

Light Tolerance-related Tree Growth Strategies and their Impacts on Key Functional Tree Traits: A Review

Estelle Nkene Mezui,^{a,b,c} Loic Brancheriau,^{b,*} Samuel Ikogou,^{c,d} and Rostand Moutou Pitti^{a,c}

Light is essential for tree growth and development, yet some species are able, or prefer, to tolerate shady conditions without adversely affecting their development. This ecological preference prompts different strategies in these species, often involving a trade-off between performance and safety in terms of mechanical support, conductivity, and pest and disease protection. Studies on the ecological strategies of trees and their associated functional traits are essential to gain further insight into biodiversity and the processes that shape wood quality from the standpoint of technological properties useful to humans. This literature review showcases current links between ecological preferences and the main functional traits of tree species, with particular emphasis on wood properties.

DOI: [10.15376/biores.19.4.NkeneMezui](https://doi.org/10.15376/biores.19.4.NkeneMezui)

Keywords: Ecological strategies; Functional traits; Shade tolerance; Wood properties

Contact information: a: Clermont Auvergne University, CNRS, Clermont Auvergne INP, Institut Pascal, F-63000 Clermont-Ferrand, France; b: CIRAD, UPR BioWooEB, University of Montpellier, 34398 Montpellier, France; c: LaReVaBois, Wood Research and Development Laboratory, 3960 Libreville, Gabon, France; d: Ecole Polytechnique de Masuku (EPM-USTM), B.P. 941 Franceville, Gabon, France; * Corresponding author: loic.brancheriau@cirad.fr

INTRODUCTION

Trees growing in forest stands compete with neighbouring trees for light, water, and nutrients. This competition affects their growth and the overall functioning of forest ecosystems in terms of biodiversity, carbon sequestration, water regulation through transpiration and oxygen production (Keleş 2019; Imbert *et al.* 2021). Forests are vital for the biosphere, but also for the diverse range of human applications of wood. During their growth, trees adopt various strategies necessary for their survival at each developmental stage (González-Melo 2022), depending on the species and its surrounding environment. The fundamental biological lifecycle processes (establishment, development, and reproduction) require the uptake of vital resources (energy and elements transfer) and adaptation to prevailing environmental conditions and variations (droughts and storms for instance). Variability in the morphological and physiological characteristics, or so-called functional traits, reflects the diversity in the ways trees perform in carrying out these biological processes. The main functional traits include wood density, specific leaf area (ratio between the surface area and unit dry mass of a leaf), maximum height, photosynthetic capacity, water potential and sap flow (raw and elaborated sap) (Wright *et al.* 2004; Kunstler *et al.* 2016; Cachinero-Vivar *et al.* 2024). Wood density is a functional trait linked to fiber characteristics in hardwoods and tracheids in softwoods. It is used as a determinant of wood quality and varies greatly between species due to their different

porosities. Higher values produce stronger woods, while lower density woods are more suitable for pulp manufacture. Furthermore, hardwoods generally have a higher density than softwoods (Saranpää 2003; Trouy 2015). Specific leaf area reflects leaf thickness. It is a parameter positively linked to the plant's photosynthetic capacity. It can be used to estimate a plant's reproductive strategy based on light and humidity levels, among other factors (Wright *et al.* 2004; Milla *et.* 2008). Photosynthetic capacity is the bioenergetic process that enables plants to synthesize organic matter using light energy, water and carbon dioxide (Wright *et al.* 2004). Water potential corresponds to the energetic state of water in a cell or leaf, for example. It represents the resultant energy of osmotic, turgor and capillary forces, among others (Cachinero-Vivar *et al.* 2024). These performances are assessed in terms of the values of the functional traits related to each function (Violle *et al.* 2007) to ensure the tree's survival, which involves conductivity, support, and pest and disease protection (fungi, insects).

There may be trade-offs between functional traits depending on environmental conditions and ecological preferences (or ecological groups) of the species (Poorter and Kitajima 2007). The ecological strategy of a species is defined by the trade-offs and values of the diverse functional traits. These strategies must be studied to enhance the overall understanding of biodiversity and related ontogenetic mechanisms, and to gain insight into the variability in the properties of the wood produced (wood quality) for various human uses (construction, furniture, packaging, paper, and energy). These strategies have been extensively studied in temperate species (Zimmermann and Brown 1971; Loehle 1988; Kolb *et al.* 1990; Del Tredici 2001; Brym *et al.* 2011; Adler *et al.* 2014; Bianchi *et al.* 2021; Cheng *et al.* 2022; Han *et al.* 2022). Conversely, little is known on the trends in tropical species (Lehnebach 2015; Levionnois 2019; Zue Ondo *et al.* 2021; González-Melo 2022; Han *et al.* 2022; Schmitt *et al.* 2022; Browne *et al.* 2023; Conti *et al.* 2023; Liu *et al.* 2023; Werden *et al.* 2023; Grady *et al.* 2024; Huanca-Nunez *et al.* 2024; Zhang *et al.* 2024), despite the high species diversity hosted in these areas. The aim of this literature review is to highlight current links between ecological preferences and the main functional traits of tree species, while focusing particularly on wood properties. The article is divided into four parts, with the concept of ecological groups described in the first part. Secondly, the links between functional characteristics and ecological groups are examined in terms of mechanical support in the next part, then in terms of hydraulic conductivity in the third part and to end up, in terms of protection against pathogens in the fourth and final part.

LIGHT DEPENDENCY AND ECOLOGICAL GROUPS

Trees are living organisms that require energy for their growth and survival (Rüger *et al.* 2011). Light in forests is highly stratified vertically while being horizontally heterogeneous, largely due to the forest gap dynamics. Light penetrates the forest and disperses from the top to the bottom of the canopy along different gradients (Niinemets and Valladares 2004; Demmig-Adams *et al.* 2017). Trees then use this light for photosynthesis (Fig. 1). Some tree species are able to survive even when there is very little available light available to them, whereas others may tolerate a certain extent of shade at some point during their lifespans without it impairing their development. These so-called understory tree species use a lower light gradient to carry out what is known as minimal photosynthesis (Demmig-Adams *et al.* 2017). Several authors have suggested characterising individuals of tree species based on their average light environment (King

1991; Clark and Clark 1992; Bongers and Sterck 1998; Sterck and Bongers 1998). The need for light is believed to be a key factor in determining species' habitat specialization (Mađerek *et al.* 2017; Schmitt *et al.* 2022). Tree species may therefore be classified into different ecological groups according to their light dependence.

A seed and seedling ecology hypothesis was put forward by Swaine and Whitmore (1988) and supported by authors such as Canham (1989) and Hubbell *et al.* (1999). Under this hypothesis, these authors claim that: "A species cannot be classified in a group without knowing the ecology of its seeds and seedlings," and they suggest classifying species in two groups, *i.e.*, pioneer and non-pioneer (or climax) species. Pioneers are species whose seeds and seedlings require full sunlight to become established and grow and their plants cannot survive under forest shade at any growth stage (Table 1) (Swaine and Whitmore, 1988; Whitmore 1989). Consequently, they are light-demanding plants. Otherwise, non-pioneer or climax species are those whose seeds and seedlings can become established and grow under forest shade throughout part or all of their lifespans. Their seedlings are thus commonly found underneath a forest canopy (Swaine and Whitmore 1988). Seeds of these non-pioneer species are larger, thereby offering the seedlings more abundant reserves necessary for their growth (Davies and Ashton 1999; Kitajima 2002; Poorter and Rose 2005).

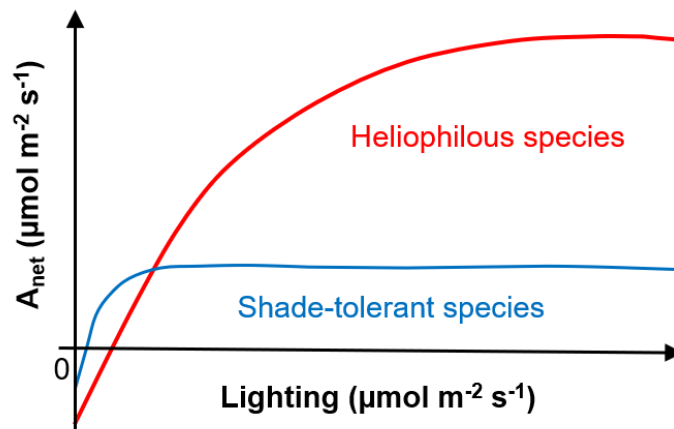


Fig. 1. Comparison of photosynthesis between heliophilous and shade-tolerant species. Photosynthetic light-response (A_{net}) measurements for shade-tolerant and shade-intolerant species grown in ambient or elevated CO_2 (+300 $\mu mol CO_2 mol^{-1}$). (adapted and redrawn from Sefcik *et al.* 2006)

The classification into pioneer and non-pioneer groups has since evolved, and most authors propose more nuanced categories of ecological groups. In the study by Blanc *et al.* (2003), the authors classify species in three groups: heliophilous (light-demanding), sciaphilous (shade-tolerant), and hemi-heliophilous (semi-shade-tolerant). The heliophilous trait is easier to distinguish than the sciaphilous trait (Blanc *et al.* 2003). Heliophilous plants require a substantial amount of light to grow. Species that can only grow in the shade are referred to as sciaphilous (Schmitt *et al.* 2022). There is also an intermediate group of so-called hemi-tolerant species. Plants of these species are able to start their life cycle in the undergrowth, but they will only be able to thrive if there is an opening in the forest canopy (Blanc *et al.* 2003). Other authors (Souza *et al.* 2014; Blundo *et al.* 2015; Shen and Cao 2017; Han *et al.* 2022; Wen *et al.* 2023; Jiang *et al.* 2024; Peng

et al. 2024) have proposed various classifications based on morphological traits, growth rates, leaf characteristics, and wood density, among others. These suggest divisions into two, three, or even seven ecological groups.

Table 1. Character of Pioneer Tree Species in Tropical Rainforests

i	Seeds germinate only in canopy spaces that are open to the sky and receive full sunlight.
ii	Plants cannot survive in the shade - young plants are never found under a closed forest canopy.
iii	Seeds are small and produced abundantly and more or less continuously.
iv	Seeds are produced early in life.
v	Seeds are dispersed by animals or the wind.
vi	Dormant seeds are generally abundant in forest soils (especially species with fleshy fruits); orthodox seeds (not known recalcitrant species).
vii	High rate of carbon fixation by seedlings; high compensation point
viii	Rapid growth in height
ix	Indeterminate growth without resting buds
x	Relatively few branches
xi	Short-lived leaves
xii	Shallow rooting
xiii	Generally pale, low density, non-siliceous wood
xiv	Leaves are susceptible to herbivory, sometimes with little chemical defence.
xv	Wide ecological range; phenotypically plastic
xvi	Often ephemeral

Not all pioneers have all the characters iii to xvi (adapted from Swaine and Whitmore 1988)

Heliophilous species grow faster and reach higher maximum heights (King 1991; Coomes and Grubb 1998; Veneklaas and Poorter 1998; Morel *et al.* 2018; Schmitt *et al.* 2022). These so-called canopy species allocate more resources to trunk rather than branch growth, which enables them to rapidly grow in height and compete for light (Poorter *et al.* 2012). Light competition is therefore beneficial for height growth (Montgomery and Chazdon 2002; Koch *et al.* 2004; R ger *et al.* 2011, 2012). The high growth rate of these species in forest gaps is also favoured by their less developed, short-lived, and physiologically active leaves (Poorter and Bongers 2006; Adler *et al.* 2014). The findings of Tenius Ribeiro *et al.* (2019) show that pioneer (*i.e.*, heliophilous) species tend to dominate in nutrient-enriched soils. Soil fertility therefore has an impact on the abundance of this ecological tree group (Xing *et al.* 2022; Ye *et al.* 2022).

For sciaphilous (shade-tolerant) species, survival rather than height growth for light is a crucial issue (Montgomery and Chazdon 2002). These species are characterised by their slow height growth (Schmitt *et al.* 2022) and high radial growth (broader trunk diameter) (Janse-Ten Klooster *et al.* 2007; Poorter *et al.* 2012). The high survival rate of these species in the forest understorey is facilitated by the formation of long-lived leaves and larger crowns (Poorter and Bongers 2006; Janse-Ten Klooster *et al.* 2007; Adler *et al.* 2014). Broader crowns improve light capture, which contributes to the trees' shade tolerance (Valladares and Niinemets 2008; Niinemets 2010; Poorter *et al.* 2012).

MECHANICAL SUPPORT FUNCTION

Mechanical support refers to all the mechanisms that enable a tree to support its own mass, maintain its vertical stance through its motricity (Martone *et al.* 2010; Trouy, 2015), while preventing damage from factors such as wind (Fournier *et al.* 2013; Trouy, 2015). The relationship between the tree diameter growth and the formed wood density depends on the species and whether it is a softwood or a hardwood (González-Melo 2022). Density variation within a growth ring is very important in softwoods. This is linked to seasonal changes and the formation of the final wood (Saranpää 2003).

Wood density is a crucial biomechanical feature because it is generally linked to all the other wood mechanical properties (Niklas and Spatz 2010; De Borst *et al.* 2012). Shade-tolerant species are denser (Lawton 1984; Thomas 1996; Muller-Landau 2004; Osunkoya *et al.* 2007; Adler *et al.* 2014) and hence more rigid than light-demanding species. These shade-tolerant species have optimal mechanical properties that provide more effective mechanical support (Table 2). Because of this higher density, shade-tolerant species have a higher survival rate than light-demanding species (Román-Dañobeytia *et al.* 2021). Wood density variations are often regarded as a trade-off for rapid competitive growth at the expense of wood quality, thereby reducing the trees' safety. However, the biomechanical safety features (bending stiffness, buckling resistance, breakage, or uprooting resistance) involve both tree shape factors and the intrinsic wood properties.

The secondary walls of normal wood consist of the S1, S2, and S3 layers. The S1 layer is made up of several lamellae, within which the cellulose microfibrils are oriented in alternating S- and Z-shaped helical structures (Salmén 2018). The S2 layer is the thickest and richest in cellulose (Salmén 2018). The cellulose fibrils within the S2 layer are almost vertical and all parallel (Salmén 2018). The angle of the microfibrils in this layer is another key parameter that impacts the performance of the mechanical support (Fournier *et al.* 2013). The S3 layer is also made up of lamellae, like S1. However, the helical texture of the microfibrils is still S-shaped. This layer is mainly made up of lignin and hemicelluloses. An increase in the microfibril angle in the S2 layer reduces the stiffness of the wood and its longitudinal stress resistance (De Borst *et al.* 2012; Trouy 2015; Maaß *et al.* 2020; Phan *et al.* 2024; Wang *et al.* 2024). This parameter varies according to the tree growth stage. Juvenile wood has a larger microfibril angle and is therefore less stiff than mature wood (Trouy 2015). Other parameters, such as the vessels and lignin content, affect the stiffness of the wood and thereby its mechanical support. A reduction in lignin content would lead to a decline in wood stiffness (Voelker *et al.* 2011; Özparpucu *et al.* 2019; Serra-Parareda *et al.* 2020; Choi *et al.* 2023). According to Zhang *et al.* (2023), lignin plays an important role in tree growth. According to the article, lignin deficiency suppresses tree growth through xylem collapse and phloem thickening. As a result, upright plants must biosynthesize lignin to provide mechanical support for secondary cell walls, enabling them to reach great heights. Yadav and Chattopadhyay (2023) support this assertion and add that lignification is an important process that provides the mechanical strength plants need to stand upright (Balk *et al.* 2023). Otherwise, regarding the vessels, it has been shown that their content, arrangement, and shape may impact the macroscopic wood stiffness (De Borst *et al.* 2012). There is a clear link between the hydraulic efficiency and mechanical support in relation to the wood physical, chemical, and anatomical properties.

Table 2. Mechanical and Physical Properties of Shade-tolerant (n = 20) and Pioneer (n = 10) Rain Forest Tree Species*

Properties	Shade-tolerant	Pioneer	<i>p</i>
Dry density, vertical stems (kg.m ⁻³)	450.0 (80.0)	270.0 (130.0)	***
Compression strength (N.mm ⁻²)	21.1 (4.5)	13.3 (8.3)	*
Modulus of rupture (N.mm ⁻²)	57.3 (13.5)	35.8 (24.1)	**
Modulus of elasticity (N.mm ⁻²)	5220.0 (1431.0)	4420.0 (1082.0)	ns

*(Adapted from Van Gelder *et al.* 2006); Mean values (\pm standard deviation) and significance levels (*p*) of *t* test; ns: $p > 0.05$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$

CONDUCTIVITY FUNCTION

The vessel size and frequency are linked to the hydraulic conductivity, with larger vessels conducting water more efficiently than narrower ones (Olson and Rosell 2013). However, larger vessels cavitate before narrower vessels (Mauseth and Stevenson 2004). Moreover, the tree height is associated with the vessel size and frequency (Preston *et al.* 2006; Martínez-Cabrera *et al.* 2011). McCulloh *et al.* (2010) found that hydraulic conductivity also varies with the trunk diameter. Although negative correlations have been found between growth-related hydraulic characteristics and wood density (Santiago *et al.* 2004; Hoeber *et al.* 2014), according to Fan *et al.* (2012), anatomical features associated with conductivity are much better descriptors of tree growth rate. Koch *et al.* (2004) and Anfodillo *et al.* (2006) highlighted a link between tree height growth and hydraulic conductivity, with tall trees requiring greater conductivity and therefore larger vessels (Olson *et al.* 2014). Light-demanding species thus have larger vessels than shade-tolerant species (Chave *et al.* 2009; González-Melo 2022). The conduction function is optimal in light-demanding species. The link between vessel size and frequency has been reported by Fan *et al.* (2012); trees with larger diameter vessels have fewer of them. Shade-tolerant species are reported to have narrower and more frequent vessels with a lower hydraulic efficiency (Searson *et al.* 2004; Preston *et al.* 2006; Hacke *et al.* 2006; Pratt *et al.* 2007). Rüger *et al.* (2011) pointed out that little is known about how the growth of species present in species-rich tropical forests differs according to their shade tolerance.

The effects of climatic conditions on tree growth vary between species, and these effects are important for gaining insight into tree stand dynamics (Oboite and Comeau 2021). The different responses of species to drought and frost could mirror the ecological groups to which they belong (Jucker *et al.* 2014; Nourtier *et al.* 2014; Latreille *et al.* 2017). Pfautsch *et al.* (2016) showed that tree height was promoted by the extent of available water. This latter availability would therefore be essential for the growth of light-demanding species. Large air bubbles are more likely to form in large vessels, which means that light-demanding species are more susceptible to freeze-thaw embolism (Pittermann and Sperry 2006; Charra-Vaskou *et al.* 2016). Shade-tolerant species are more drought resistant (Adler *et al.* 2014; Jucker *et al.* 2014), which is facilitated because the vessels are smaller and more numerous, according to Baas *et al.* (2004). Recent studies (Rüger *et al.* 2020; Guillemot *et al.* 2022) have also indicated a natural tendency for slow-growing species to better withstand drought (Fig. 2). In such cases, embolism due to drought stress depends on the pore size in pit primary walls rather than on the vessel size (Cochard and Granier 1999). Levionnois *et al.* (2021) also revealed the low predictive power of vessel

diameter on resistance to embolism due to drought as compared to the cell wall diameter-thickness ratio.

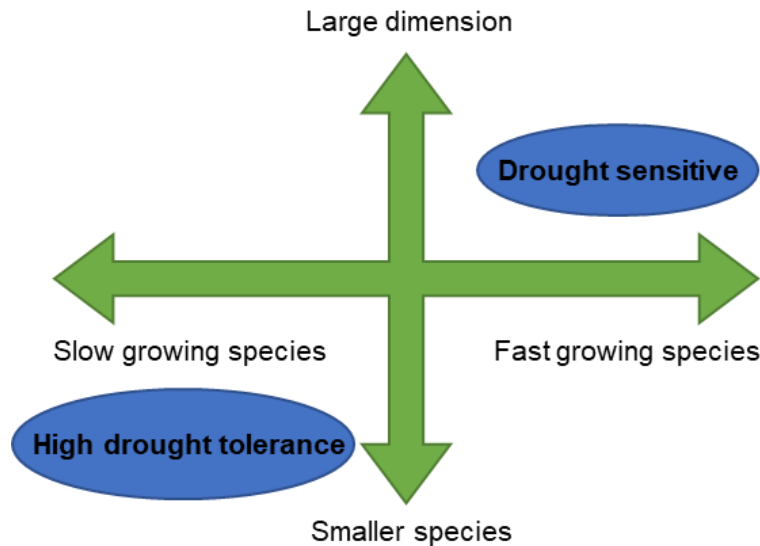


Fig. 2. Correlation between drought tolerance vs. size and growth rate of trees (redrawn from Guillemot *et al.* 2022)

PROTECTION FUNCTION

The main properties involved in wood durability are the quantity and composition of heartwood extractives (Wink 2010; Martín and López 2023). Extractives are low molecular weight secondary organic compounds (Fig. 3). Secondary metabolites that give the wood its external stress resistance properties are synthesised during the heartwood extractive formation process (Hillis 1971). Such formation and distribution to the heartwood enables it to withstand attacks by fungi and wood-eating insects. This protection enables the heartwood to maintain its strength over time, thus preserving the integrity of the tree. The wood density is also related to its durability (Chave *et al.* 2006; Nock *et al.* 2009). High wood density is associated with enhanced protection against fungal attack (Falster 2006; Larjavaara and Muller-Landau 2010).

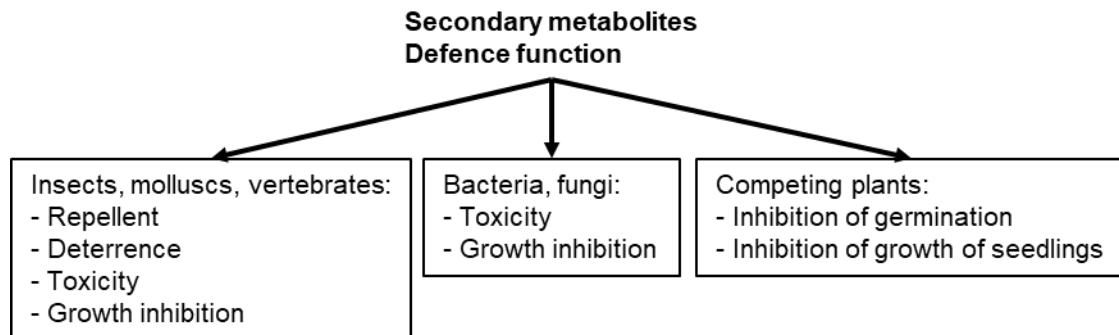


Fig. 3. Defence function of plant secondary metabolites (redrawn from Wink 2010)

Most variability in wood durability (including the proportion of heartwood) is genetically controlled (Pâques 2001). Environmental, silvicultural management, and stand site factors have a more limited impact (Harju *et al.* 2001; Taylor *et al.* 2002). The extractive content generally increases from the pith to the outer heartwood, peaking in the heartwood-sapwood transition zone. The extractive content decreases longitudinally with the tree height, whereas it increases as the tree ages (Hillis 1987). The heartwood of species with a long lifespan is more durable (Wheeler *et al.* 1989).

Shade-tolerant species and light-demanding species are both sensitive to external stresses at the juvenile wood stage, yet light-demanding species are more sensitive, given their growth-defence trade-off at this development stage (González-Melo 2022). Tree ageing is linked to tree survival, *i.e.*, a trait of shade-tolerant species. These species will presumably always produce more wood (higher extractive content) than light-demanding species, as confirmed by the findings of various authors (Dudt and Shure 1994; Coley and Barone 1996; Falster 2006; Imaji and Seiwa 2010; Sillett *et al.* 2010; Mađerek *et al.* 2017; González-Melo 2022). This investment in the protective function of shade-tolerant species is reflected, for instance, in their high phenolic compound and tannin contents, as well as their low herbivory levels (Dudt and Shure 1994; Imaji and Seiwa 2010; Mađerek *et al.* 2017). This latter point should nevertheless be considered with caution because studies on heartwood extractive formation products have revealed a range of different strategies regarding this process. In a comparative study of the natural durability of highly durable species from French Guiana, Amusant *et al.* (2014) proposed that there are two types of strategy: extractive quantity *vs.* extractive quality. These authors suggested that the natural durability of *Vouacapoua americana* is due to its high quantity of extractives, whereas that of *Bocoa prouacensis* is due to the high quality and/or specificity and toxicity of its extractives rather than to their high quantity.

CONCLUDING REMARKS

Trees - as they grow - fulfil the mechanical support, conduction, and protection functions necessary for their survival. The functional features of trees reflect the different ways in which a specific function can be achieved. A single species cannot be the best performer for all functions and under all growth conditions, which leads us to the trade-off concept. The functional traits of a species reflect its ecological strategy. Previously published studies highlighted the main characteristics of species while sketching a portrait of target species according to their degree of shade tolerance.

Heliophilous species may grow rapidly to reach great heights, while having a slender trunk. These light-demanding species have larger and fewer vessels, which means that their conduction function is efficient and optimal. However, they become more vulnerable to drought-induced cavitation. Sciophilous species are slow growing with larger trunk diameters (not slender). The crowns are broad and the trees have long-lived leaves, contrary to heliophilous species. These shade-tolerant species have denser and stiffer wood with better mechanical support, which is compatible with their slenderness. Their hydraulic conductivity is, however, less effective given that the vessels are narrower and more numerous. Thus, their xylem is more resistant to cavitation. Sciophilous species have better pest and disease protection with higher extractive levels alongside their high wood density. Unfortunately, little bibliographical information is available on the protective function.

Overall, minimal research has focused on functional traits associated with the ecological strategies of tropical tree species, despite their great diversity.

The integrative nature of wood density should be highlighted. This technological property appears to be the only feature that dovetails with all tree functions. Wood density is also linked to many of its physical and mechanical properties. Yet the wood density alone cannot explain everything. Rather, trees (and wood) are the result of a complex and extremely refined evolutionary process. These properties, which we have classified as technological, physical, anatomical, chemical, and mechanical, are interdependent. Few studies have jointly focused on all these properties, but gaining greater insight into them would enhance our understanding of different growth strategies and the development of wood quality.

REFERENCES CITED

- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., and Franco, M. (2014). “Functional traits explain variation in plant life history strategies,” *Proceedings of the National Academy of Sciences* 111(2), 740-745. DOI: 10.1073/pnas.1315179111
- Amusant, N., Nigg, M., Thibaut, B., and Beauchêne, J. (2014). “Diversity of decay resistance strategies of durable tropical woods species: *Bocoa prouacensis* Aublet, *Vouacapoua americana* Aublet, *Inga alba* (Sw.) Wild,” *International Biodeterioration & Biodegradation* 94, 103-108. DOI: 10.1016/j.ibiod.2014.06.012
- Anfodillo, T., Carraro, V., Carrer, M., Fior, C., and Rossi, S. (2006). “Convergent tapering of xylem conduits in different woody species,” *New Phytologist* 169(2), 279-290. DOI: 10.1111/j.1469-8137.2005.01587.x
- Baas, P., Ewers, F. W., Davis, S. D., and Wheeler, E. A. (2004). “Evolution of xylem physiology,” in: *The Evolution of Plant Physiology*, Elsevier Academic Press, London, UK, pp. 273-295. DOI: 10.1016/B978-012339552-8/50016-0
- Balk, M., Sofia, P., Neffe, A. T., and Tirelli, N. (2023). “Lignin, the lignification process, and advanced, lignin-based materials,” *International Journal of Molecular Sciences* 24(14), article 11668. DOI: 10.3390/ijms241411668
- Bianchi, E., Bugmann, H., and Bigler, C. (2021). “Light availability predicts mortality probability of conifer saplings in Swiss mountain forests better than radial growth and tree size,” *Forest Ecology and Management* 479, article ID 118607. DOI: 10.1016/j.foreco.2020.118607
- Blanc, L., Flores, O., Molino, J. F., Gourlet-Fleury, S., and Sabatier, D. (2003). “Diversity and groupings of arborescent species in the forests of French Guiana,” *Revue Forestière Française* 55, 131-146. DOI: 10.5555/20043148194
- Blundo, C., Malizia, L. R., and González-Espinosa, M. (2015). “Distribution of functional traits in subtropical trees across environmental and forest use gradients,” *Acta Oecologica* 69, 96-104.
- Bongers, F., and Sterck, F. J. (1998). “Architecture and development of rainforest trees: responses to light variation,” *Dynamics of Tropical Communities* 125-162. DOI: 10.5555/19980612804
- Browne, L., Markesteijn, L., Manzané-Pinzón, E., Wright, S. J., Bagchi, R., Engelbrecht, B. M., and Comita, L. S. (2023). “Widespread variation in functional trait–vital rate

- relationships in tropical tree seedlings across a precipitation and soil phosphorus gradient,” *Functional Ecology* 37(2), 248-260. DOI: 10.1111/1365-2435.14213
- Brym, Z. T., Lake, J. K., Allen, D., and Ostling, A. (2011). “Plant functional traits suggest novel ecological strategy for an invasive shrub in an understory woody plant community,” *Journal of Applied Ecology* 48(5), 1098-1106. DOI: 10.1111/j.1365-2664.2011.02049.x
- Cachinero-Vivar, A. M., Navarro-Cerrillo, R. M., Cabrera-Puerto, R. J., and Pérez-Priego, O. (2024). “Impact of thinning on leaf economics, plant hydraulics, and growth dynamics,” *Forest Ecology and Management* 562, article 121914. DOI: 10.1016/j.foreco.2024.121914
- Canham, C. D. (1989). “Different response to gaps among shade-tolerant tree species,” *Ecology* 70(3), 548-550. DOI: 10.2307/1940200
- Charra-Vaskou, K., Badel, E., Charrier, G., Ponomarenko, A., Bonhomme, M., Foucat, L., Mayr, S., and Améglio, T. (2016). “Cavitation and water fluxes driven by ice water potential in *Juglans regia* during freeze-thaw cycles,” *Journal of Experimental Botany* 67(3), 739-750. DOI: 10.1093/jxb/erv486
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E. (2009). “Towards a worldwide wood economics spectrum,” *Ecology Letters* 12, 351-366. DOI: 10.1111/j.1461-0248.2009.01285.x
- Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. T., and Webb, C. O. (2006). “Regional and phylogenetic variation of wood density across 2456 neotropical tree species,” *Ecological Applications* 16(6), 2356-2367. DOI: 10.1890/1051-0761(2006)016[2356:RAPVOW]2.0.CO;2
- Cheng, X., Ping, T., Li, Z., Wang, T., Han, H., and Epstein, H. E. (2022). “Effects of environmental factors on plant functional traits across different plant life forms in a temperate forest ecosystem,” *New Forests* 53(1), 125-142. DOI: 10.1007/s11056-021-09847-0
- Choi, S. J., Lee, Z., Kim, S., Jeong, E., and Shim, J. S. (2023). “Modulation of lignin biosynthesis for drought tolerance in plants,” *Frontiers in Plant Science* 14, article 1116426. DOI: 10.3389/fpls.2023.1116426
- Clark, D. A., and Clark, D. B. (1992). “Life history diversity of canopy and emergent trees in a neotropical rain forest,” *Ecological Monographs* 62(3), 315-344. DOI: 10.2307/2937114
- Cochard, H., and Granier, A. (1999). “Fonctionnement hydraulique des arbres forestiers (Hydraulic functioning of forest trees),” *Revue Forestiere Francaise* 51(2), 121-134. DOI: 10.4267/2042/5425
- Coley, P. D., and Barone, J. A. (1996). “Herbivory and plant defenses in tropical forests,” *Annual Review of Ecology and Systematics* 27, 305-335. DOI: 10.1146/annurev.ecolsys.27.1.305
- Conti, L., Valencia, E., Galland, T., Götzenberger, L., Lepš, J., E-Vojtkó, A., and De Bello, F. (2023). “Functional trait trade-offs define plant population stability across different biomes,” *Proceedings of the Royal Society B* 290(2001), article 20230344. DOI: 10.1098/rspb.2023.0344
- Coomes, D. A., and Grubb, P. J. (1998). “A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships,” *Functional Ecology* 12(3), 426-435. DOI: 10.1046/j.1365-2435.1998.00211.x

- Davies, S. J., and Ashton, P. S. (1999). "Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (*Euphorbiaceae*) in Borneo," *American Journal of Botany* 86(12), 1786-1795. DOI: 10.2307/2656675
- De Borst, K., Bader, T. K., and Wikete, C. (2012). "Microstructure-stiffness relationships of ten European and tropical hardwood species," *Journal of Structural Biology* 177(2), 532-542. DOI: 10.1016/j.jsb.2011.10.010
- Del Tredici, P. (2001). "Sprouting in temperate trees: A morphological and ecological review," *The Botanical Review* 67(2), 121-140. DOI: 10.1007/BF02858075
- Demmig-Adams, B., Stewart, J. J., and Adams, III, W. W. (2017). "Environmental regulation of intrinsic photosynthetic capacity: An integrated view," *Current Opinion in Plant Biology* 37, 34-41. DOI: 10.1016/j.pbi.2017.03.008
- Dudt, J. F., and Shure, D. J. (1994). "The influence of light and nutrients on foliar phenolics and insect herbivory," *Ecology* 75(1), 86-98. DOI: 10.2307/1939385
- Falster, D. S. (2006). "Sapling strength and safety: The importance of wood density in tropical forests," *New Phytologist* 171(2), 237-239. DOI: 10.1111/j.1469-8137.2006.01809.x
- Fan, Z. X., Zhang, S. B., Hao, G. Y., Ferry Slik, J. W., and Cao, K. F. (2012). "Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density," *Journal of Ecology* 100(3), 732-741. DOI: 10.1111/j.1365-2745.2011.01939.x
- Fournier, M., Dlouhá, J., Jaouen, G., and Almeras, T. (2013). "Integrative biomechanics for tree ecology: Beyond wood density and strength," *Journal of Experimental Botany* 64(15), 4793-4815. DOI: 10.1093/jxb/ert279
- González-Melo, A. (2022). "Wood anatomical traits mediate life-history variations at the sapling, but not at the adult stage," *Trees* 36, 1337-1347. DOI: 10.1007/s00468-022-02293-1
- Grady, J. M., Read, Q. D., Record, S., Rüger, N., Zarnetske, P. L., Dell, A. I., and Enquist, B. J. (2024). "Life history scaling in a tropical forest," *Journal of Ecology* 112(3), 487-500. DOI: 10.1111/1365-2745.14245
- Guillemot, J., Martin-StPaul, N. K., Bulascoschi, L., Poorter, L., Morin, X., Pinho, B. X., le Maire, G., Bittencourt, P., Oliveira, R. S., Bongers, F., *et al.* (2022). "Small and slow is safe: On the drought tolerance of tropical tree species," *Global Change Biology* 28(8), 2622-2638. DOI: 10.1111/gcb.16082
- Hacke, U. G., Sperry, J. S., Wheeler, J. K., and Castro, L. (2006). "Scaling of angiosperm xylem structure with safety and efficiency," *Tree Physiology* 26, 689-701. DOI: 10.1093/treephys/26.6.689
- Han, X., Huang, J., and Zang, R. (2022). "Soil nutrients and climate seasonality drive differentiation of ecological strategies of species in forests across four climatic zones," *Plant and Soil* 473(1-2), 517-531. DOI: 10.1007/s11104-022-05303-w
- Han, X., Xu, Y., Huang, J., and Zang, R. (2022). "Species diversity regulates ecological strategy spectra of forest vegetation across different climatic zones," *Frontiers in Plant Science* 13, article 807369. DOI: 10.3389/fpls.2022.807369
- Harju, A. M., Venäläinen, M., Beuker, E., Velling, P., and Viitanen, H. (2001). "Genetic variation in the decay resistance of scots pine wood against brown rot fungus," *Canadian Journal of Forest Research* 31, 1244-1249. DOI: 10.1139/x01-059
- Hillis, W. E. (1971). "Distribution, properties and formation of some wood extractives," *Wood Science and Technology* 5(4), 272-289. DOI: 10.1007/BF00365060

- Hillis, W. E. (1987). *Heartwood and Tree Exudates*, Springer Series in Wood Science (SSWO, volume 4), Springer Berlin, Heidelberg, Berlin, Germany.
- Hoerber, S., Leuschner, C., Köhler, L., Arias-Aguilar, D., and Schuldt, B. (2014). “The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate,” *Forest Ecology and Management* 330, 126-136. DOI: 10.1016/j.foreco.2014.06.039
- Huanca-Nunez, N., Chazdon, R. L., and Russo, S. E. (2024). “Trait-mediated variation in seedling performance in Costa Rican successional forests: Comparing above-ground, below-ground, and allocation-based traits,” *Plants* 13(17), article 2378. DOI: 10.3390/plants13172378
- Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J., and De Lao, S. L. (1999). “Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest,” *Science* 283(5401), 554-557. DOI: 10.1126/science.283.5401.554
- Hudson, I., Wilson, L., and van Beveren, K. (1998). “Vessel and fibre property variation in *Eucalyptus globulus* and *Eucalyptus nitens*: Some preliminary results,” *IAWA Journal* 19(2), 111-130.
- Imaji, A., and Seiwa, K. (2010). “Carbon allocation to defense, storage, and growth in seedlings of two temperate broad-leaved tree species,” *Oecologia* 162(2), 273-281. DOI: 10.1007/s00442-009-1453-3
- Imbert, J. B., Blanco, J. A., Candel-Pérez, D., Lo, Y. H., González de Andrés, E., Yeste, A., and Chang, S. C. (2021). “Synergies between climate change, biodiversity, ecosystem function and services, indirect drivers of change and human well-being in forests,” in: *Exploring Synergies and Trade-offs between Climate Change and the Sustainable Development Goals*, Springer, Singapore. DOI: 10.1007/978-981-15-7301-9_12
- Janse-Ten Klooster, S. H., Thomas, E. J. P., and Sterck, F. J. (2007). “Explaining interspecific differences in sapling growth and shade tolerance in temperate forests,” *Journal of Ecology* 95(6), 1250-1260. DOI: 10.1111/j.1365-2745.2007.01299.x
- Jiang, Y., Chen, Z., Lin, H., Deng, R., Liang, Z., Li, Y., and Liang, S. (2024). “Trait-based community assembly and functional strategies across three subtropical karst forests, Southwestern China,” *Frontiers in Plant Science* 15, article 1451981. DOI: 10.3389/fpls.2024.1451981
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., and Coomes, D. A. (2014). “Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests,” *Journal of Ecology* 102(5), 1202-1213. DOI: 10.1111/1365-2745.12276
- Keleş, S. (2019). “An assessment of hydrological functions of forest ecosystems to support sustainable forest management,” *Journal of Sustainable Forestry* 38(4), 305-326. DOI: 10.1080/10549811.2018.1547879
- King, D. A. (1991). “Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings,” *Ecology* 72(4), 485-492. DOI: 10.2307/2389630
- Kitajima, K. (2002). “Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three *Bignoniaceae* species,” *Functional Ecology* 16(4), 433-444. DOI: 10.1046/j.1365-2435.2002.00641.x
- Koch, G. W., Sillett, S. C., Jennings, G. M., and Davis, S. D. (2004). “The limits to tree height,” *Nature* 428, 851-854. DOI: 10.1038/nature02417

- Kolb, T. E., Steiner, K. C., McCormick, L. H., and Bowersox, T. W. (1990). "Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy," *Forest Ecology and Management* 38, 65-78. DOI: 10.1016/0378-1127(90)90086-Q
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., *et al.* (2016). "Plant functional traits have globally consistent effects on competition," *Nature* 529, 204-207. DOI: 10.1038/nature16476
- Larjavaara, M., and Muller-Landau, H. C. (2010). "Rethinking the value of high wood density," *Functional Ecology* 24(4), 701-705.
- Latreille, A., Davi, H., Huard, F., and Pichot, C. (2017). "Variability of the climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients," *Forest Ecology and Management* 396, 150-159. DOI: 10.1016/j.foreco.2017.04.012
- Lawton, R. O. (1984). "Ecological constraints on wood density in a tropical Montane rain forest," *American Journal of Botany* 71(2), 261-267. DOI: 10.1002/j.1537-2197.1984.tb12512.x
- Lehnebach, R. (2015). *Study of the Ontogenic Variability of the Woody Profile in Some Tropical Forest Species in French Guiana*, Doctoral Dissertation, University of Montpellier, France. (in French)
- Levionnois, S. (2019). *Diversity and Variability of Vascular and Hydraulic Leaf Shoot Architecture in Canopy Trees of a Tropical Rainforest*, Doctoral Dissertation, University of French Guyana, France. (in French)
- Levionnois, S., Jansen, S., Wandji, R. T., Beauchêne, J., Ziegler, C., Coste, S., Stahl, C., Delzon, S., Authier, L., and Heuret, P. (2021). "Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees," *New Phytologist* 229(3), 1453-1466. DOI: 10.1111/nph.16942
- Liu, L., Xia, H., Quan, X., and Wang, Y. (2023). "Plant trait-based life strategies of overlapping species vary in different succession stages of subtropical forests, Eastern China," *Frontiers in Ecology and Evolution* 10, article 1103937. DOI: 10.3389/fevo.2022.1103937
- Loehle, C. (1988). "Tree life history strategies: The role of defenses," *Canadian Journal of Forest Research* 18(2), 209-222. DOI: 10.1139/x88-032
- Maaß, M. C., Saleh, S., Militz, H., and Volkert, C. A. (2020). "The structural origins of wood cell wall toughness," *Advanced Materials* 32(16), article 1907693. DOI: 10.1002/adma.201907693
- Mađerek, E., Zadworny, M., Mucha, J., and Karolewski, P. (2017). "Light as a regulator of structural and chemical leaf defenses against insects in two *Prunus* species," *Acta Oecologica* 85, 18-24. DOI: 10.1016/j.actao.2017.09.002
- Martín, J. A., and López, R. (2023). "Biological deterioration and natural durability of wood in Europe," *Forests* 14(2), article 283. DOI: 10.3390/f14020283
- Martinez-Cabrera, H. I., Schenk, H. J., Cevallos-Ferriz, R. S., and Jones, C. S. (2011). "Integration of vessel traits, wood density, and height in angiosperm shrubs and trees," *American Journal of Botany* 98, 915-922. DOI: 10.3732/ajb.1000335
- Martone, P. T., Boiler, M., Burgert, I., Dumais, J., Edwards, J., MacH, K., Rowe, N., Rugeberg, M., Seidel, R., and Speck, T. (2010). "Mechanics without muscle: Biomechanical inspiration from the plant world," *Integrative and Comparative Biology* 50(5), 888-907. DOI: 10.1093/icb/icq122

- Mauseth, J. D., and Stevenson, J. F. (2004). "Theoretical considerations of vessel diameter and conductive safety in populations of vessels," *International Journal of Plant Sciences* 165(3), 359-368. DOI: 10.1086/382808
- McCulloh, K., Sperry, J. S., Lachenbruch, B., Meinzer, F. C., Reich, P. B., and Voelker, S. (2010). "Moving water well: Comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse-porous saplings from temperate and tropical forests," *New Phytologist* 186(2), 439-450. DOI: 10.1111/j.1469-8137.2010.03181.x
- Metz, M. R., Wright, S. J., Zimmerman, J. K., Hernández, A., Smith, S. M., Swenson, N. G., and Garwood, N. C. (2023). "Functional traits of young seedlings predict trade-offs in seedling performance in three neotropical forests," *Journal of Ecology* 111(12), 2568-2582. DOI: 10.1111/1365-2745.14195
- Milla, R., Reich, P. B., Niinemets, Ü., and Castro-Díez, P. (2008). "Environmental and developmental controls on specific leaf area are little modified by leaf allometry," *Functional Ecology* 22(4), 565-576. DOI: 10.1111/j.1365-2435.2008.01406.x
- Montgomery, R., and Chazdon, R. (2002). "Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps," *Oecologia* 131, 165-174. DOI: 10.1007/s00442-002-0872-1
- Morel, H., Lehnebach, R., Cigna, J., Ruelle, J., Nicolini, E., and Beauchene, J. (2018). "Basic wood density variations of *Parkia velutina* Benoist, a long-lived heliophilic Neotropical rainforest tree," *Bois et Forêts des Tropiques* 335(1), 59-69. DOI: 10.19182/bft2018.335.a31518
- Muller-Landau, H. C. (2004). "Interspecific and inter-site variation in wood specific gravity of tropical trees," *Biotropica* 36(1), 20-32. DOI: 10.1111/j.1744-7429.2004.tb00292.x
- Niinemets, Ü., and Valladares, F. (2004). "Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: Optimality and constraints," *Plant Biology* 6(03), 254-268. DOI: 10.1055/s-2004-817881
- Niinemets, Ü. (2010). "A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance," *Ecological Research* 25, 693-714. DOI: 10.1007/s11284-010-0712-4
- Niklas, K. J., and Spatz, H. C. (2010). "Worldwide correlations of mechanical properties and green wood density," *American Journal of Botany* 97(10), 1587-1594. DOI: 10.3732/ajb.1000150
- Nock, C. A., Geihofer, D., Grabner, M., Baker, P. J., Bunyavejchewin, S., and Hietz, P. (2009). "Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand," *Annals of Botany* 104(2), 297-306. DOI: 10.1093/aob/mcp118
- Nourtier, M., Chanzy, A., Cailleret, M., Yingge, X., Huc, R., and Davi, H. (2014). "Transpiration of silver fir (*Abies alba* mill.) during and after drought in relation to soil properties in a Mediterranean mountain area," *Annals of Forest Science* 71(6), 683-695. DOI: 10.1007/s13595-012-0229-9
- Oboite, F. O., and Comeau, P. G. (2021). "Climate sensitive growth models for predicting diameter growth of western Canadian boreal tree species," *Forestry* 94(3), 363-373. DOI: 10.1093/forestry/cpaa039
- Olson, M. E., and Rosell, J. A. (2013). "Vessel diameter-stem diameter scaling across woody angiosperms and the ecological causes of xylem vessel diameter variation," *New Phytologist* 197(4), 1204-1213. DOI: 10.1111/nph.12097

- Olson, M. E., Anfodillo, T., Rosell, J. A., Petit, G., Crivellaro, A., Isnard, S., León-Gómez, C., Alvarado-Cárdenas, L. O., and Castorena, M. (2014). “Universal hydraulics of the flowering plants: Vessel diameter scales with stem length across angiosperm lineages, habits and climates,” *Ecology Letters* 17(8), 988-997. DOI: 10.1111/ele.12302
- Osunkoya, O. O., Sheng, T. K., Mahmud, N. A., and Damit, N. (2007). “Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island,” *Austral Ecology* 32(2), 191-201. DOI: 10.1111/j.1442-9993.2007.01678.x
- Özparpucu, M., Gierlinger, N., Cesarino, I., Burgert, I., Boerjan, W., and Rüggeberg, M. (2019). “Significant influence of lignin on axial elastic modulus of poplar wood at low microfibril angles under wet conditions,” *Journal of experimental botany* 70(15), 4039-4047. DOI: 10.1093/jxb/erz180
- Pâques, L. (2001). “Genetic control of heartwood content in larch,” *Silvae Genetica* 50(2), 69-75. DOI: 10.5555/20013137863
- Peng, Y., Cui, G., Li, H., Wang, N., Zheng, X., Ding, H., and Fang, Y. (2024). “Can CSR strategy classes determined by StrateFy explain the species dominance and diversity of a forest community?,” *Forests* 15(8), article 1412. DOI: 10.3390/f15081412
- Pfautsch, S., Harbusch, M., Wesolowski, A., Smith, R., Macfarlane, C., Tjoelker, M. G., Reich, P. B., and Adams, M. A. (2016). “Climate determines vascular traits in the ecologically diverse genus *Eucalyptus*,” *Ecology Letters* 19(3), 240-248. DOI: 10.1111/ele.12559
- Phan, N. T., Auslender, F., Gril, J., and Moutou Pitti, R. (2024). “Effects of cellulose fibril cross-linking on the mechanical behavior of wood at different scales,” *Wood Science and Technology* 58, 1555-1583. DOI: 10.1007/s00226-024-01569-8
- Pittermann, J., and Sperry, J. S. (2006). “Analysis of freeze-thaw embolism in conifers. The interaction between cavitation pressure and tracheid size,” *Plant Physiology* 140(1), 374-382. DOI: 10.1104/pp.105.067900
- Poorter, L., and Bongers, L. (2006). “Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups,” *Ecology* 87, 1289-1301. DOI: 10.1890/0012-9658(2006)87[1289:AOMTST]2.0.CO;2
- Poorter, L., and Kitajima, K. (2007). “Carbohydrate storage and light requirements of tropical moist and dry forest tree species,” *Ecology* 88(4), 1000-1011. DOI: 10.1890/06-0984
- Poorter, L., and Rose, S. A. (2005). “Light-dependent changes in the relationship between seed mass and seedling traits: A meta-analysis for rain forest tree species,” *Oecologia* 142, 378-387. DOI: 10.1007/s00442-004-1732-y
- Poorter, L., Lianes, E., Moreno-de las Heras, M., and Zavala, M. A. (2012). “Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate,” *Plant Ecology* 213(5), 707-722. DOI: 10.1007/s11258-012-0032-6
- Pratt, R. B., Jacobsen, A. L., Ewers, F. W. and Davis, S. D. (2007). “Relationships among xylem transport, biomechanics and storage in stems and roots of nine *Rhamnaceae* species of the California chaparral,” *New Phytologist* 174, 787-798. DOI: 10.1111/j.1469-8137.2007.02061.x
- Preston, K. A., Cornwell, W. K., and DeNoyer, J. L. (2006). “Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms,” *New Phytologist* 170, 807-818. DOI: 10.5555/20063132632

- Román-Dañobeytia, F., Cabanillas, F., Lefebvre, D., Farfan, J., Alferez, J., Polo-Villanueva, F., Llacsahuanga, J., Vega, C. M., Velasquez, M., Corvera, R., *et al.* (2021). "Survival and early growth of 51 tropical tree species in areas degraded by artisanal gold mining in the Peruvian Amazon," *Ecological Engineering* 159, article ID 106097. DOI: 10.1016/j.ecoleng.2020.106097
- Rüger, N., Berger, U., Hubbell, S. P., Vieilledent, G., and Condit, R. (2011). "Growth strategies of tropical tree species: Disentangling light and size effects," *PLoS ONE* 6(9). DOI: 10.1371/journal.pone.0025330
- Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., Lopez O. R., Wirth, C., and Fariori, C. E. (2020). "Demographic trade-offs predict tropical forest dynamics," *Science* 368(6487), 165-168. DOI: 10.1126/science.aaz4797
- Rüger, N., Wirth, C., Joseph Wright, S., and Condit, R. (2012). "Functional traits explain light and size response of growth rates in tropical tree species," *Ecology* 93(12), 2626-2636. DOI: 10.1890/12-0622.1
- Salmén, L. (2018). "Wood cell wall structure and organisation in relation to mechanics," in: *Plant Biomechanics*, Springer Cham. DOI: 10.1007/978-3-319-79099-2_1
- Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., and Jones, T. (2004). "Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees," *Oecologia* 140, 543-550. DOI: 10.1007/s00442-004-1624-1
- Saranpää, P. (2003). "Wood density and growth," in: *Wood Quality and its Biological Basis*, Wiley-Blackwell.
- Schmitt, S., Tysklind, N., Heuertz, M., and Hérault, B. (2022). "Selection in space and time: Individual tree growth is adapted to tropical forest gap dynamics," *Molecular Ecology* 2022, article 16392. DOI: 10.1111/mec.16392
- Searson, M. J., Thomas, D. S., Montagu, K. D., and Conroy, J. P. (2004). "Wood density and anatomy of water-limited eucalypts," *Tree Physiology* 24(11), 1295-1302. DOI: 10.1093/treephys/24.11.1295
- Sefcik, L. T., Zak, D. R., and Ellsworth, D. S. (2006). "Photosynthetic responses to understory shade and elevated carbon dioxide concentration in four northern hardwood tree species," *Tree Physiology* 26, 1589-1599. DOI: 10.1093/treephys/26.12.1589
- Serra-Parareda, F., Tarrés, Q., Espinach, F. X., Vilaseca, F., Mutjé, P., and Delgado-Aguilar, M. (2020). "Influence of lignin content on the intrinsic modulus of natural fibers and on the stiffness of composite materials," *International Journal of Biological Macromolecules* 155, 81-90. DOI: 10.1016/j.ijbiomac.2020.03.160
- Shen, X., and Cao, L. (2017). "Tree-species classification in subtropical forests using airborne hyperspectral and LiDAR data," *Remote Sensing* 9(11), article 1180. DOI: 10.3390/rs9111180
- Sillett, S. C., van Pelt, R., Koch, G. W., Ambrose, A. R., Carroll, A. L., Antoine, M. E., and Mifsud, B. M. (2010). "Increasing wood production through old age in tall trees," *Forest Ecology and Management* 259(5), 976-994. DOI: 10.1016/j.foreco.2009.12.003
- Souza, A. F., Forgiarini, C., Longhi, S. J., and Oliveira, J. M. (2014). "Detecting ecological groups from traits: a classification of subtropical tree species based on ecological strategies," *Brazilian Journal of Botany* 37, 441-452. DOI: 10.1007/s40415-014-0084-z

- Sterck, F. J., and Bongers, F. (1998). "Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees," *American Journal of Botany* 85(2), 266-272. DOI: 10.2307/2446315
- Swaine, M. D., and Whitmore, T. C. (1988). "On the definition of ecological species groups in tropical rain forests," *Vegetatio* 75(1), 81-86. DOI: 10.1007/BF00044629
- Taylor, A. M., Gartner, B. L., and Morrell, J. J. (2002). "Heartwood formation and natural durability. A review," *Wood and Fiber Science* 34, 587-611. DOI: 10.5555/20023166786
- Tenius Ribeiro, J. C., Nunes-Freitas, A. F., Fidalgo, E. C. C., and Uzêda, M. C. (2019). "Forest fragmentation and impacts of intensive agriculture: Responses from different tree functional groups," *PLoS ONE* 14(8), article ID e0212725. DOI: 10.1371/journal.pone.0212725
- Thomas, S. C. (1996). "Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees," *American Journal of Botany* 83(5), 556-566. DOI: 10.1002/j.1537-2197.1996.tb12739.x
- Trouy, M. C. (2015). *Wood Anatomy: Formation, Functions and Identification*, Quae, Versailles, France. (in French)
- Valladares, F., and Niinemets, Ü. (2008). "Shade tolerance, a key plant feature of complex nature and consequences," *Annual Review of Ecology, Evolution, and Systematics* 39(1), 237-257. DOI: 10.1146/annurev.ecolsys.39.110707.173506
- Van Gelder, H. A., Poorter, L., and Sterck, F. J. (2006). "Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community," *New Phytologist* 171(2), 367-378. DOI: 10.1111/j.1469-8137.2006.01757.x
- Veneklaas, E. J., and Poorter, L. (1998). "Growth and carbon partitioning of tropical tree seedlings in contrasting light environments," in: *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences*, H. Lambers, L. Poorter, and M. M. I. van Vuuren (Eds.), Backhuys Publishers, Leiden, Netherlands, pp. 337-361.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). "Let the concept of trait be functional!. *Oikos* 116(5), 882-892. DOI: 10.1111/j.0030-1299.2007.15559.x
- Voelker, S. L., Lachenbruch, B., Meinzer, F. C., and Strauss, S. H. (2011). "Reduced wood stiffness and strength, and altered stem form, in young antisense 4CL transgenic poplars with reduced lignin contents," *New Phytologist* 189(4), 1096-1109. DOI: 10.1111/j.1469-8137.2010.03572.x
- Wang, X., Zhao, W., Zhang, Y., Shi, J., Shan, S., and Cai, L. (2024). "Exploring wood micromechanical structure: Impact of microfibril angle and crystallinity on cell wall strength," *Journal of Building Engineering* 90, article 109452. DOI: 10.1016/j.job.2024.109452
- Wen, Y., Chen, C., Sun, T., Yang, Y., Han, X., He, B., and Lu, X. (2023). "The change pattern of CSR ecological strategy of trees and seedlings during different succession stages in tropical lowland rainforests," *Frontiers in Forests and Global Change* 6, article 1236933. DOI: 10.3389/ffgc.2023.1236933
- Werden, L. K., Averill, C., Crowther, T. W., Calderón-Morales, E., Toro, L., Alvarado, J. P., and Powers, J. S. (2023). "Below-ground traits mediate tree survival in a tropical dry forest restoration," *Philosophical Transactions of the Royal Society B* 378(1867), article 20210067. DOI: 10.1098/rstb.2021.0067

- Wheeler, E. A., Baas, P., and Gasson, P. E. (1989). "IAWA List of microscopic features for hardwood identification," *IAWA Bulletin* 10, 219-332.
- Whitmore, T. (1989). "Canopy gaps and the two major groups of forest trees," *Ecology* 70(3), 536-538.
- Wink, M. (2010). *Annual Plant Reviews, Volume 39: Functions and Biotechnology of Plant Secondary Metabolites*, John Wiley & Sons, Hoboken, NJ, USA. DOI: 10.1002/9781444320503.ch1
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., and Villar, R. (2004). "The worldwide leaf economics spectrum," *Nature* 428(6985), 821-827. DOI: 10.1038/nature02403
- Xing, S., Cheng, X., Kang, F., Wang, J., Yan, J., and Han, H. (2022). "The patterns of N/P/K stoichiometry in the *Quercus wutaishanica* community among different life forms and organs and their responses to environmental factors in northern China," *Ecological Indicators* 137, article ID 108783. DOI: 10.1016/j.ecolind.2022.108783
- Yadav, S., and Chattopadhyay, D. (2023). "Lignin: The building block of defense responses to stress in plants," *Journal of Plant Growth Regulation* 42(10), 6652-6666. DOI: 10.1007/s00344-023-10926-z
- Ye, X., Wang, F., Hu, X., Lin, Y., Sun, R., Liang, X., and Chen, F. (2022). "Experimental approach alters N and P addition effects on leaf traits and growth rate of subtropical *Schima superba* (Reinw. ex Blume) seedlings," *Forests* 13(2), article 141. DOI: 10.3390/f13020141
- Zhang, S., Wang, B., Li, Q., Hui, W., Yang, L., Wang, Z., and Wu, A. M. (2023). "CRISPR/Cas9 mutated p-coumaroyl shikimate 3'-hydroxylase 3 gene in *Populus tomentosa* reveals lignin functioning on supporting tree upright," *International Journal of Biological Macromolecules* 253, article 126762. DOI: 10.1016/j.ijbiomac.2023.126762
- Zhang, C., Gu, R., Lin, L., and Russo, S. E. (2024). "Functional traits and ecological niches as correlates of the interspecific growth–mortality trade-off among seedlings of 14 tropical tree species," *Functional Ecology* 38(9), 1888-1901. DOI: 10.1111/1365-2435.14624
- Zimmermann, M. H., and Brown, C. L. (1971). *Trees: Structure and Function*, Springer-Verlag, New York, NY, USA.
- Zue Ondo, J. L., Ruelle, J., Dlouhá, J., and Fournier, M. (2021). "Characterisation and variability of physical and structural properties of kevazingo, *Guibourtia tessmannii*, and okoumé, *Aucoumea klaineana*, wood from natural forests in Gabon," *Bois et Forêts Des Tropiques* 347, 41-57. DOI: 10.19182/bft2021.347.a31939

Article submitted: August 06, 2024; Peer review completed: September 21, 2024;
Revised version received: October 7, 2024; Accepted: October 9, 2024; Published:
October 23, 2024.

DOI: 10.15376/biores.19.4.NkeneMezui