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A whole-plant functional scheme predicting the early growth of tropical tree species: evidence from 15 tree species in Central Africa

Ariane Mirabel[1,2] · Dakis-Yaoba Ouédraogo[1] · Hans Beeckman[4] · Claire Delvaux[4] · Jean-Louis Doucet[1] · Bruno Hérault[2,3] · Adeline Fayolle[1]

Abstract

Key message **This study highlighted the consistency of a functional scheme integrating leaf, stem and root traits, biomass allocation and stem anatomy for 15 tropical tree species at the seedling stage. This functional scheme was shaped by the trade-offs for resource use and the hydraulics of the plants and was found to determine seedling growth.**

Abstract Functional traits determine plant functioning, performance and response to the environment and define species functional strategy. The functional strategy of 15 African tree species was assessed by (1) highlighting the structure of traits covariance and the underlying functional trade-offs, (2) inferring a whole-plant functional scheme and (3) testing the correlation of the functional scheme with plant performance for two early developmental stages (seedlings and saplings). We selected 10 seedlings for each of the 15 species studied from a nursery in south-eastern Cameroon and measured 18 functional traits, including leaf, stem and root traits, biomass allocation and stem anatomy. We assessed the height and diameter growth of the seedlings and the DBH growth and survival for the saplings of nearby plantations. Multivariate analyses highlighted the covariations among the functional traits of the leaf/stem/root, biomass allocation ratios and stem anatomy. The major trait covariation axes were driven by two trade-offs, first between resource acquisition and conservation and second between hydraulic safety and efficiency. The axes were integrated into a Bayesian network inferring a functional scheme at the whole-plant scale, which was found to predict the growth of the seedlings but not the performance of the saplings. The functional strategies of the seedlings were determined by an integrated whole-plant scheme reflecting the trade-offs for resource use and plant hydraulics. The scheme predicted the growth of the seedlings through mechanistic pathways from the wood stem to all the plant traits, but it appeared to shift at the stage of the saplings.

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✉ Ariane Mirabel
    Ariane.Mirabel@ecofog.gf

1   TERRA Teaching and Research Center, Gembloux Agro-Bio Tech, Passage des Déportés 2, 5030 Gembloux, Belgium

2   Cirad, UR Forest and Societies, Montpellier, France

3   INPHB (Institut National Polytechnique Félix Houphouët Boigny), Yamoussoukro, Ivory Coast

4   Service of Wood Biology, Royal Museum of Central Africa (RMCA), Tervuren, Belgium

Introduction

A key objective of plant community ecology is to understand how functional traits determine the phenotypic response of plants to environmental factors and their effects on ecosystem processes and services (Wright and Westoby 2001; Lavorel and Garnier 2002; Hérault et al. 2011; Aubry-Kientz et al. 2013). Functional traits encompass morphological, phenological and physiological characteristics of plants measurable at the individual scale (Violle et al. 2007). They have been largely adopted in trait-based approaches to describe the species through their biological attributes. Thus, functional traits reduce the dimensionality of species-rich ecosystems and facilitate the comparison of communities and ecosystems, therefore easing the inferences on the

dynamics and functioning of tropical forests (Scheiter et al. 2013).

The search for contrasting functional types able to discriminate species led to a consensus on the relevance of some major continuous trait axes (Reich 2014). The most frequently reported is the leaf economics spectrum (Reich et al. 1997; Wright et al. 2004). One end of the spectrum corresponds to species with tough, dense and long-lived leaves. On the other end are the species with light, large and short-lived leaves (Reich et al. 1997). These species display higher photosynthetic rates but greater susceptibility to damage and herbivory (Caldwell et al. 2015). The leaf economics spectrum also fits a slow-fast continuum of species strategies from the conservation of resources through long-lived, dense tissues in stressful environments to the potentially fast acquisition of resources when they are available (Chapin 1980). A similar continuum proved consistent for root traits (Bardgett et al. 2014; Valverde-Barrantes et al. 2017) and stem traits (Chave et al. 2009). The stem economics spectrum based on stem traits and properties was recently proposed and consistently predicted the performance of the plants (Chave et al. 2009; Baraloto et al. 2010). The spectrum specifically highlighted the central role of wood density in determining the hydraulic and mechanical functions of the plant (Fortunel et al. 2013; Beeckman 2016). Functional traits and economic spectra of the leaf, stem and root were well documented separately, but it remains unclear how they correlate with each other, specifically for tropical tree species. While leaf/stem/root traits appeared decoupled for tropical woody species at the adult stage in French Guiana and Peru (Baraloto et al. 2010; Fortunel et al. 2012), they proved to be correlated in several empirical studies and a literature review. Such coupling would argue for an integrated economics spectrum at the whole-plant scale (Freschet et al. 2010; Bucci et al. 2012; Reich 2014; Valverde-Barrantes et al. 2017). The correlation of functional traits with biomass allocation ratios and stem anatomical traits also remains unclear. Correlations with biomass allocation would be expected, as these are also shaped by resource-use trade-offs between managing with limited resources and maintaining the functions of organs (Poorter et al. 2011; Kleyer and Minden 2015). Similarly, stem anatomy integrates different microscopic and macroscopic observation scales and might highlight the mechanisms underlying plant performance (Beeckman 2016). Thus, it has been demonstrated for roots (Hummel et al. 2007) and suggested for wood (Lachenbruch and Mcculloh 2014) that anatomical traits explained interspecific variations in other key traits. Specifically, the combination of fibre and vessel features and the partitioning of stem tissues alone would reflect the vital balance between stem hydraulic and mechanical functions (Chave et al. 2009; Fan et al. 2012). However, anatomical traits and their role in shaping other functional trait values

remain to be clarified through broad multi-trait approaches as proposed by Fortunel et al. (2013) and Poorter et al. (2010), who related wood density to fibre and vessel traits.

Functional traits are expected to shape the average performance of species and its variation according to the environment (Violle et al. 2007; Rüger et al. 2012). The functional trade-offs underlying trait covariations would then correlate with the demographic trade-offs balancing plant growth and survival. Such a correlation, mediated by the availability of resources, was suggested between the resource acquisition-conservation trade-off and the demographic growth-mortality trade-off (Reich et al. 2003; Reich 2014). However, in practice, correlations between functional traits and performance either proved inconsistent (Paine et al. 2015; Gibert et al. 2016) or varied across different climates and soils (Kitajima and Poorter 2008; Poorter et al. 2008; Russo et al. 2008; Rüger et al. 2012). If some properties, such as the wood density and species maximum height, consistently determined plant mean growth (Poorter and Rozendaal 2008; Wright et al. 2010; Rüger et al. 2012), the role of other key traits for plant performance remained unclear. For example, leaf traits proved to be correlated to seedling growth for 250 Australian species (Westoby and Wright 2003), as well as growth and mortality for 53 tropical tree species (Poorter and Bongers 2006). However, no leaf trait consistently predicted the average specific growth rate of 171 Neotropical tree species (Rüger et al. 2012) or the maximum growth rate and the magnitude of ontogenetic changes in growth for 50 tree species in French Guiana (Hérault et al. 2011). The leaf traits predicted the sapling growth of 37 subtropical tree species only when considered in combination rather than individually (Li et al. 2017).

In studying the role of functional traits and strategies in tropical forest dynamics, early development stages should be carefully examined. Indeed, little is known about the trait-growth relationships in these early development stages, although they correspond to crucial differentiation between species due to the harsh environment of the forest understory (displaying low light and seasonal drought) (Markesteijn and Poorter 2009; Paine et al. 2015). This lack of knowledge is partly attributed to the mismatch between pantropical functional trait databases that usually register the trait values of mature trees and the fact that important changes in the trait-performance relationships may occur during plant ontogeny (Visser et al. 2016). In this study, we examined the seedlings of 15 tropical tree species in south-eastern Cameroon for which the functional characteristics and juvenile traits are poorly documented (Markesteijn et al. 2011; Verbeeck et al. 2011). We examined a large set of 18 traits, including leaf, stem and root traits, biomass allocation (leaf/stem and shoot/root ratios) and stem anatomical traits (tissue proportion, vessel density and diameter and fibre wall thickness). The functional traits were measured on seedlings with similar

development stages raised under optimal conditions in a nursery. In addition, the seedling traits were completed with additional traits at the species level, including seed mass, maximum height, phenology and performance at the sapling stage. We performed multi-trait analyses to highlight the correlation map and trait covariation axes to identify the primary functional trade-offs. Specifically, we questioned the consistency of the widespread resource acquisition-conservation trade-off, the coupling between the leaf/stem/root traits and the correlations of seedling functional traits with additional traits at the species level. These analyses allowed us to infer an integrative functional scheme at the whole-plant scale. We then examined the correlations of this whole-plant scheme with the performance at both the seedling and sapling stages to identify the mechanistic pathways of plant functioning from anatomical traits to performance through functional traits.

Materials and methods

Study site and species

We selected 15 tree species, mostly timber species, widespread across the lowland mixed-moist forests of the Guineo-Congolian Region (White 1983). The species were grown in south-eastern Cameroon in the nursery of the Pallisco® Logging Company (3°34′N; 13°24′E) and germinated from seeds collected in the nearby forests. For each species, the seeds were collected from a set of determined mother trees within a 100 km radius in the Forest Management Units of the company. Mother trees are monitored monthly for phenology and yearly for growth in the frame of the DynAfFor project (https://www.dynaffor.org/localisation-des-sites). The seeds collected were germinated without storage and grown in the controlled conditions of the nursery, following the protocols applied for seedlings intended for forest enrichment and reforestation (Doucet et al. 2009, 2016). The seedlings were planted in nutrient-enriched soils (black soils from villages, i.e. compost), constantly shaded and watered daily. The annual average temperature in the area is 24 °C, and the annual rainfall varies between 1500 and 2000 mm year^{-1}. The 15 species belong to 9 families and 13 genera. Additional information on leaf phenology at the adult stage (deciduous or evergreen), dispersal mode (animal, wind or unassisted dispersal) and regeneration guild (pioneer, non-pioneer light demander, shade-bearer) at the species level were extracted from Meunier et al. (2015) and complemented by field expertise (J. L. Doucet, pers. com.). The maximum tree height (H_{max} in m), maximum diameter at breast height (D_{max} in m) and seed length (SL in cm) were extracted from the CoForTrait database (Bénédet et al. 2014). The wood density (WD in mg mm^{-3}) was extracted

from the Global Wood Density Database (Zanne et al. 2009) and the seed mass (SM in mg, measured for air-dried seeds) from the Seed Information Database (Royal Botanic Gardens Kew 2016). Table 1 summarizes the information of the 15 species. Most of the species were deciduous ($n = 12$ species) and light-demanding at the adult stage, either pioneers ($n = 5$) or non-pioneer light-demanders ($n = 8$). Most of the species had seeds dispersed by wind ($n = 7$) or animals ($n = 7$). The maximum tree height ranged from 22 m (*Diospyros crassiflora* [Ebenaceae]) to 50 m (*Entandrophragma utile* [Meliaceae]), and the wood density ranged from 0.33 (*Triplochiton scleroxylon* [Malvaceae]) to 0.89 mg mm^{-3} (*Desbordesia glaucescens* [Irvingiaceae]).

Trait measurements

A total of 18 traits were measured following standard protocols (Pérez-Harguindeguy et al. 2013). Leaf, stem and root traits were selected based on their relevance as proxies of tree species functional strategy (Garnier and Shipley 2001; Borchert 1994; Ostonen et al. 2014) and according to practical constraints, specifically the time-consuming measurements of root traits. The traits measured also encompassed biomass allocation ratios (Poorter et al. 2011) and the anatomical traits of the stem (Fortunel et al. 2013). For each species, ten seedlings aged from 4 to 10.5 months (Table 1) were selected among the healthier ones, considering their size, number of leaves and potential damage. The total leaf and stem biomass and nine of the leaf and stem functional traits were measured on all ten seedlings (10 seedlings × 9 traits). In addition, the leaf nitrogen content, root biomass, specific root length and stem anatomical traits were measured for a subset of five seedlings per species (5 seedlings × 18 traits, Table 2).

Leaf/stem/root traits

For all ten seedlings per species, the number of leaves (N_{leaves}) was counted at the time of sampling. The third leaf from the apex was collected and stored for 6 h in the refrigerator to stabilize its metabolism. The petiole length and two perpendicular median diameters were then measured with a calliper, and the leaf was scanned to measure the leaf area (LA in mm^2) using ImageJ software (Rasband 2015). The leaf was then oven dried for 72 h at 65 °C, after which the whole leaf and the petiole alone were weighed. The leaf and petiole dry mass allowed the computation of the specific leaf area (leaf area per unit dry mass; SLA in m^2 kg^{-1}), the leaf dry matter content (leaf dry mass per unit leaf fresh mass; LDMC in mg g^{-1}), the specific petiole length (petiole fresh length per unit petiole dry mass; SPL in cm g^{-1}) and the petiole mass fraction (petiole dry mass per unit leaf dry mass; PMF in g g^{-1}). For the subset of five seedlings, the

Table 1 List of the 15 studied species with their botanical family, regeneration guild, leaf phenology deciduous (Dec.) or evergreen (Eve.), dispersal mode (from Meunier et al. 2015), average maximum height and diameter seed length (from Bénédet et al. 2014), wood density at species level (from Zanne et al. 2009) and seed mass (from Royal Botanic Garden Kew 2016)

Scientific name (common name)	Family	Guild	Leaf habit	Dispersal mode	H_{max}, m	D_{max}, m	Specific wood density, mg mm^{-3}	Seed length, cm	Seed mass, mg	Seedlings in nursery Age, month	H_{Inc}, mm day^{-1}	D_{Inc}, mm day^{-1}	Saplings in plantation Survival %	DBH growth, mm year^{-1}
Afzelia bipindensis (Doussié)	Fabaceae, Caesalpiniodea	NPLD	Dec.	Animal	28.75	1	0.73	2.5	–	6.7	2.54	2.41×10^{-2}	54.7	5.75
Antrocaryon klaineanum (Ozambili)	Anacardiaceae	P	Dec.	Animal	30	1	0.50	1	–	9.9	3.29	1.78×10^{-2}	–	–
Autranella congolensis (Mukulungu)	Sapotaceae	NPLD	Dec.	Animal	30	1.5	0.78	3.3	–	7.4	0.95	1.40×10^{-2}	100	6,41
Baillonella toxisperma (Moabi)	Sapotaceae	NPLD	Dec.	Animal	38.75	3	0.72	2.5	–	7.4	2.02	1.85×10^{-2}	58.7	6.76
Desbordesia glaucescens (Alep)	Irvingiaceae	SB	Eve.	Wind	30	1.75	0.89	2.25	–	6.3	1.20	9.59×10^{-3}	–	–
Diospyros crassiflora (Ebène)	Ebenaceae	SB	Eve.	Animal	22.5	1	0.86	1.5	–	7.3	0.92	1.27×10^{-2}	–	–
Entandrophragma candollei (Kosipo)	Meliaceae	NPLD	Dec.	Wind	40	2	0.57	1.7	370	9.6	0.46	1.52×10^{-2}	–	–
Entandrophragma cylindricum (Sapelli)	Meliaceae	NPLD	Dec.	Wind	40	2	0.57	1.5	312	8.7	0.648	1.15×10^{-2}	72.6	1.71
Entandrophragma utile (Sipo)	Meliaceae	NPLD	Dec.	Wind	50	2.5	0.53	5	300	4.4	1.44	2.51×10^{-2}	73.4	5
Erythrophleum suaveolens (Tali)	Fabaceae, Caesalpiniodea	P	Dec.	Unassisted	30	1.45	0.84	1.05	425	4	1.52	1.56×10^{-2}	88	7,3

Table 1 (continued)

Scientific name (common name)	Family	Guild	Leaf habit	Dispersal mode	H_{max}, m	D_{max}, m	Specific wood density, mg mm^{-3}	Seed length, cm	Seed mass, mg	Seedlings in nursery			Saplings in plantation	
										Age, month	H_{Inc}, mm day^{-1}	D_{Inc}, mm day^{-1}	Survival %	DBH growth, mm year^{-1}
Milicia excelsa (Iroko)	Moraceae	P	Dec.	Animal	36.25	1.6	0.56	0.2	2.5	4.7	2.00	2.09×10^{-2}	44	1.67
Pouteria altissima (Aningré)	Sapotaceae	NPLD	Eve.	Animal	40	1	0.46	1.5	–	7.4	1.18	1.19×10^{-2}	–	–
Pterocarpus soyauxii (Padouk)	Fabaceae	NPLD	Dec.	Wind	40	1.2	0.66	1.5	–	7.4	0.92	1.19×10^{-2}	81.3	5.01
Terminalia superba (Fraké)	Combretaceae	P	Dec.	Wind	35	1	0.46	0.605	110	5.1	3.46	2.38×10^{-2}	84	19.8
Triplochiton scleroxylon (Ayous)	Malvaceae	P	Dec.	Wind	40	2	0.33	0.65	292	10.5	2.16	1.72×10^{-2}	83	42.9

Abbreviations for regeneration guild correspond to *P* pioneers, *NPLD* non-pioneers light-demanders, *SB* Shade Bearers

Table 2 List of the 18 functional traits measured on 15 tropical tree species at the seedling stage, including leaf, stem and root traits, biomass allocation ratios and stem anatomical traits. Sampling effort (number of seedlings measured for each species), trait name, corresponding abbreviation, unit, average value and standard deviation for the whole dataset, trait function and corresponding references are given for each trait

Rep.	Trait	Notation	Unit	Average ($\pm$ standard deviation)	Function	References
Functional traits						
Leaves						
10	Number of leaves	N_{leaves}		7.56 (± 3.54)	Resource capture	Westoby and Wright (2003)
10	Leaf area	LA	mm^2	$6.83 \cdot 10^3$ ($\pm 6.47 \cdot 10^3$)	Resource capture	Reich et al. (2003)
10	Specific leaf area	SLA	m^2 kg^{-1}	2.62 (± 0.99)	Resource capture, defense	Garnier et al. (2001)
10	Leaf dry matter content	LDMC	mg g^{-1}	307.99 (± 78.06)	Resource capture, defense	Wright et al. (2010) and Garnier et al. (2001)
5	Leaf nitrogen content	LNC	mg g^{-1}	21.4 (± 5.2)	Resource capture	Garnier et al. (2001) and Poorter and Bongers (2006)
10	Petiole Diameter	PDm	mm	1.46 (± 0.44)	Support, conduction	Poorter and Rozendaal (2008)
10	Specific petiole length	SPL	m g^{-1}	1.99 (± 3.16)	Resource capture, Support, conduction	Poorter and Rozendaal (2008)
10	Petiole mass fraction	PMF	mg g^{-1}	66.39 (± 36.84)	Support, conduction	Kitajima and Poorter (2008)
Stem						
10	Stem density	SD	mg mm^{-3}	0.11 (± 0.04)	Support, defense, conduction	Chave et al. (2009) and Baraloto et al. (2010)
10	Saturated water content	SWC	%	218.69 (± 93.98)	Conduction, stock	Borchert (1994) and Chave et al. (2009)
Roots						
5	Specific root length	SRL	m g^{-1}	20.93 (± 20.95)	Resource capture	Bardgett et al. (2014)
Biomass allocation						
10	Leaf/stem ratio	Leaf/stem	g g^{-1}	1.32 (± 0.84)	Support, resources capture	Poorter et al. (2011)
5	Shoot/root ratio	Shoot/root	g g^{-1}	2.67 (± 0.94)	Resources capture	Bardgett et al. (2014)
Stem anatomy						
5	Fibre wall thickness	FWT	µm	8.47 (± 5.03)	Support, conduction	Fortunel et al. (2013)
5	Vessel diameter	VDm	µm	28.55 (± 11.50)	Conduction	Fan et al. (2012)
5	Vessel density	Vd	µm^{-2}	96.43 (± 57.06)	Conduction	Fan et al. (2012) and Poorter et al. (2010)
5	Pith fraction	PF	µm µm^{-1}	0.37 (± 0.13)	Support, conduction	Spicer (2014)
5	Bark/wood ratio	Bark/wood	µm µm^{-1}	0.68 (± 0.61)	Defense	Lawes et al. (2013)

dry leaf was stored in silica gel for later determination of the leaf nitrogen content (nitrogen mass per unit leaf dry mass; LNC in mg g^{-1}) using the Kjeldahl method.

A 5-cm long stem sample was collected at a third of the plant height for the ten seedlings per species. The fresh volume of the samples was computed from its length and diameter. The stem sample was weighed first immediately after cutting and then after soaking for 24 h in tap water once the tissues were water-saturated. The weights and volume were combined to compute the stem density (SD in mg mm^{-3}) and saturated water content (stored water mass per unit stem fresh mass; SWC in %).

For the subset of five seedlings per species, the roots were cleaned with water and sorted to obtain a sample of the secondary roots (diameters < 2 mm) with at least 10 absorptive roots. The sample was stained for 24 h in a 0.1% methylene blue solution and scanned to measure the root length using QGIS software (Development Team Quantum GIS 2015). The root sample was oven dried for 72 h at 65 °C and weighed to compute the specific root length (root length per unit dry mass; SRL, in m g^{-1}).

Biomass allocation

For all ten seedlings, the leaf and stem compartments were separated. For the subset of five seedlings, the root compartment was also separated. The leaves and roots were oven dried for 72 h at 65 °C, and the stem was oven dried for

72 h at 103 °C. All the compartments were then weighed to compute the leaf/stem and shoot/root ratios (in g g^{-1}).

Stem anatomy

After the measurement of the stem functional traits (SD and SWC), the stem samples were stored in 38° alcohol to prevent tissue drying. In the lab, five thin sections of the samples were cut using a mechanical microtome (12–16 μm thick), stained in a safranin/alcian blue mixture before dehydration in ethanol at 50, 75, 95 and 100% and mounted. The best thin section was selected for each sample under the microscope, and pictures were taken at various objective magnifications. Anatomical traits were measured with image analysis using ImageJ software (Fig. 1). The widths of the pith, wood and bark were measured with the 2.5 magnification objective lens (Fig. 1a) to compute the pith fraction (pith thickness per unit section radius; PF in μm μm^{-1}) and the bark/wood ratio (bark thickness per unit wood section radius; bark/wood in μm μm^{-1}). The vessel surface density (number of vessels per unit surface area; Vd in n μm^{-2}, Fig. 1b) was measured with the 20 magnification objective lens by counting the vessels in a 0.25 mm^2 area. The average vessel diameter (VDm in μm) and fibre wall thickness (FWT in μm) were measured from 30 randomly selected vessels and wood fibres (Fig. 1c) with the 40 magnification objective lens.

Performance measurements

At the seedling stage, the height and diameter absolute increments were computed at the time of the sampling. Prior to the trait measurements, the height of all ten seedlings and two perpendicular diameters were measured at a third of the total plant height (to avoid the remaining cotyledons). The height and diameter of the seedlings were normalized by their age in days, known from the precise recording of the

germination of the seeds, to compute the height and diameter increments (H_{Inc} and D_{Inc} in mm day^{-1}) of the seedlings.

At the sapling stage, the DBH growth rates (mean and maximum) and survival in plantation were extracted from Doucet et al. (2016, Table 1) for 10 of the 15 study species. The species missing were *Antrocaryon klaineanum* [Anacardiaceae], *D. glaucescens* [Irvingiaceae], *D. crassiflora* [Ebenaceae], *Entandrophragma candollei* [Meliaceae] and *Pouteria altissima* [Sapotaceae] (Table 1). Seedlings grown in the same nursery and conditions as those of the seedlings used for trait measurements were planted in 14 plots installed between 2009 and 2014 during the rainy season. At the time of planting, the seedling height was 50 cm high on average, with a 2.1 cm standard deviation, and the seedling diameter at 10 cm above the stem base ranged from 5.0 to 11.5 mm. The plots were located between 10 and 70 km from the nursery in highly degraded areas along roads on Ferralsols (Doucet et al. 2016). The understory was clearcut before planting by keeping only the high-value species and the trees with a DBH greater than 50 cm. At the time of planting, the remaining canopy cover ranged from 8.2 to 70.5%. The plots corresponded to a mixture of species planted in pure-species blocks (15 × 15 m planted with 25 conspecific seedlings). Species were planted in blocks where their shade tolerance matched the canopy openness. Thus, the mixture of species differed for each plot. The number of species varied from 2 to 10 per plot. After plantation, 75% of the seedlings were planted in fully open areas (81% of the pioneers and 62% of the non-pioneer species). Doucet et al. (2016) analysed sapling performance using a DBH growth model. A linear mixed model was adjusted on 4621 surviving saplings with species and species-time interaction as fixed effects and individuals as random effects. The fixed model parameters were extracted for each species to obtain their mean DBH growth rate (in mm year^{-1}). The maximum DBH growth rates (in mm year^{-1}) of species were computed as the mean growth rate of the best performing individuals (i.e. the best 10% of stems) obtained by extracting the
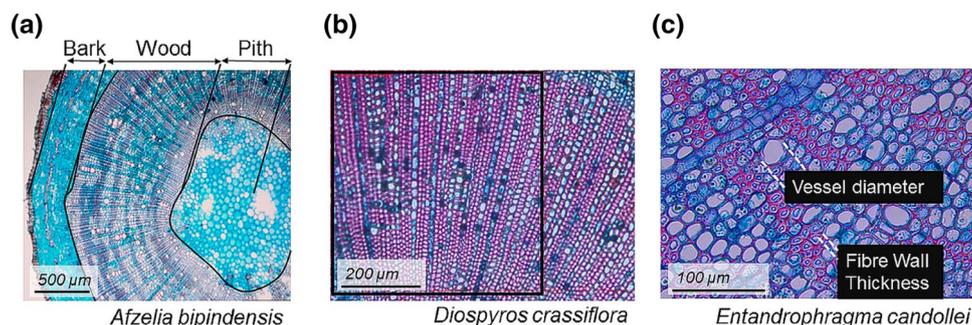
Fig. 1 Protocol for stem anatomy measurements: **a** tissues proportion was measured with the 2.5 magnification objective lens, **b** vessel density was measured with the 200 magnification objective lens based on vessel count on 0.25 mm^2 and **c** vessel diameter and fibre wall thickness were measured with the 400 magnification objective lens for 30 vessels and fibres randomly selected

best linear unbiased estimate of the random effects for each individual. The species survival (%) at 690 days after planting was estimated using the Kaplan–Meier estimator, which gives the probability at time *t* of individuals surviving since planting (Kaplan and Meier 1958).

Data analyses

The correlation map and the main correlation axes among the leaf, stem and root functional traits, biomass allocation ratios and stem anatomical traits at the seedling stage were highlighted with a principal component analysis (PCA). To account for the trait intraspecific variability, trait analyses were performed at an individual scale rather than on species averages.

A first analysis was conducted on the 18 trait values measured on the subset of five seedlings. The analysis was confirmed with a second one conducted on the nine trait values measured on all 10 seedlings. In addition, trait covariations were examined using pairwise Pearson multiple correlation tests with *P* values adjusted for multiple tests using the Holm correction (Holm 1979). The seedling height and diameter increments were added to the PCA analysis as supplementary variables. This allowed mapping the seedling growth parameters in the functional space to compute their interrelation with other functional traits without changing the definition of the PCA axes.

To assess the relationships between trait values and both literature-based trait information and species-level performance, non-parametric correlation tests were performed between species-level performance and species mean trait values and scores on the first two PCA axes. Spearman correlation tests were performed for quantitative variables (wood density, seed length and mass, growth and survival at the seedling and sapling stages), and Kruskal–Wallis tests were performed for qualitative variables (regeneration guild and leaf phenology).

The contributions of the traits to the PCA axes were calculated as their relative inertia, i.e. the square of the trait coordinates relative to the eigenvalue of the axis considered. The traits defining more than 10% of the two first axes were integrated into a Bayesian network. The Bayesian analysis inferred a directed acyclic graph (DAG) corresponding to a whole-plant functioning scheme. To preserve the logic of the axes, the DAG was constrained by preventing links between traits of the two axes. To test the mechanistic pathways across scales, the direction of the relationships was imposed from anatomical traits to organ functional traits and performance variables and from all traits to performance variables. To account for the intraspecific dependencies among all the traits and performance, the regression coefficients (*r*) were computed using a mixed model with species as a grouping variable.

All analyses were conducted within the R environment version 3.1.3 (R Core Team 2014) using the ade4 package for multivariate analysis (Dray and Dufour 2007), the psych package for multiple correlation tests (Revelle 2015), the abn package for Bayesian network analysis (Lewis 2016) and the plotrix package for figures (Lemon 2006).

Results

Among the 15 tropical tree species studied, the most variable traits at the seedling stage were the SPL (2.0 ± 3.16 m g^{-1}) and the SRL (20.93, $\pm$ 20.95 m g^{-1}), both showing a 100-fold variation, and the LA ($6.83 \pm 6.47 \times 10^3$ mm^2) (Table 2). The measures were in the range of the values previously reported at the adult stage (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). The SLA ranged from 1.18 (*D. crassiflora* [Ebenaceae]) to 4.45 m^2 kg^{-1} (*Milicia excelsa* [Moraceae]), the LDMC from 180.62 (*Terminalia superba* [Combretaceae]) to 477.80 mg g^{-1} (*D. crassiflora*), the LNC from 13.3 (*D. crassiflora*) to 30.0 mg g^{-1} (*M. excelsa*) and the SRL from 3.37 (*Baillonella toxisperma* [Sapotaceae]) to 74.07 mg g^{-1} (*M. excelsa*).

Trait covariations

The trait covariations among the 15 tropical tree species at the seedling stage highlighted a strong coupling between the leaf, stem and root functional traits. The first covariation axis was shaped at the whole-plant scale by a trade-off between resource acquisition and conservation. The second covariation axis highlighted the strong correlations between the biomass allocation ratios and vessel traits determined by a plant hydraulics trade-off (Fig. 2).

The multivariate analysis of trait correlations (PCA) conducted at the seedling stage ($n = 75$, 5 seedlings × 15 species) for the 18 functional traits highlighted two major trait axes (43% of the total variance, Fig. 2). The first axis (29% of the explained variance) was defined by the leaf, stem and root functional traits involved in the resource acquisition-conservation trade-off. In particular, the contributions of SLA, LDMC, SWC, SD and SRL ranged from 9.2 to 14.8% of the axis definition. The first axis opposed species with dense tissues (high LDMC, SD and FWT), such as true Ebony, *D. crassiflora*, against species with large exchange surfaces (high SLA, SRL and SWC), such as Limba/Fraké, *T. superba*. This axis also highlighted the correlation between the SD and FWT ($r = 0.36$, $P = 0.077$).

The second axis (14% of the explained variance) was defined by functional traits more likely to be involved in plant hydraulics. In particular, it was defined by the coordination between the vessel density, petiole mass fraction and bark/wood biomass allocation ratio. Biomass allocation

(a)

(b)
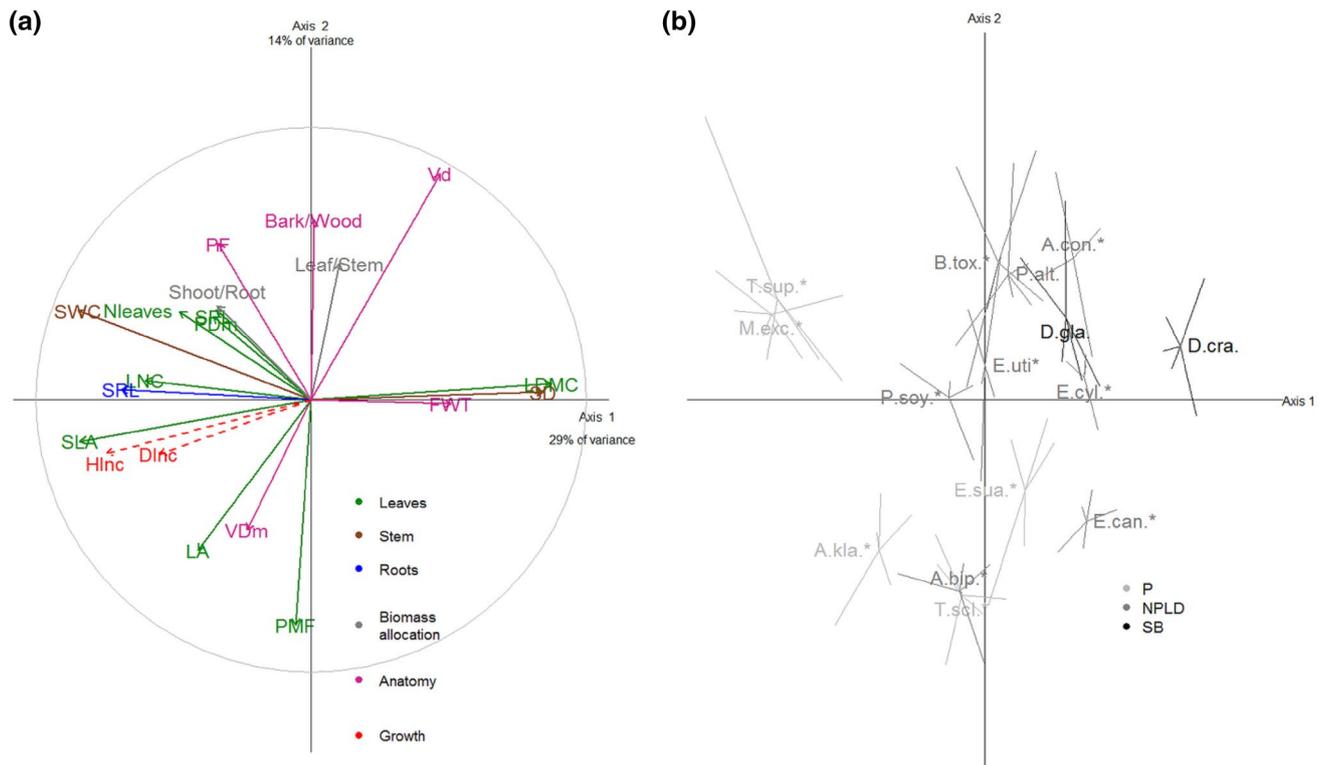
Fig. 2 **a** PCA of the 18 functional traits measured on 15 tropical tree species at the seedling stage (*n* = 5 seedlings). The correlation circle is given for the 18 traits with a colour code corresponding to leaf (green), stem (brown) and roots (blue) traits, biomass allocation ratios (grey) and stem anatomy (pink). The height and diameter increments of seedlings are displayed as supplementary variables (red). **b** Location of the 15 studied species in the factorial plan defined by the two first trait axes, radiating lines linking individuals to the corresponding barycenter of each species. Deciduous species are indicated by asterisk and the grey levels indicates regeneration guild from pioneers (P, light grey), to non-pioneer light-demanders (NPLD, dark grey) and shade bearers (SB, black). Species are named by the Genus first letter and species three first letters. Traits abbreviations are given in Table 2

and anatomical traits contributed from 12.5 to 19.6% of the second axis definition. On the positive end of the axis were species such as Mukulungu, *Autranella congolensis* [Meliaceae], with a high allocation of shoot biomass to the leaves and a high allocation of total biomass to the shoot. On the negative end of the axis were species such as Ayous, *T. scleroxylon* [Malvaceae], with large vessels and an important petiole mass fraction. These results were confirmed by both pairwise Pearson correlation tests (Table S1) and the results of the PCA conducted on the restricted set of 9 traits available for 10 seedlings per species (*n* = 150, Fig. S1). The third axis (10% of the total variance) was primarily defined by the leaf/stem ratio, LA and petiole diameter. It was redundant with the second axis, and its interpretation supported similar concepts.

Considering the additional information at the species level, positive correlations were found with species mean scores on the first PCA axis (resource use). The species wood density and seed size (both length and mass) were positively correlated with the scores on the first axis (*r* = 0.58, *P* = 0.023 for WD; *r* = 0.54 = 3, *P* = 0.065 and *r* = 0.77,

P = 0.072 for seed length and mass, respectively; Table S2). The results of the Kruskal–Wallis tests also showed significant relationships between the first axis and the species regeneration guild (*P* = 0.037). Thus, species with positive scores on the first trait axis displayed dense leaves, dense wood and large seeds and were shade-tolerant. Parallel species with negative scores displayed lighter leaves and wood and smaller seeds and were either pioneers or non-pioneer light-demanders. There were no significant relationships between the second trait axis (plant hydraulics) and any additional trait at the species level (Table S2).

Relationships between the traits and performance

The functional traits of the seedlings were significantly correlated to growth at both the seedling and sapling stages. However, there was a strong shift in some trait-growth relationships between the two ontogenetic stages.

At the seedling stage, scores on the first axis were significantly and positively correlated with the height increment in the nursery (Fig. 2; Table 3). Seedling height increments

Table 3 Pearson correlation coefficients for the 15 species between seedlings' height and diameter absolute increments and their 18 functional traits, biomass allocation ratios and stem anatomical traits and coordinates along the two main trait-PCA axes

	Seedlings in nursery ($n=15$ species)		Saplings in plantation ($n=10$ species)		
	H_{Inc} (mm day^{-1})	D_{Inc} (mm day^{-1})	Mean DBH$_{Inc}$ (mm year^{-1})	Max DBH$_{Inc}$ (mm year^{-1})	Survival (%)
Seedling traits					
Leaves					
N_{leaves}	**0.50****	**0.33****	− 0.07	0.22	0.05
LA	**0.59****	0.30	0.37	0.31	− 0.37
SLA	**0.51****	**0.39****	− 0.28	0.12	− 0.31
LDMC	**− 0.51****	**− 0.41****	0.24	0.05	0.15
LNC	0.33	0.34	− 0.27	− 0.3	− 0.32
PDm	**0.43****	0.25	0.19	− 0.08	− 0.33
SPL	0.13	0.07	− 0.37	− 0.16	0.03
PMF	0.19	0.07	0.52	**0.61***	0.24
Stem					
SD	**− 0.57****	**− 0.44****	0.08	− 0.09	0.38
SWC	**0.45****	**0.32****	− 0.19	0.05	− 0.19
Roots					
SRL	**0.36****	0.22	0.1	0.26	− 0.07
Biomass allocation					
Leaf/stem	**− 0.31****	**− 0.19****	− 0.31	0.05	0.24
Shoot/root	**0.43****	0.11	**0.78****	0.54	0.14
Stem anatomy					
FWT	**− 0.41****	− 0.15	0.01	− 0.25	0.26
VDm	**0.34****	**0.42****	0.15	0.05	− 0.37
Vd	**− 0.43****	**− 0.43****	− 0.26	− 0.42	0.21
PF	**0.45****	0.18	0.12	− 0.08	− 0.04
Bark/wood	**− 0.22****	− 0.09	− 0.38	**− 0.58***	− 0.14
PCA coordinates					
Axis 1	**0.75****	0.56	− 0.02	− 0.26	0.26
Axis 2	0.17	0.17	− 0.16	− 0.25	0.18
Growth values					
H_{inc}	/	/	**0.58***	0.43	− 0.13
D_{inc}	/	/	− 0.04	0.21	0.35

Spearman correlation coefficients between the same seedlings' information and species mean and maximum growth rates at the sapling stage, and survival rate at 690 days in plantation. Significant correlations are showed in bold and significance levels are indicated with ** $P<0.05$ and * $P<0.1$

were also correlated with individual traits, including the functional traits of the leaf (LA, SLA, LDMC and PDm), stem (SD and SWC) and root (SRL), and with biomass allocation ratios (shoot/root and leaf/stem ratios) and anatomical traits (VDm, Vd, FWT, PF and bark/wood ratio). At the species level, the only correlation was between the height increment of the seedlings and the species regeneration guild ($P=0.047$). Pioneers and non-pioneer light-demanders showed average height increments of 2.5 mm day^{-1} and 1.3 mm day^{-1} respectively.

At the sapling stage, there was no relationship between sapling performance in the plantations and the average scores of species on the two trait axes. However, some seedling individual traits were correlated with sapling performance in the plantation. The sapling mean DBH growth measured in the plantation was positively correlated with the seedling shoot/root ratio ($r=0.78$ and $P=0.012$). Similarly, the maximum sapling DBH growth was positively correlated with the petiole mass fraction of the seedlings and the bark/wood ratio ($r=0.61$, $P=0.066$ and $r=−0.58$, $P=0.088$, respectively, Table 3). For example, Ayous, *T. scleroxylon*, saplings had the highest maximum and mean growth rates in the plantation, and the seedlings displayed the highest petiole mass fraction and bark/wood ratio and the third highest shoot/root ratio.

The only correlation between the seedling and sapling stage growths was a weak correlation between the seedling height increment and sapling DBH increment. However,

important growth at the seedling stage tended to correspond to the highest mean growth rate in the plantations. For example, *T. scleroxylon* had the fourth highest height increment at the seedling stage (2.2 mm day^{-1}) and the highest mean growth rate at the sapling stage (19.8 mm year^{-1}). In contrast, Sapelli, *Entandrophragma cylindricum* [Meliaceae], had the second lowest height increment at the seedling stage (0.5 mm day^{-1}) and the second lowest mean growth rate at the sapling stage (1.67 mm year^{-1}).

Inferred seedling functional scheme

Based on the PCA analysis, we used the traits linked to the main axes and the seedling growth values to construct a directed acyclic graph (DAG) and infer the functional scheme at the whole-plant scale (Fig. 3). The DAG was constructed with the functional traits (SD, SWC, SRL, LA, SLA, LNC, LDMC and PMF), biomass allocation (leaf/stem) and anatomical traits (bark/wood ratio, PF and Vd). The leaf/stem ratio and SD were directly related to the height increment ($r = -0.24$ and $r = -0.32$, respectively). Traits involved in the first trait axis shaped by the functional

trade-off for resources use were related to the growth in the height and diameter through the stem density ($r = -32$ and $r = -61$, between the SD and increments in height and diameter, respectively). Vessel density was a determinant of the biomass allocation ratios ($r = 0.14$ between Vd and the leaf/stem ratio) and some of the leaf traits ($r = -0.12$ between Vd and PMF). Although the fibre wall thickness had been input as a variable to draw the DAG, it did not stand out significantly. Traits involved in the second PCA axis shaped by the trade-off between hydraulic safety and efficiency were directly related to the height increment ($r = -0.17$ for the bark/wood ratio and $r = 0.30$ for PF).

Discussion

Trait covariations have been widely documented within organs sampled individually using the definition of the worldwide Leaf Economics Spectrum (Wright et al. 2004) and the Stem Economics Spectrum (Chave et al. 2009). However, the consistency of the trait covariations at the whole-plant scale remains a topic of debate (Baraloto et al.
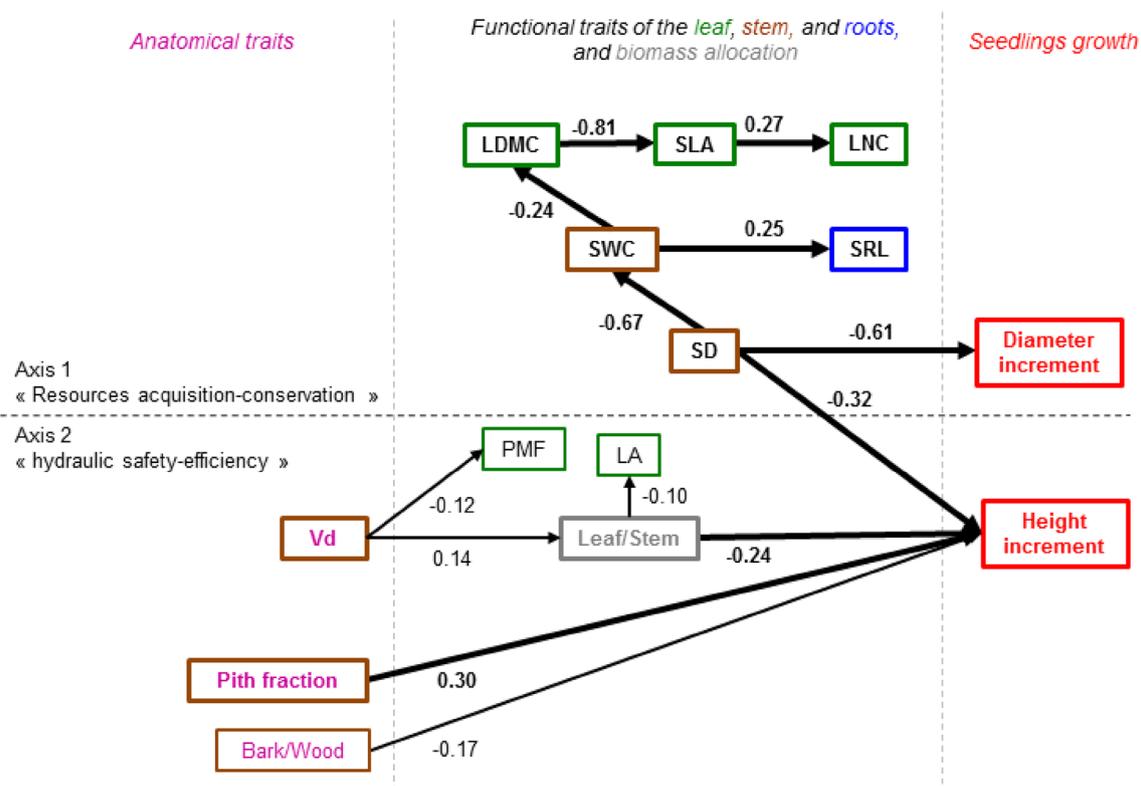
Fig. 3 Directed acyclic graph (DAG) inferred from a Bayesian network analysis based on the functional traits determining more than 10% of the PCA axis and their relations to the seedlings' growth. The regression coefficients indicating the relationship between nodes were calculated from a mixed model with seedlings species as group-

ing variable. The direction of the arrows was imposed from anatomical traits to functional traits, biomass allocation ratios and seedlings' growth. Growth variables were defined as terminal nodes and no connections between traits defining the different axes were allowed

2010; Freschet et al. 2010; Reich 2014). In this study, we examined the covariations among 18 functional traits of all plant organs (leaf/stem/root), biomass allocation ratios and anatomical traits of the stem for 15 tropical tree species at the seedling stage. Trait measurements were conducted on individuals of the same life-cycle stage (seedling) grown in comparable conditions; thus avoiding the variability due to the environment and plant ontogeny (Rüger et al. 2012). Our results highlighted two orthogonal axes of trait covariations. The first axis, specifically driven by *D. crassiflora, M. excelsa* and *T. superba*, corresponded to the coordination of the leaf, stem and root traits. This trait coordination supported the coupling among all the organs and was not entirely consistent with the conclusions of Baraloto et al. (2010) and Fortunel et al. (2012). This result suggested that leaf and stem coupling is specific to light-demanding species (Makesteijn et al. 2011; Martínez-Garza et al. 2013). However, our results were consistent with the integrated whole-plant functional coordination proposed by Reich (2014) and revealed among functional groups by Martínez-Garza et al. (2013) for 24 Mexican tree species. The first trait axis corresponded to the global trade-off between resource acquisition and conservation (Kitajima and Poorter 2008) and the reflected species light requirement. The definition of the axis largely depended on the stem density determined by the fibre wall thickness (FWT) as demonstrated by Fortunel et al. (2013) and Powell et al. (2017). The first trait axis was also related to the growth of the seedlings and could be additionally interpreted as a "fast-slow" continuum (Reich 2014). Species with high light demand and an "acquisitive" strategy showed faster growth than more shade-tolerant species with a "conservative" strategy.

The second axis of the trait covariations was shaped by the coordination of the biomass allocation ratios (leaf/stem ratio and petiole mass fraction) and the vessel traits (density and diameter). This second axis was interpreted as the trade-off between safety and the efficiency of hydraulic conductivity (Fortunel et al. 2013; Lachenbruch and Mcculloh 2014; Beeckman 2016). This axis illustrates the trade-off, already reported for 42 coexisting species in Bolivia (Poorter et al. 2010), between the number and size of the vessels. The axis opposed species with small numerous vessels, which limits the cavitation risks and enforces the safety of hydraulic conduction, against species with fewer large vessels, which allows a more efficient hydraulic conductivity (Markesteijn et al. 2011). The axis with more efficient hydraulic conductivity, ensured by a large vessel diameter and a low vessel density, was associated with leaf traits recognized to imply a high water demand (large leaf area and specific leaf area). Such an association was consistent with the observations of a wide range of species and functional types in Amazonia (Powell et al. 2017).

In addition to the descriptive multivariate analyses, the functional scheme inferred confirmed the consistency of a whole-plant functional scheme. It was driven by the functional trade-offs for resource use and plant hydraulics and highlighted the mechanistic pathways between the hierarchical scales from the anatomical traits to functional traits of all the organs (Fig. 3) and eventually to plant growth. Specifically, the anatomical traits of the vessel density, bark/wood ratio and pith fraction determined the functional traits of all the organs (SD, SWC, SLA, LDMC and SRL). In turn, the functional traits of the organs predicted the individual growth in height and diameter (Reich 2014; Beeckman 2016). This result emphasized the importance of hydraulic conductivity for plant growth at the seedling stage (Fan et al. 2012; Poorter et al. 2010), although the regression coefficients of the correlations remained low. It also emphasized the need to account for a large set of anatomical traits to define species functional strategy: the fibre wall thickness, usually thought as a key trait to consider (Fan et al. 2012), did not significantly integrate into the scheme. In addition, the functional scheme confirmed the central role of wood density (Chave et al. 2009; Wright et al. 2010; Lachenbruch and Mcculloh 2014). As previously noted, stem density determined the seedling growth and other key functional traits, consistent with the pioneer study of Poorter and Bongers 2006 and several other studies and meta-analyses (Poorter et al. 2008; Rüger et al. 2012; Gibert et al. 2016).

The functional traits of the seedlings proved predictive of plant growth at the seedling stage. However, only three traits predicted sapling growth (the shoot/root ratio, the petiole mass fraction and the bark/wood ratio), and none predicted sapling survival. Such disconnection in tree performance between ontogenetic stages has already been reported across the whole life-cycle and had been related to tree size (Hérault et al. 2011; Rüger et al. 2012; Prado-Junior et al. 2016). Thus, in a meta-analysis, Gibert et al. (2016) reported the disappearance of some trait-growth relationships during the ontogeny. Similarly, Visser et al. (2016) showed that during the whole life-cycle, the performance was first primarily determined by seed mass and adult stature at the seedling stage and by wood density at the sapling and adult stages. Therefore, we found an integrative role of stem density (SD) during plant development. At the seedling stage, stem density was strongly correlated to height and diameter increments (respectively, $r = -0.57$ and $r = -0.44$, $P < 0.05$), while Doucet et al. (2016) identified a correlation between performance and wood density from a global database at the sapling stage. In contrast, it is only at the seedling stage that the leaf traits (LA, SLA, LDMC and petiole diameter) fully integrated into the "fast-slow" economics spectrum and consistently predicted plant growth (Wright et al. 2010). Among the leaf traits, only the petiole mass fraction was

related to the average specific growth rate at the sapling stage. Petioles that ensure the leaf mechanical support and sap conduction compensate for the hydrostatic constraints resulting from the plant height and leaf transpiration surface (Niinemets et al. 2004; Cavaleri et al. 2010). Petiole allometry directly depends on the plant growth rate at any stage. In contrast, the other leaf traits did not relate to the sapling growth rate and displayed significant variation, as already experienced in another in situ experiment, particularly for tropical tree species (Poorter et al. 2008; Lloyd et al. 2010; Hérault et al. 2011; Markesteijn et al. 2011; Rüger et al. 2012). In particular, the SLA proved unsuitable for predicting the seedling growth rates (Paine et al. 2015), suggesting its strong dependence on the environment, as demonstrated for 15 tropical tree species (Philipson et al. 2014) and 37 subtropical tree species (Li et al. 2017). In addition, trait de-correlation with sapling growth may come from a shift in the role of the traits during the ontogeny. This was theorized by Falster et al. (2011) and revealed by the meta-analysis of Gibert et al. (2016) and for tropical tree species in Central Panama (Visser et al. 2016) and Australia (Sendall et al. 2018). The shift in the role of the traits would also be stronger for light-demanding species whose growth depends first on the efficiency of light interception and second on water use, thus involving different leaf traits (Delagrange et al. 2008; Poorter et al. 2008; Wright et al. 2010; Prado-Junior et al. 2016; Sendall et al. 2018). Our results based on not only classical functional traits but also biomass allocation and stem anatomical traits are consistent with those of Wright et al. (2010), who already mentioned that "[al]though WD [Wood Density] provides a promising start, a successful trait-based ecology of tropical forest trees will require consideration of additional traits". This motivates the focus on new traits, such as the petiole mass fraction or diameter, and additional development of standardized protocols (Garnier and Shipley 2001) to fit the particularities of the tropical tree species.

Our analyses produced a consistent functional scheme at the whole-plant scale for light-demanding and some shade-tolerant species. This integrative scheme was shaped by two major functional trade-offs and highlighted the mechanistic pathway from the anatomical and organ functional traits that determine plant growth. Put in perspective with contradictory results (Baraloto et al. 2010; Fortunel et al. 2012; Paine et al. 2015), the consistency of the whole-plant scheme argues for the need to consider the specificity of central African species ecology (Verbeeck et al. 2011). It also argues for the consideration of ontogenetic shifts in the species functional strategies (Hérault et al. 2011; Gibert et al. 2016) and advocates an individual-based approach to avoid confusing intraspecific, environmental and ontogenetic variability of the functional traits (Rüger et al. 2012; Visser et al. 2016).

Compliance with ethical standards

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