persistence (Rüger et al., 2018), which underpins the existence of the fast-slow plant continuum. If trees invest in the construction of nutrient-poor but durable tissues, which require larger investments in terms of energy, carbon and time, these 'slow-safe-strategists' are then more susceptible to rapid environmental changes (Reich, 2014). Accordingly, fast-growing species have a high instantaneous nutrient acquisition (Méndez-Alonzo et al., 2012), building nutrient-rich but comparably short-lived tissues. These species can grow more effectively while investing the same amount of C than species on the slow end of the spectrum, by producing lower WSG and thinner leaves. In turn fast-strategists are more susceptible to environmental stressors, such as resource scarcity or herbivory (Chave et al., 2009; Li et al., 2018; Reich, 2014; Sack et al., 2013). It thus seems intuitive, that fast-strategists have been found to be drought-avoiding in contrast to slow-strategists being drought-tolerant (Méndez-Alonzo et al., 2012).

The prediction of demographic dynamics, such as tree mortality and tree growth rates has been the subject of various investigations (McDowell et al., 2011; Anderegg et al., 2016; Hartmann et al., 2018). Leaf functional traits have generally proven to be weak predictors for growth rates as well as tree death (Rosas et al., 2021; Rüger et al., 2012). Wood density, on the other hand, has been shown to be strongly inversely related to relative growth rates (Chao et al., 2008; Rüger et al., 2012; Kleinschmidt et al., 2020; Rosas et al., 2021). Nevertheless, a more detailed elucidation on how other leaf water relations traits, as well as leaf isotopic compositions, affect tree growth and mortality is still required.

Hydraulic traits are key for plants to adapt to contrasting environmental conditions, which is why they are assumed to be subjected to strong selective pressure (Liu et al., 2015; Sanchez-Martinez et al., 2020). The phylogenetic signal can be used to assess whether closely related species have more similar trait values than there would be expected by chance. In previous studies, hydraulic traits turned out to be moderately to strongly dependant on phylogeny (Liu et al., 2015). These findings were explained by the fact that traits related to water availability

are shaped through stabilizing selection. However, questions about phylogenetic influence on leaf hydraulic traits have remained largely unanswered.

Hypotheses/Research questions

Given that drought events are forecasted to become more frequent and more severe with climate change, a holistic understanding of eco-physiological drought responses in tropical tree communities is urgently required. Disentangling the relationship of hydraulic traits among each other, but also with the leaf and stem economics spectra, as well as inspecting their linkage with plant demographic processes will contribute considerably to the understanding of tropical forest ecosystems and eventually support their conservation. The aim of this study therefore was to examine **1a)** the coordination between hydraulic traits of 114 abundant tree species in an old-growth rainforest in French Guiana. **1b)** The coordination between leaf water relations traits and traits representing the leaf and stem economics spectrum will be assessed. **2)** Furthermore, we set out to build a model to predict mean annual species stem diameter growth (DGR) by incorporating functional traits of different functional dimensions. **3)** We tested whether mean annual species tree mortality (m) can be explained by a combination of functional traits. **4)** Finally, we analysed the phylogenetic signal in leaf hydraulic traits in comparison to other functional traits across species.

We hypothesized that following, **1a)** that species mean hydraulic traits show a typical trade-off. More specifically, we expected no correlation between g_{\min} and π_0 , assuming that these traits vary independently from each other, which corresponds to the findings of Marechaux et al. (2019). In contrast, π_0 and LSWC will be tightly linked, as fast-risky strategists tend to be drought-avoiding (Méndez-Alonzo et al., 2012), which implies that they have a high LSWC as well as a high π_0 . Trees on the slower end of the spectrum, however, are drought tolerant, which becomes manifest by both, low LSWC and low π_0 .

In **H1b)** we speculated that the leaf hydraulic dimension is decoupled from other functional trait syndromes, such as the leaf and stem “soft” traits, indicating that hydraulic traits cannot be inferred from commonly measured leaf or stem traits (Maréchaux et al., 2019). However,

we expected that WSG represents an exception to this, being closely linked to stem water capacitance and hydraulics.

H2) Furthermore, leaf hydraulic traits do not substantially explain the variation in mean tree annual growth. We expected that a combination of (soft) functional traits will weakly predict tree growth, with WSG negatively and dominantly explaining tree growth patterns.

H3) Mean annual mortality can only be poorly explained by leaf hydraulic traits, as drought induced mortality only explains a small fraction of overall tree mortality. High π_o is an indicator for drought-avoidance, high LSWC and lower $\delta^{18}\text{O}$ or g_{\min} provide more time before leaf desiccation, all potentially decreasing the probability of tree death during dry periods. Thus, we hypothesise that those traits potentially act in concert, having a moderate influence on tree mortality.

H4) Leaf hydraulic traits and traits involved in nutrient acquisition display substantial phylogenetic signal in comparison with leaf morphological traits. Correspondingly, we assumed that leaf $\delta^{13}\text{C}$ and SLA are non-conserved across the phylogeny, whereas nutrient sourcing traits (leaf C:N) leaf hydraulic traits and leaf $\delta^{18}\text{O}$ should have comparably strong phylogenetic signals.

3.3 Material & Methods

Study site

The fieldwork was conducted in a tropical rainforest located in the Atlantic lowlands of French Guiana. With the dominance of Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae, the floristic composition at the site is that of a typical Guianan rainforest (Rutishauser et al. 2016). On average 150 - 220 tree species (with more than 10 cm diameter at breast height) can be found per hectare.

Sampling was carried out at the Paracou experimental site ($5^{\circ}16'26''\text{N}$, $52^{\circ}55'26''\text{W}$), managed by CIRAD (2016) through the joint research unit EcoFog. The experimental site (see Figure 1) is part of the Guyafor network, which is dedicated to long-term monitoring of tropical forest biodiversity and dynamics (Jolivot et al., 2008; Guyafor Database, 2017). As outlined in Figure 2, trees were randomly sampled from thirteen 6.25-ha plots, which are either disturbed through selective logging (plot 3, 4, 5, 7-9 & 12) or control plots covered by old-growth forest (plot 1, 6, 11 & 13- 15).



Figure 1: Typical aspect of the study site at Paracou Research Station. Lowlands (left), as photographed here facing slightly upwards, have a distinct structure, appearance and tree species composition compared to plateaus (right).

The site comprises an old-growth wet tropical forest with small hills, plateaus, and slopes as well as valleys, which are seasonally inundated (see Figure 2). The research site is characterized by a mean annual air temperature of 26°C with an annual range of 1 to 1.5 °C (CIRAD, 2016). A mean annual rainfall of 3,041 mm was recorded at Paracou, with a minimum in September and a maximum in May. Typically, a long dry season occurs mid-August to December. In addition, a shorter dry season usually occurs in March. Precipitation can be less than 50 mm/month during these periods (Aguilos et al., 2019).



Figure 2: Schematic outline of sampled plots at the Paracou Research Station (left) and locations of the sampled individuals including topographic levels (valley, slope and plateau; CIRAD, 2016), created with ArcGIS Pro (ESRI, 2010).

Sampling design

With an annual - biennial tree census at the experimental site, all trees ≥ 10 cm in diameter at breast height have been tagged, mapped, and identified to species level since 1984. For this project we selected the 114 most important tree species, based on total basal area. In cooperation with the Metradica project (Boisseaux et al., unpublished data), we sampled 114 co-occurring tree species, of which 103 species with at least three replicates were selected (see Appendix, Table 1). Those species belong to 86 genera and 37 plant families. To

standardize trees according to light availability, we chose individuals with a Dawkins' Index of 2 – 4 (Dawkins, 1958). This means that trees which get either some natural light, partial upper lighting or even complete upper lighting were sampled exclusively (see Appendix, Figure 1). Before sampling, suitable trees were located and pre-checked in terms of accessibility, their Dawkins' Index, as well as their overall health status.

Sampling

Depending on prevalence, three to 29 replicates were sampled per tree species, respectively. Healthy and partially sunlit branches were collected with a BigShot slingshot. The acquired branches were screened for diseases and damage and heavily impaired or diseased ones were rejected. Branches were re-cut to smaller sprigs, containing three to five leaves, for re-saturation. A pre-selection of leaves for subsequent measurements was performed, taking age, health status, and potential fractures into account. Only fully developed, but not senescent leaves, with no severe signs of disease or herbivory were selected. Leaf samples were instantly placed into pre-labelled Ziploc bags with wet towel papers and stored in dark cooling boxes until being processed further in the lab. Dawkins' indices of the trees as well as the respective branch, recorded the tree ID number, as well as weather conditions at the time of sampling, and supplementary comments were noted on a field data sheet.

Trait measurements

We here subsume the following properties as leaf hydraulic traits: minimum leaf hydraulic conductance (g_{min}), leaf saturated water content (LSWC), osmotic potential at full saturation (π_o), and relative (leaf) water content (RWC). The other traits are related to the leaf economics spectrum und the stem economics spectrum, see Table 1.

Leaf minimal conductance and leaf area

Following the protocol of Sack et al. (2003) g_{min} was estimated in the following manner: Firstly, an intact and re-hydrated leaf was selected per individual. The petiole was cut off and instantly covered with nail polish to avoid water loss through the petiole. The initial weight of

the leaf was measured with a precision balance and noted with a precision of 0.0001 g in an excel sheet, changes recorded with time, as well as room temperature and air humidity at the measurement time point. The leaf was then placed with the adaxial side facing down onto a grid above a ventilator. After 30 minutes the leaf was weighed again and put under the ventilator. This was repeated every 30 minutes for at least 3.5 h to monitor the leaf water mass loss over time.

The saturated water pressure (VP_{sat} , in kPa) was estimated through the mean measured temperature (T) in degrees Celsius according to the Arden Buck equation (Buck, 1996):

$$VP_{sat} = 0.61121 \times \exp \exp ((18.678 - 234.5) T \times (257.14 T + T))$$

The vapor pressure deficit (VPD) was then calculated, using VP_{sat} , the atmospheric pressure (101.3 kPa, P_{atm}) and the mean relative humidity (RH):

$$VPD = \frac{VP_{sat}}{P_{atm}} \times \left(1 - \left(\frac{RH}{100} \right) \right)$$

Between leaf weight measurements, every leaf was scanned, and the leaf area (cm²) was calculated with the aid of the ImageJ software (Schneider et al., 2012). The following formula was employed to estimate g_{min} :

$$g_{min} = \frac{-\Delta \text{ leaf mass}}{\Delta \text{ time} \times 60} \times \frac{1}{VPD} \times \frac{1000}{18} \times \frac{10\ 000}{\text{leaf area} \times 2}$$

Leaf relative water content and leaf saturated water content

During sampling one leaf per individual was instantaneously put into a pre-weighed Zip-Loc bag, to avoid weight loss caused by transpiration during transport. The samples were weighed in the bags (FBW). To calculate leaf fresh weight (FW), bag weight was subtracted from FBW. The fresh leaves were instantly wrapped into paper towels that had been soaked with de-ionized water. For saturation, the soaked leaves were kept for 24 h in the fridge, after which they were superficially dried and instantly weighted again to estimate the saturated weight (SW). The leaves were then dried in a drying oven at 65 °C for about a week.

Consequently, dry weights (DW) of the leaves were measured. RWC and LSWC were then both calculated according to the protocol of Blackman et al. (2019) as follows:

$$RWC = \frac{(FW - DW)}{(SW - DW)} \times 100$$

$$LSWC = \frac{(SW - DW)}{DW}$$

As some difficulties occurred during ascertaining leaf FW, multiple RWC measurements had to be discarded from the dataset.

Leaf water potential at saturation

For the measurement of π_0 we followed the protocol of Bartlett et al. (2012). Collected leaves were instantly wrapped into pre-soaked paper towels and enclosed in Zip-Lock bags. After transport they were stored in the fridge for 24 h to ensure full re-hydration. Prior to measurement, leaf disks were sampled with a 5 mm cork borer. Primary and secondary venations were avoided while coring. The discs were instantly wrapped into aluminum foil and immersed in liquid nitrogen for a minimum of 5 minutes. Subsequently the discs were perforated 15 times with a metal needle and then placed into the vapor pressure osmometer (VAPRO 5520, Wescor). The equilibrium solute concentration value C_0 (mmol kg⁻¹) was recorded when the difference between consecutive measures was less than 4 mmol kg⁻¹. This value was converted into MPa using the Van't Hoff equation (Maréchaux et al., 2015):

$$\pi_0 = - \frac{2.5}{100} \times C_0$$

Carbon and oxygen isotopic composition and leaf C:N ratios

To create a composite sample, the dried leaves from g_{\min} , π_0 and RWC analyses were chopped and shredded with forceps. Samples were filled into 2 ml Eppendorf tubes. Two to three steel

balls were added respectively for grinding with a ball mill with at maximum speed, i.e. 100 rotations per minute for five minutes, until samples were ground into a fine powder.

For carbon isotope analysis 1-2 mg of each leaf sample was weighed into tin capsules with a precision balance and the respective weight was noted at the μg scale. For the measurement of foliar oxygen isotopic compositions, the ground samples were dried again for about 24 h at 65 °C in the drying oven. Aliquots of 0.2 – 0.4 mg per sample were weighed into silver capsules.

All carbon isotope measurements, as well as leaf carbon and nitrogen contents, were conducted with an EA-Isolink (EA IRMS), consisting of a Flash Elemental Analyzer, linked by a Conflo IV Universal Interface to a Delta V isotope ratio mass spectrometer (IRMS). Oxygen isotope ratios were measured with a high temperature pyrolysis unit (TCEA) coupled to a Delta V IRMS instrument.

Other functional traits

Table 1: Overview of functional traits and demographic rates that were incorporated in the statistical analyses; including units, functional dimension (LES = leaf economics spectrum, SES = stem economics spectrum, LWR = leaf water relations, or demography), functional significance, and predicted relation to drought tolerance (DT). Positive anticipated relations are marked with '+', negative links are indicated with '-', and no linkage is signified with '/'.

Trait	Meaning	Unit	Dimension	Functional significance	DT correlation
$\delta^{23}\text{C}$	Leaf C isotope ratio	‰	LWR	Proxy of intrinsic water-use efficiency, photosynthesis	+
$\delta^{18}\text{O}$	Leaf O isotope ratio	‰	LES	Proxy for stomatal conductance	+
g_{min}	Minimum leaf conductance	$\text{mmol m}^{-2} \text{s}^{-1}$	LWR	Water conservation after stomatal closure	-
LSWC	Leaf saturated water content	g g^{-1}	LWR	Potential to store water	+
π_o	Osmotic potential at full hydration	MPa	LWR	Determinant of turgor loss point	-
RWC	Relative (leaf) water content	%	LWR	Water storage	+
C:N	Leaf C:N ratio	unitless	LES	Resource capture (N – use efficiency)	/
L_{thick}	Laminar thickness	mm	LES	Biomechanical stability	/
SLA	Specific leaf area	$\text{m}^2 \text{kg}^{-1}$	LES	Light capture & mechanical stability	/
B_{thick}	Trunk bark thickness	mm	SES	Defence and transport	/
WSG	Wood specific gravity	unitless	SES	Resistance and capacitance	+
m	Annual mortality rate	$\% \text{ year}^{-1}$	demography	Survival and persistence	-
DGR	Annual diameter growth rate	cm year^{-1}	demography	Growth and productivity	-

For the assessment of correlations with prevalent functional traits representing the leaf and stem economics spectrum, existing data were obtained from previous studies at the Paracou Research Station, French Guyana. Species mean trait values of leaf thickness (L_{thick}), specific leaf area (SLA), wood specific gravity (WSG) and bark thickness (B_{thick}) were retrieved from Baraloto et al. (2010) and Fortunel et al. (2012). A detailed overview of all traits used in this study can be viewed in Table 1.

Demographic rates

Data from the Paracou Research Station from annual and biannual censuses between 1984 and 2020 (Guyafor database, 2017) on species-specific annual diameter growth rates (DGR, cm/year) of all individuals representing our sampled species were calculated with the 'ForestData' package in R. Estimation of the annual species-specific mortality rates were conducted following the protocol of Sheil & May (1996). Annual mortality rates (m) were estimated with N_0 and N_t being the population counts at the beginning and at the end of each measurement interval (t). With the following formula species tree mortality was calculated per year and subsequently annual species means were estimated:

$$m = 1 - \left(\frac{N_t}{N_0}\right)^{1/t}$$

Data analyses

All statistical analyses were performed with the statistical software R version 4.1.1 (R Core Team, 2021).

Data preparation and outlier analysis

Species with less than 3 replicates were removed from the list. Finally, 103 of the 114 sampled tree species were used in the analysis (see Appendix, Table 1). For each trait boxplots were created per botanical family. The whiskers extend from the hinge to the minimum and maximum no further than $1.5 \times \text{IQR}$ (inter-quartile range). Data points which were located below or above the whiskers were removed. This data elimination was complemented by carefully checking comments (measurement errors, leaf scars, oxidation, etc.), which had

been noted during trait measurements. To assess whether data were normally distributed Shapiro Wilk tests were performed for each trait. If required traits were transformed accordingly by either using natural logarithm, x^2 , x^3 or $\sqrt[3]{x}$ (see Table 2).

Depending on the type of statistical evaluation as well as which parameters are crucial for it, the number of used species (n) varies among analyses (see Appendix, Table 2).

Hydraulic trait coordination

To assess the dimensionality of trait coordination, a centred and scaled principal component analysis (PCA) was performed with g_{min} , π_o , RWC, LSWC, $\delta^{13}C$, $\delta^{18}O$, SLA, B_{thick} , L_{thick} , C:N and WSG across the species mean dataset without missing values ($n = 74$). Trait loading and PCA visualization was carried out using the R packages 'FactoMineR' (Lê et al., 2008) and 'factoextra' (Kassambara & Mundt, 2020). A matrix of pairwise Pearson correlations of the gapless dataset ($n = 74$) was created with all included functional traits and demographic rates. To visualize the relationships, a simplified colour scheme was created with the App BioRender.com (BioRender, 2021).

Trait-demography linkage

The coupling of demographic rates with functional traits was investigated with pairwise Pearson correlations in all 103 species. One linear model including all functional traits was fitted to predict mean annual species diameter growth rates (DGR) and mean annual species mortality rates (m), respectively. The models were then trimmed down using `stepAIC()` from the 'MASS' R package (Venables & Ripley, 2002) to avoid overparameterization. As `stepAIC` cannot deal with missing values, only 64 species with complete trait data were used to fit the linear models.

Phylogenetic signal

For the creation of a phylogenetic tree of the 103 species, we used the 'V.PhyloMaker' R package (Jin & Qian, 2019). An ultrametric tree with species-level resolution was built.

Species mean trait values were calculated and their phylogenetic signal was estimated as Pagel's λ by using the R packages 'phylobase' (Hackathon et al., 2020) and 'adephylo' (Jombart & Dray, 2008).

3.4 Results

Trait coordination

The studied tropical tree species displayed wide variation along the leaf economics, stem economics and leaf hydraulics spectrum, as well as a large variation in their demographic rates (stem increment and mortality, see Table 2).

Table 2: Overview of statistical parameters of functional traits and demographic rates. Trait abbreviations are explained in Table 1. Number of species (*n*), means, minima, maxima, standard deviations (SD), units and transformations used to correspond to the normality assumption are given.

	<i>n</i>	Mean	Min.	Max.	SD	Unit	Transformation
$\delta^{13}\text{C}$	91	-32.092	-33.95	-29.026	1.050	‰	$\sqrt[3]{x}$
$\delta^{18}\text{O}$	91	30.829	27.233	34.033	1.751	‰	x^3
g_{min}	103	4.488	1.153	14.321	2.476	$\text{mmol m}^{-2} \text{s}^{-1}$	$\log(x)$
LSWC	103	153.933	88.095	254.484	3.250	g g^{-1}	$\log(x)$
Π_0	103	-1.412	-2.472	-0.751	0.279	MPa	-
RWC	103	95.676	81.697	99.192	3.191	%	-
C:N	91	31.467	17.222	49.280	7.587	unitless	-
L_{thick}	85	0.250	0.155	0.411	0.054	mm	-
SLA	87	11.034	4.485	21.241	3.346	$\text{m}^2 \text{kg}^{-1}$	-
B_{thick}	72	4.245	0.500	10.468	1.937	mm	-
WSG	79	0.639	0.413	0.905	0.110	unitless	x^2
<i>m</i>	91	0.007	0.000	0.058	0.010	$\% \text{ year}^{-1}$	$\log(x)$
DGR	91	0.668	0.084	2.722	0.522	cm year^{-1}	$\log(x)$

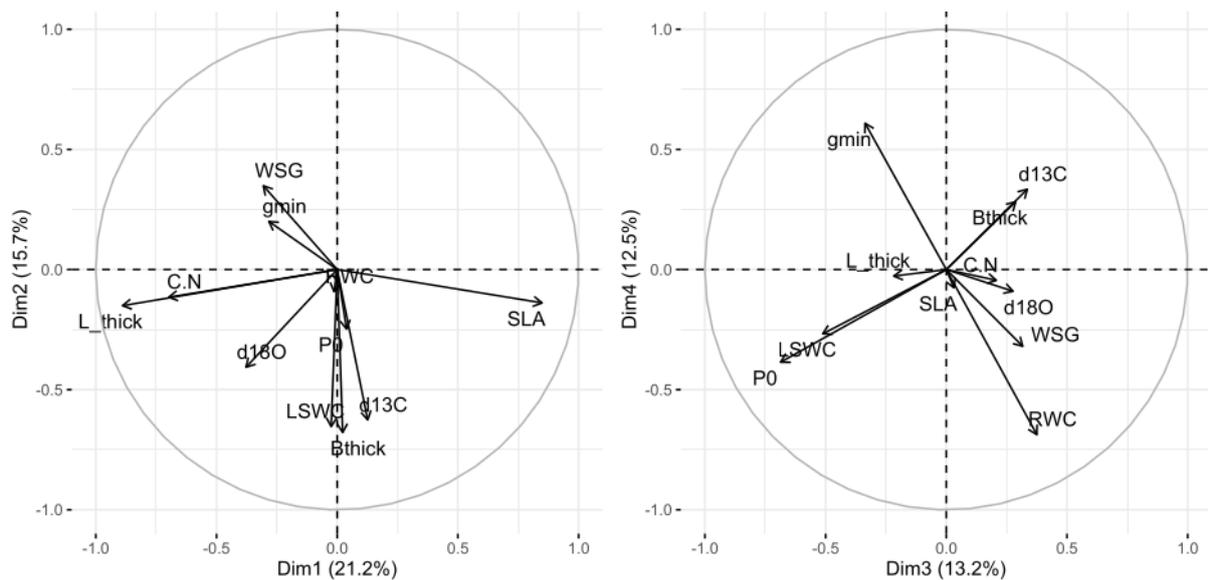


Figure 3: Biplot of principal component analysis of functional trait variability across the 103 studied tree species. The explained variances of the first two (left) and the third and fourth (right) principal component axes (%) are depicted in brackets. All trait abbreviations are explained in Table 1. When required, variables were transformed to meet the normality assumption (see Table 2).

Table 3: PCA loading scores of the nine functional traits and explained variances per principal component (PC) in % are shown. Trait abbreviations are given in Table 1.

Principal Component	PC 1	PC 2	PC 3	PC 4
Explained variance	21.20%	15.70%	13.20%	12.50%
Trait	Trait loadings			
B_{thick}	0.02	-0.68	0.29	0.28
C:N	-0.70	-0.12	0.21	-0.04
δ¹³C	0.13	-0.63	0.34	0.33
δ¹⁸O	-0.38	-0.41	0.28	-0.09
g_{min}	-0.28	0.20	-0.34	0.61
L_{thick}	-0.89	-0.15	-0.22	-0.03
LSWC	-0.03	-0.65	-0.51	-0.27
π_o	0.04	-0.25	-0.69	-0.39
RWC	-0.01	-0.09	0.38	-0.69
SLA	0.85	-0.14	0.03	-0.08
WSG	-0.31	0.35	0.32	-0.32

Table 4: Pearson correlation coefficients (*r*) of species mean trait values from 103 tree species are shown above the diagonal. *P*-values of pairwise correlations are depicted below the diagonal. Note that *g_{min}*, *LSWC*, *δ¹⁸O*, *δ¹³C*, mean annual mortality (*m*) as well as mean annual growth (*DGR*) have been transformed (according to Table 2) to meet the assumption of normality. Bold font indicates significant correlations ($p < 0.05$).

	π _o	g _{min}	LSWC	RWC	C:N	SLA	L _{thick}	δ ¹³ C	δ ¹⁸ O	WSG	B _{thick}	m	DGR
π _o		0.08	0.37	-0.03	-0.15	-0.01	0.08	-0.07	-0.16	-0.12	-0.06	0.19	0.19
g _{min}	0.454		0.01	-0.42	0.10	-0.18	0.25	-0.02	-0.04	0.03	-0.03	0.08	0.03
LSWC	<0.001	0.961		-0.17	-0.24	0.22	0.19	0.06	0.05	-0.30	-0.01	0.20	0.00
RWC	0.774	<0.001	0.095		-0.12	0.14	-0.26	0.11	-0.01	0.05	0.09	0.04	0.01
C:N	0.188	0.375	0.036	0.283		-0.40	0.43	-0.09	0.22	0.25	0.15	-0.18	-0.03
SLA	0.920	0.122	0.064	0.247	<0.001		-0.67	0.05	0.11	-0.08	-0.26	0.19	-0.23
L _{thick}	0.517	0.036	0.040	0.028	<0.001	<0.001		-0.05	0.14	-0.06	0.04	-0.12	-0.09
δ ¹³ C	0.531	0.871	0.628	0.354	0.417	0.691	0.681		0.16	-0.11	0.34	0.25	0.15
δ ¹⁸ O	0.155	0.740	0.643	0.905	0.054	0.353	0.226	0.169		0.20	0.04	-0.26	-0.43
WSG	0.327	0.816	0.013	0.657	0.040	0.488	0.639	0.361	0.091		-0.23	-0.20	-0.31
B _{thick}	0.607	0.802	0.961	0.447	0.199	0.028	0.730	0.003	0.768	0.053		0.07	0.26
m	0.050	0.443	0.051	0.702	0.107	0.099	0.297	0.015	0.020	0.095	0.542		0.15
DGR	0.0586	0.756	0.997	0.906	0.793	0.047	0.467	0.189	<0.001	0.009	0.024	0.145	

In the PCA analysis, the two first components explained 21.2 % and 15.7 %, respectively (see Figure 3). The first axis represents a dimension characterized by relationships between leaf functional traits, such as SLA, leaf C:N and L_{thick}, as outlined in Table 3. The second dimension was predominantly driven by variations in B_{thick}, leaf δ¹³C and LSWC. Taking the first four axes into consideration, a total of 62.6 % of trait variance was accounted for. The co-variation

between π_0 and LSWC were represented in the third PC axis, whereas the fourth PC axis was primarily linked to the relationship between RWC and g_{\min} (see Table 3).

As Table 4 shows, strong correlations were found between LSWC and π_0 ($r = 0.37$, $p < 0.001$), and RWC and g_{\min} ($r = -0.42$, $p < 0.001$). Traits representing the LES were predominantly correlated to each other, but not with leaf hydraulics. Exceptions to this were the weak links between L_{thick} and RWC ($r = -0.26$, $p = 0.028$), L_{thick} and g_{\min} ($r = 0.25$, $p = 0.036$) and between L_{thick} and LSWC ($r = 0.19$, $p = 0.101$). WSG, as a representative of the SES, was correlated to LSWC ($r = -0.30$, $p = 0.013$) and leaf $\delta^{18}\text{O}$ ($r = 0.2$, $p = 0.091$). B_{thick} was strongly associated with $\delta^{13}\text{C}$ ($r = 0.34$, $p = 0.003$). The trait relationships are additionally visualized in a simplified colour scheme in Figure 4.

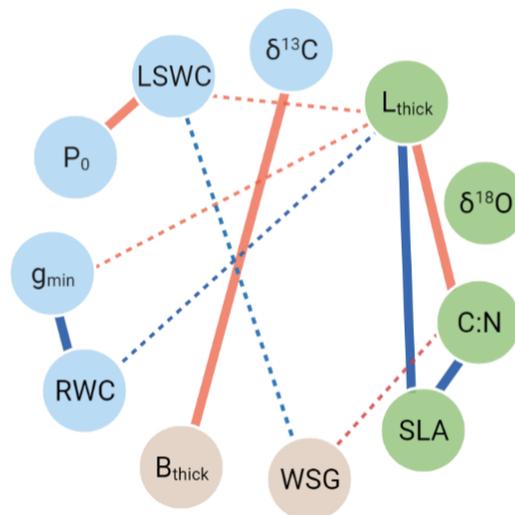


Figure 4: A schematic overview of the pairwise Pearson correlations between plant functional traits ($n = 103$). Trait abbreviations correspond to those listed in Table 1. Positive correlations are signified with a red line, whereas negative correlations are marked with a dark blue line. Strongly significant correlations ($p < 0.001$) are indicated with a thick continuous line, moderately significant correlations ($p < 0.01$) as a thin continuous line and weakly significant correlations ($p < 0.05$) are signified with a dotted line. Leaf water relations traits and hydraulic traits are coloured in light blue, LES in green and SES in light brown. The scheme was created with BioRender.com (2021).

Trait-demography relationships

As depicted in the pairwise correlation matrix (Table 4), DGR was strongly negatively correlated with leaf $\delta^{18}\text{O}$ ($r = -0.43$, $p < 0.001$) as well as WSG ($r = -0.31$, $p = 0.009$). However, in the multiple linear regression predicting tree growth, leaf $\delta^{18}\text{O}$ was the only significant predictor, being negatively linked to DGR (see Table 5 and Figure 5). A significant, but weak correlation was also detected between B_{thick} and growth ($r = 0.26$, $p = 0.024$; see Table 4).

Mean annual tree mortality exhibited a weak negative pairwise correlation with leaf $\delta^{18}\text{O}$ ($r = -0.26$, $p = 0.02$; Table 4) and a weak positive correlation with $\delta^{13}\text{C}$ ($r = 0.25$, $p = 0.015$).

Table 5: Linear model predicting mean annual diameter growth rates (DGR) across 103 tropical tree species, showing coefficient estimates, standard errors (SE), significance levels (p values), species numbers (n) and R^2 values. Trait values were transformed (see Table 2) when necessary to meet the assumption of normality.

	Estimate	SE	p
Intercept	-0.0071	0.0770	0.927
$\delta^{18}\text{O}$	-0.0001	< 0.0001	< 0.001
WSG	-0.9574	0.5780	0.102
$\delta^{13}\text{C}$	0.5683	0.4787	0.239
n = 103	$R^2 = 0.254$	$p < 0.0001$	

Table 6: Linear model predicting mean annual mortality rates (m) across 103 tropical tree species, showing coefficient estimates, standard errors (SE), significance levels (p values), species number (n) and R^2 values. Trait values were transformed (see Table 2) when necessary to meet the assumption of normality.

	Estimates	SE	p
Intercept	-0.0390	0.1036	0.708
$\delta^{18}\text{O}$	-0.0001	< 0.0001	0.005
LSWC	0.6530	0.4645	0.163
n = 103	$R^2 = 0.101$	$p = 0.009$	

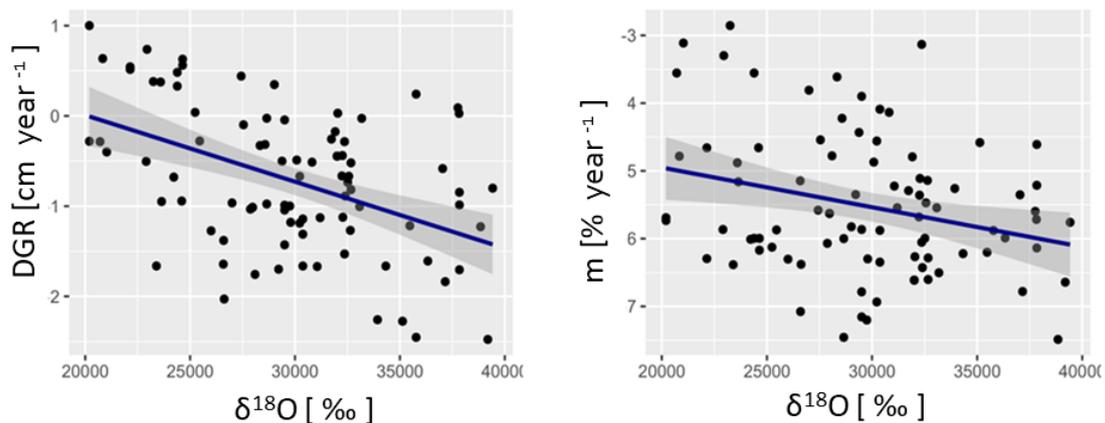


Figure 5: Linear trait-demography relationships for tree diameter growth rates (DGR) versus leaf $\delta^{18}\text{O}$ (left), and tree annual mortality rates (m) versus leaf $\delta^{18}\text{O}$ (right). Note that all parameters were transformed according to Table 2.

A simplified linear model predicting mean annual tree diameter growth rate with leaf $\delta^{18}\text{O}$, WSG and leaf $\delta^{13}\text{C}$ yielded an R^2 of 0.254 and a p-value of < 0.001 , with leaf $\delta^{18}\text{O}$ being the sole significant variable ($p < 0.001$, see Table 6 and Figure 5). Similarly, by fitting a trimmed linear model to explain mean annual tree mortality with leaf $\delta^{18}\text{O}$ and LSWC gave an R^2 of 0.101 and a p value of 0.009, in which only leaf $\delta^{18}\text{O}$ was significant ($p = 0.005$, see Table 6).

Phylogenetic signal

Table 7: Parameters describing the phylogenetic signal (λ) including result from log-likelihood ratio test (LogL), p-values and numbers of included species (n). Significant values are marked in bold.

Trait	λ	logL	p-value	n
Π_o	0.40	-14.65	0.07	103
g_{\min}	0.60	-238.82	0.00	103
RWC	0.21	-229.74	0.04	103
LSWC	0.36	-529.26	0.00	103
$\delta^{18}\text{O}$	0.30	-170.36	0.03	91
$\delta^{13}\text{C}$	0.13	-125.87	0.53	91
C:N	0.51	-294.76	0.00	91
SLA	0.25	-220.63	0.13	87
L_{thick}	0.22	122.54	0.08	85
WSG	0.56	66.97	0.00	79
B_{thick}	0.79	18.51	0.00	79

Strong phylogenetic signals were detected for B_{thick} ($\lambda = 0.79$) and g_{\min} ($\lambda = 0.6$), followed by WSG ($\lambda = 0.56$) and leaf C:N ($\lambda = 0.51$). Additionally, the phylogenetic dependences of LSWC ($\lambda = 0.36$), leaf $\delta^{18}\text{O}$ ($\lambda = 0.30$) and RWC ($\lambda = 0.21$) were significant, which is shown in Table 7.

3.5 Discussion

Trait coordination

According to our expectations, we found a strong positive correlation between LSWC and π_o . This conforms to what Ishida and his co-authors reported for 32 subtropical and tropical tree species (2008). A high concentration of solutes (ergo a high π_o) implies a high leaf water content. On the one hand LSWC and π_o are structurally coordinated (Bartlett et al., 2016), as a higher concentration of solutes causes a higher osmotic potential in the leaf, which allows a higher water-holding potential. Méndez-Alonzo et al. (2012) attributes this linkage to concerted convergence, as fast-risky strategists tend to be drought-avoiding, meaning that they have a high π_o and also a high LSWC. The opposite is true for slow-safe strategists, which tend to have lower LSWCs and simultaneously lower (more negative) water potentials, the latter being essential to maintain hydraulic conductivity (Ziegler et al., 2019).

As anticipated, traits that are commonly referred to as representatives of the leaf economics spectrum (Wright et al., 2004; Baraloto et al., 2010) were principally uncorrelated with leaf water relations (see Figure 4). The sole exception to this was L_{thick} , which exhibited a weak negative relationship with RWC and weak positive correlations with g_{min} and LSWC. The linkage of L_{thick} to hydraulic characteristics corresponds to the results of Ishida et al. (2008). Greater laminar thickness can potentially prevent leaf dehydration by curtailing transpiration, allowing the leaf to contain higher amounts of water per dry mass (LSWC) without losing too much of it. Sack et al. (2003) equally reported an association of L_{thick} with g_{min} and leaf conductance. This can be partially attributed to the fact that thicker leaves tend to have more stomata on the adaxial surface (Muir et al., 2014). A higher number of stomata is likely to imply larger transpiration losses when stomata are open. However, there is a strong negative correlation between stomata size and density, and smaller stomata can react faster to water deficit (Kardiman & Ræbild, 2018). Anyway, g_{min} should be primarily affected by the cuticle thickness and not by stomatal numbers and sizes (Kerstiens 1996 & Sack et al. 2003).

WSG was related to all three functional dimensions to some extent, being moderately inversely related to LSWC and weakly positively correlated to leaf C:N. This conforms to the expectations, as previous studies have postulated, that WSG represents a trade-off between

biomechanical stability and water capacitance (Méndez-Alonzo et al., 2012; Hietz et al. 2017). This means that trees building light wood have greater vessel lumina for water storage (Méndez-Alonzo et al., 2012). According to Hietz et al. (2017) low WSG in fast-risky strategists is only indirectly related to hydraulic conductivity, as both are linked to growth. The weak positive link between WSG and leaf C:N can be explained by functional integration. Both represent conservative strategies: dense wood and thick nutrient-poor leaves. It might be conjectured, that the flow rate at which nutrients are transported through the xylem, which is negatively affected by wood density, is also negatively influencing plant nutrient use efficiency, which in turn affects leaf nutrient concentrations.

The strong inverse relationship between RWC and g_{\min} is as an indication that higher minimum transpiration, both through stomata and the cuticle, promotes water loss and causes a decrease in leaf turgescence. In other words, if less water is lost when stomata are closed, there will be more water left. As RWC merely represents the momentary leaf water status, which underlies environmental and diurnal fluctuations, it should probably not be considered as a 'robust' leaf hydraulic trait.

π_0 and g_{\min} were uncorrelated, which conforms with expectations, based on what Marechaux et al. found in their study (2019). These traits obviously vary independently from each other across our tree species set and represent different drought response strategies in tropical trees.

Representative traits of the leaf economics spectrum, such as SLA, L_{thick} and leaf C:N, were tightly coupled (see Figure 4). A high laminar thickness implies high investments of dry matter per leaf area (low SLA). LMA and leaf nutrient concentrations are globally negatively correlated (Wright et al., 2004), as they represent a structural trade-off on the fast-slow trait continuum. Fast-growing plants have nutrient-rich leaves, but a low investment in dry mass per leaf area, or in other words show higher SLA and lower L_{thick} . Resource-conservative species, however, invest more in a higher leaf mass per area, which is associated with a higher leaf lifespan (Ishida et al., 2008). The leaves of those slow-strategist plant species are thicker, but poorer in leaf nitrogen, hence exhibiting higher leaf C:N ratios.

The strong association of B_{thick} and leaf $\delta^{13}\text{C}$ was surprising, and not underlined here by co-variation with other traits influencing leaf-level carbon isotope discrimination and water-use efficiency. This relationship could be because trees with thick barks are more conservative in

their water use, restricting leaf photosynthetic CO₂ uptake, for which we did not find any indications. As existing research does not point towards a consistent linkage between B_{thick} and leaf $\delta^{13}\text{C}$ (Baraloto et al., 2010; Fortunel et al., 2012), this relationship might be spurious. Peuke et al. (2006) found that the leaf carbon isotope composition is strongly impacted by environmental factors, especially soil water availability. Our sampling, having been exclusively carried out during the dry season, could have led to seasonal deviances in leaf $\delta^{13}\text{C}$ values. This underpins the findings of Brodribb et al. (2002), who claimed that in South American rainforests coordination of leaf hydraulic traits with other functional traits are significantly weaker during the wet season compared to dry season.

Generally, leaf oxygen and carbon isotopic signatures were not at all related to leaf hydraulic traits. This is surprising, as $\delta^{13}\text{C}$ is understood to reflect the ratio between photosynthetic rate and stomatal conductance and $\delta^{18}\text{O}$ has proven to be indicative for transpiration and stomatal conductance (Prieto et al., 2018; Scheidegger et al., 2000). The linkage between these photosynthetic traits leaf hydraulic traits has been suggested by Santiago et al. (2004) and Blackman et al. (2016), the latter showing a tight coupling of $\delta^{13}\text{C}$ and stomatal conductance in eucalyptus species. The results from Prieto et al. (2018) supported this hypothesis, by investigating herbaceous grassland species in the Mediterranean region. By conducting a similar analysis with tree species in a tropical forest ecosystem, Li et al. (2015) reported that leaf $\delta^{13}\text{C}$ was unaffected by leaf hydraulics. Soil water availability in wet tropical forests is likely non-limiting, and consequently, a tight coordination of plant water and carbon gain may not be required in tree species in wet tropical forests. A tight coordination of water use and photosynthetic carbon gain might thus not be essentially selected for in the fast-slow continuum to the same extent as in drier regions. In order to test this hypothesis, a direct comparison of functional trait coordination between dry and wet tropical forests is required, which clearly represents an interesting topic for future investigations.

Trait-demography associations

Intriguingly, leaf $\delta^{18}\text{O}$ was the strongest predictor for both, tree growth and mortality. These results provide some striking insights, but also raise novel questions. Leaf oxygen isotope composition is widely referred to as an indicator for stomatal conductance and leaf transpiration (Barbour, 2007; Cernusak et al., 2009; Prieto et al., 2018). To our knowledge this

is the first attempt to link the leaf oxygen isotope composition with trait-demography relationships. In fact, Cherubini and his co-authors (2021) postulated, that stem oxygen isotopic composition are a better indicator for tree vitality and growth than other, more commonly used traits. This gives rise to the speculation that a similar concept can be applied to leaf $\delta^{18}\text{O}$. Prieto et al. (2018) claimed that low leaf $\delta^{18}\text{O}$, and thus high stomatal conductance, is linked to high leaf nutrient concentrations, through “enhanced transpiration-driven mass flow of soil nutrients to roots and uptake of dissolved nutrients”, which could consequently increase stem growth rates. This would conform to the fast-slow continuum theory, as fast-strategists have nutrient-rich, but short-lived leaves. Qi et al. (2021) indeed stated, that in evergreen species the diameter growth rate is strongly dependent on g_s and maximum photosynthetic rate as this clearly allows a more efficient assimilation. Equally, the negative association of $\delta^{18}\text{O}$ with tree mortality can be explained as nutrient-acquisitive species favour short-term carbon and nutrient gains over tissue longevity. This equally demonstrates the trade-off between hydraulic efficiency and hydraulic safety. As low $\delta^{18}\text{O}$ implies an increased hydraulic flow, this comes with a higher risk of cavitation and stem embolism (Seibt et al., 2008), which in turn could entail a lower chance of tree survival. Nevertheless, Prieto et al. (2018) warned that using leaf $\delta^{18}\text{O}$ as an indicator for stomatal conductance should be done cautiously, because oxygen isotope fractionation is influenced by a wide range of factors, such as ambient temperature and air humidity, and the $\delta^{18}\text{O}$ signature of the source water. We thus conclude that our explanations for the substantial impact of $\delta^{18}\text{O}$ on productivity and mortality remain speculative; and that a profound elucidation of its role in those complex processes requires further investigation.

The strong inverse relation between WSG and DGR was expected, since a negative linkage of wood density and stem growth rates has been established repeatedly (Nascimento et al., 2005; Chave et al., 2009; Rüger et al., 2012; Hietz et al., 2017). Accordingly, species with low wood density grow faster, whereas species with high wood density grow slower. These findings are in consensus with the common view that fast-strategists with low wood densities prioritize short-term over long-term benefits (Hietz et al., 2017). This is a consequence of the clear trade-off between low construction costs and low maintenance costs with respect to decreased stem respiration (Chave et al., 2009; Rüger et al., 2012). In high wood specific gravity species, a smaller wood volume is produced per unit of biomass. In addition, dense wood tends to have a lower conduit fraction, which can cause decreased xylem water flow,

and in turn negatively affects nutrient transport and ultimately productivity (Rüger et al., 2012).

The weak explanatory power of leaf $\delta^{13}\text{C}$ for stem diameter growth shows that photosynthetic water use efficiency is not strongly linked to leaf-level carbon isotope fractionation across the studied tropical tree species. Plant photosynthesis is decisive for the rate at which tree biomass is produced, though plant carbon allocation and differences in respiratory costs can blur this relationship. Especially when water is scarce, plant water use efficiency has a crucial controlling effect on plant growth (Seibt et al., 2008). However, as the explanatory power of leaf $\delta^{13}\text{C}$ for tree growth was small and non-significant, evidently plant water use efficiency and realized growth are decoupled in this ecosystem. Similarly, LSWC had a very small effect on annual tree mortality. Leaf saturated water content should be a key parameter for tree survival rates, as more leaf water offers the plant a longer time frame before turgor is lost and the leaf finally desiccates. Even though plants are able to recover from turgor loss, repeated turgor loss events have been shown to increase the risk of desiccation and irreversible cellular damage (Sapes et al., 2019), causing tree mortality during extended drought events.

Phylogenetic signal

A strong phylogenetic signal signifies that closely related species resemble each other more than as if drawn randomly from a phylogenetic tree (Münkemüller et al., 2012). We found moderate to high phylogenetic signals in B_{thick} , g_{min} , WSG and leaf C:N. Our results therefore correspond to the findings of Liu et al. (2015), who claimed that stem characteristics and leaf traits involved in nutrient acquisition, as well as their water budget, are highly phylogenetically conserved. Usually, strong phylogenetic dependence is associated with stabilizing selection or a lack of genetic variation. It can also be caused by macro-ecological factors, which prevent adaptation to new niches or genetic constraints such as pleiotropic genes (Losos, 2008). Considering stabilizing selection this would imply that these traits responded evolutionary to differences in nutrient or water availability within these wet tropical forests.

In contrast, L_{thick} , SLA, leaf $\delta^{13}\text{C}$, leaf $\delta^{18}\text{O}$ and RWC turned out to be rather weakly phylogenetically constrained. Since RWC reflects the momentary leaf water status and is hence likely to be susceptible to fluctuations in precipitation and diurnal variations in microclimate, its phylogenetic independence is not surprising. With respect to L_{thick} , SLA, and leaf oxygen and carbon isotopic compositions the weak phylogenetic signal shows that these traits are affected by quick environmental changes which require rapid adaptations, or topographic differences in environmental conditions. Consequently, they are subject to strong selective pressures and are thus evolving at a faster evolutionary rate (Liu et al., 2015). SLA and L_{thick} , as well as oxygen and carbon isotopic compositions are essentially linked to light capture, photosynthesis, and transpiration, which are processes that are strongly affected by microclimatic fluctuations, such as light and moisture availability. Phylogenetic lability in light-capture characteristics might be opposed to rather conserved traits involved in plant nutrient and water relations (Liu et al., 2015), which are subjected to stabilizing selection. This concept is visualised in a simplified scheme in Figure 6.

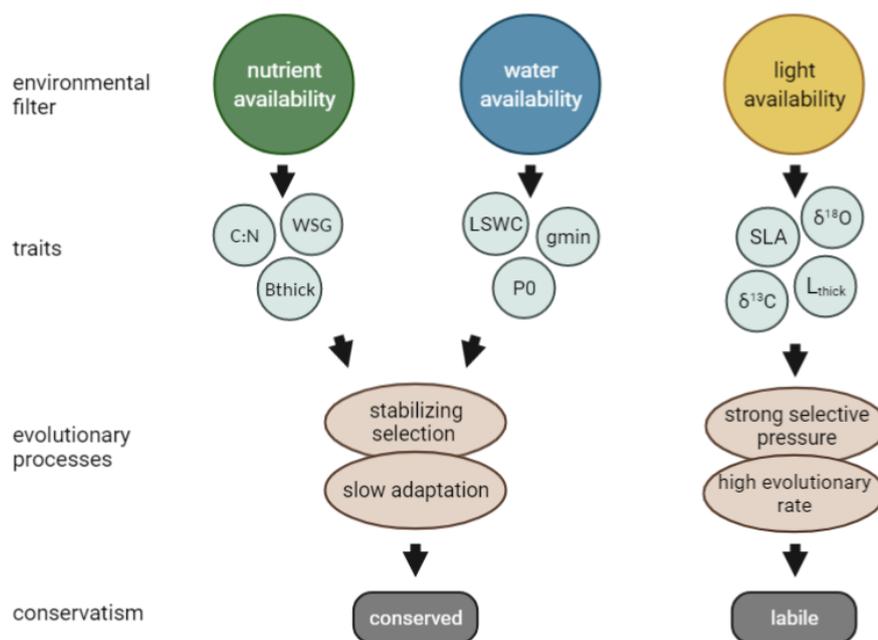


Figure 6: A simplified scheme to explain the differential patterns in phylogenetic signals. Environmental filters (nutrients, water, and light) drive adaptation of functional traits through evolutionary time. Quick fluctuations in light availability result in a high evolutionary rate and thus phylogenetic independence in the respective traits. In contrast, traits involved in plant nutrient and water capture are more likely to be subjected to stabilizing selection, which causes phylogenetic conservatism. The scheme was created with BioRender.com (2021).

Nutrient-sourcing traits as well as leaf hydraulics (except for RWC), however, were subject to a rather lagging adaptive process. As g_{\min} exhibits the highest phylogenetic signal among leaf hydraulic traits, it might be assumed to be a long-term adaptation mechanism to water scarcity in tropical ecosystems. The exceptionally strong phylogenetic signal in bark thickness ($\lambda = 0.79$) could be due to the fact that this trait is under a stronger genetic control and that anatomy less easily altered by environmental conditions.

3.6. Conclusion

With respect to the research hypotheses, I conclude that

1a) As suggested, some hydraulic traits are tightly coordinated among each other, whereas others seem to vary independently from each other. More specifically, I could verify that LSWC and π_o show a strong positive relation, which is attributed to the inherent relationship between leaf saturated water content and its osmotic potential. In other words, a high LSWC implies a high leaf solute concentration, which is synonymous to a low π_o . RWC and g_{min} were found to be strongly negatively associated, which can be explained by a simple mechanistic link: if less water is lost after stomatal closure, the momentary water content will be generally higher. Moreover, g_{min} and π_o were unrelated, as they are structurally and functionally independent.

1b) The hypothesis that leaf hydraulic traits are decoupled from stem and leaf functional traits could not be verified. Exceptions to the independence of leaf hydraulic traits from other plant economic spectra were laminar thickness, leaf oxygen and carbon isotopic compositions and, conforming to our hypothesis, WSG. The latter was moderately linked to LSWC, but also to leaf C:N. This is probably due to functional integration, as high WSG reflects the resource-conservative strategy, which is equally true for a high leaf C:N. L_{thick} was a weak indicator for LSWC and g_{min} , as leaf thickness is decisive for how much water can be held in leaves, and is also linked to stomatal density, which in turn is linked to transpirational water losses.

2) As suspected, leaf hydraulics did not substantially explain diameter increment or mortality at this site. Leaf $\delta^{18}O$, however, played a crucial role in predicting these demographic rates. To our knowledge this is the first attempt to link the leaf oxygen isotope composition with tree diameter growth and mortality rates. We conclude, that more negative leaf $\delta^{18}O$ signatures imply higher stomatal conductance, promoting tree nutrient uptake and growth. This conforms to earlier studies, claiming the strong interrelation of stomatal conductance and assimilation rate with DGR. Tree growth was also slightly negatively linked to WSG, which matches the findings of others. Denser wood implies a slower stem growth: this also confirms the fast-slow continuum theory,

stating that costly tissues, such as dense wood, come at higher costs of dry mass and time.

3) The hypothesis, that leaf hydraulic traits only have a poor explanatory power in predicting tree mortality rates, were verified. Considering the functional traits measured in this study, leaf $\delta^{18}\text{O}$ was the single best predictor for tree survival. Stomatal conductance interferes with xylem water conductivity, potentially influencing the likelihood of embolism, and eventually reducing the probability for a tree to die. LSWC was found to be a weak second predictor, increasing the time before desiccation, and reducing the risk of irreversible turgor loss. Nevertheless, the precise role that $\delta^{18}\text{O}$ plays in both stem increment and mortality remains speculative, and hence raises interesting questions for further research.

4) Most leaf water relations traits and nutrient-sourcing traits (leaf C:N and WSG) showed moderate to high phylogenetic signals, signalling that they are subject to strong stabilizing selection and rather slow environmental changes. As opposed to this, light capturing traits, such as leaf $\delta^{13}\text{C}$ and SLA were more phylogenetically labile.

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5. Appendix

Table 1: Complete list of the 103 sampled species with their respective botanical families and replicate count ($n \geq 3$) is shown. Species marked with an '*' were complemented with replicates from the collaborating project Metradica (Boisseaux et al., unpublished data).

Species	Family	n	Species	Family	n
<i>Abarema jupunba</i> var. <i>jupunba</i>	Fabaceae	5	<i>Licania densiflora</i>	Chrysobalanaceae	3
<i>Amphirrhox longifolia</i>	Violaceae	5	<i>Licania membranacea</i> *	Chrysobalanaceae	21
<i>Bellucia arborescens</i>	Melastomataceae	6	<i>Licania micrantha</i> *	Chrysobalanaceae	12
<i>Bocoa prouacensis</i> *	Fabaceae	29	<i>Licania ovalifolia</i>	Chrysobalanaceae	5
<i>Brosimum guianense</i>	Moraceae	4	<i>Mabea piriri</i>	Euphorbiaceae	4
<i>Carapa surinamensis</i> *	Meliaceae	13	<i>Manilkara bidentata</i> *	Sapotaceae	11
<i>Caryocar glabrum</i>	Caryocaraceae	7	<i>Maytenus oblongata</i>	Celastraceae	5
<i>Casearia javitensis</i>	Salicaceae	6	<i>Miconia acuminata</i>	Melastomataceae	8
<i>Caryocar glabrum</i>	Caryocaraceae	7	<i>Miconia minutiflora</i>	Melastomataceae	5
<i>Casearia javitensis</i>	Salicaceae	6	<i>Miconia tschudyoides</i>	Melastomataceae	6
<i>Catostemma fragrans</i>	Malvaceae	5	<i>Moronobea coccinea</i> *	Clusiaceae	11
<i>Cecropia obtusa</i>	Urticaceae	5	<i>Mouriri crassifolia</i>	Melastomataceae	6
<i>Cecropia sciadophylla</i>	Urticaceae	6	<i>Oxandra asbeckii</i>	Annonaceae	9
<i>Chaetocarpus schomburkianus</i> *	Peraceae	16	<i>Parinari campestris</i>	Chrysobalanaceae	5
<i>Chrysophyllum prieurii</i> *	Sapotaceae	16	<i>Parkia nitida</i>	Fabaceae	4
<i>Chrysophyllum sanquinolentum</i> *	Sapotaceae	13	<i>Pogonophora schomburgkiana</i>	Peraceae	5
<i>Conceveiba guianensis</i> *	Euphorbiaceae	18	<i>Poraqueiba guianensis</i> *	Metteniusaceae	11
<i>Cordia sagotii</i>	Cordiaceae	6	<i>Posoqueria latifolia</i>	Rubiaceae	5
<i>Couratari multiflora</i>	Lecythidaceae	6	<i>Pourouma melinonii</i>	Urticaceae	5
<i>Dendrobangia boliviana</i>	Metteniusaceae	6	<i>Pouteria guianensis</i>	Sapotaceae	6
<i>Dicorynia guianensis</i> *	Fabaceae	24	<i>Pradosia cochlearia</i> *	Sapotaceae	15
<i>Drypetes variabilis</i>	Putranjivaceae	5	<i>Protium opacum</i> *	Burseraceae	18
<i>Duguetia calycina</i>	Annonaceae	6	<i>Protium stevensonii</i>	Burseraceae	4
<i>Duroia longiflora</i>	Rubiaceae	5	<i>Protium subserratum</i>	Burseraceae	7
<i>Eperua falcata</i> *	Fabaceae	25	<i>Pterocarpus officinalis</i> *	Fabaceae	10
<i>Eperua grandiflora</i> *	Fabaceae	19	<i>Qualea rosea</i> *	Vochysiaceae	10
<i>Eschweilera congestiflora</i>	Lecythidaceae	6	<i>Recordoxylon speciosum</i> *	Fabaceae	10
<i>Eschweilera coriacea</i> *	Lecythidaceae	22	<i>Sandwithia guyanensis</i>	Euphorbiaceae	6

Species	Family	n	Species	Family	n
<i>Eschweilera decolorans</i>	Lecythidaceae	6	<i>Schefflera decaphylla</i>	Araliaceae	5
<i>Eschweilera sagotiana</i> *	Lecythidaceae	18	<i>Sextonia rubra</i> *	Lauraceae	9
<i>Garcinia benthamiana</i>	Clusiaceae	5	<i>Sterculia pruriens</i> *	Malvaceae	8
<i>Garcinia madruno</i>	Clusiaceae	3	<i>Swartzia guianensis</i>	Fabaceae	5
<i>Goupia glabra</i>	Goupiaceae	8	<i>Swartzia polyphylla</i>	Fabaceae	5
<i>Guarea pubescens</i> subsp. <i>pubescens</i>	Meliaceae	4	<i>Symphonia globulifera</i> *	Clusiaceae	10
<i>Gustavia hexapetala</i> *	Lecythidaceae	15	<i>Symphonia sp.1</i> *	Clusiaceae	11
<i>Hebepetalum humiriifolium</i>	Linaceae	6	<i>Tachigali melinonii</i> *	Fabaceae	19
<i>Hevea guianensis</i>	Euphorbiaceae	6	<i>Talisia hexaphylla</i>	Sapindaceae	4
<i>Hirtella bicornis</i> var. <i>bicornis</i>	Chrysobalanaceae	7	<i>Tapirira guianensis</i>	Anacardiaceae	5
<i>Homalolepis cedron</i>	Simaroubaceae	6	<i>Tapirira obtusa</i>	Anacardiaceae	6
<i>Hymenopus heteromorphus</i> *	Chrysobalanaceae	33	<i>Tapura capitulifera</i> *	Dichapetalaceae	10
<i>Inga alba</i>	Fabaceae	3	<i>Theobroma guianense</i>	Malvaceae	7
<i>Inga loubryana</i>	Fabaceae	5	<i>Thyrsodium guianense</i>	Anacardiaceae	5
<i>Inga stipularis</i>	Fabaceae	5	<i>Tovomita brevistaminea</i>	Clusiaceae	7
<i>Iryanthera hostmannii</i> *	Myristicaceae	10	<i>Tovomita caloneura</i>	Clusiaceae	5
<i>Iryanthera sagotiana</i> *	Myristicaceae	13	<i>Tovomita obovata</i>	Clusiaceae	4
<i>Jacaranda copaia</i> subsp. <i>copaia</i> *	Bignoniaceae	18	<i>Trymatococcus oligandrus</i>	Moraceae	6
<i>Laetia procera</i>	Salicaceae	9	<i>Unonopsis rufescens</i>	Annonaceae	6
<i>Lecythis persistens</i> subsp. <i>aurantiaca</i> *	Lecythidaceae	16	<i>Virola michelii</i> *	Myristicaceae	12
<i>Lecythis poiteauii</i> *	Lecythidaceae	14	<i>Vismia sessilifolia</i>	Hypericaceae	5
<i>Leptobalanus sprucei</i>	Chrysobalanaceae	6	<i>Vouacapoua americana</i> *	Fabaceae	18
<i>Licania alba</i> *	Chrysobalanaceae	18	<i>Xylopia nitida</i>	Annonaceae	5
<i>Licania canescens</i> *	Chrysobalanaceae	10			

Table 2: Number of incorporated species (*n*) in the respective analyses. Depending on the type of analysis, required species with crucial missing values were removed. * Number depends on the trait in focus, see Table 7 for detailed information.

Type of analysis	n
Principal component analysis	74
Pairwise Pearson correlation	103
StepAIC model simplification	67
Linear model fitting	103
Phylogenetic Signal	79-103*

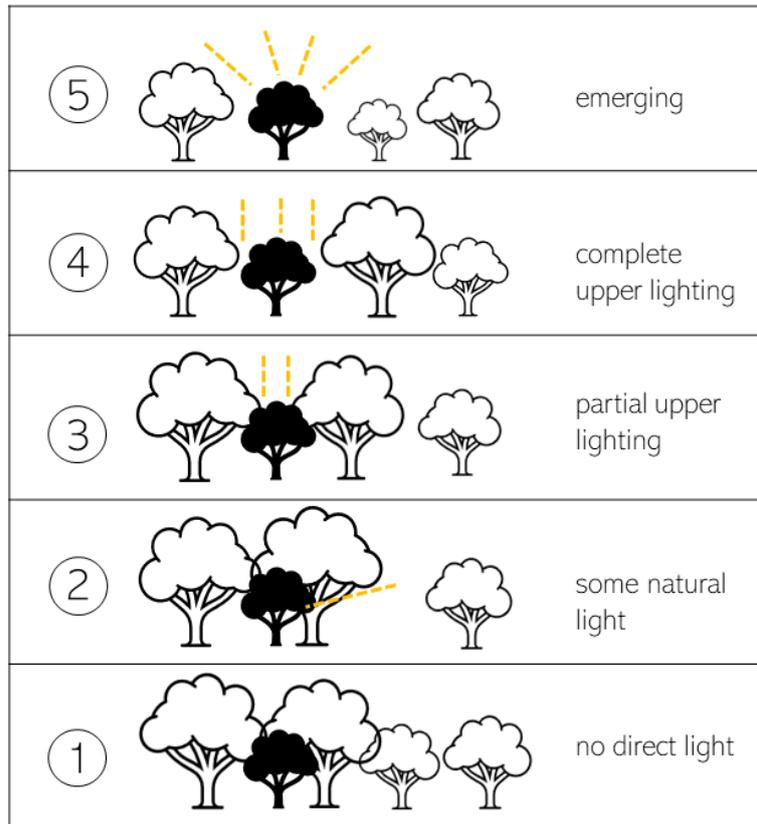


Figure 1: Schematic outline of the Dawkins' Index ranking which describes tree crown positioning (Dawkins, 1958), created with MS PowerPoint (Microsoft Corporation, 2018). To standardize light conditions, individuals classified as 2-4 (some natural light, partial upper lighting, or complete upper lighting) were targeted during sampling.