Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance

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Summary

1. Water availability is the main determinant of species' distribution in lowland tropical forests. Species' occurrence along water availability gradients depends on their ability to tolerate drought.

2. To identify species' traits underlying drought-tolerance we excavated first year seedlings of 62 dry and moist forest tree species at the onset of the dry season. We evaluate how morphological seedling traits differ between forests, and whether functional groups of species can be identified based on trait relations. We also compare seedling traits along independent axes of drought and shade-tolerance to assess a hypothesized trade-off.

3. Seedlings of dry forest species improve water foraging capacity in deep soil layers by an increased below-ground biomass allocation and by having deep roots. They minimize the risk of cavitation by making dense stems, and reduce transpiration by producing less leaf tissue. Moist forest seedlings have large leaf areas and a greater above-ground biomass, to maximize light interception, and long, cheap, branched root systems, to increase water and nutrient capture.

4. Associations among seedling traits reveal three major drought strategies: (i) evergreen drought-tolerant species have high biomass investment in enduring organs, minimize cavitation and minimize transpiration to persist under dry conditions; (ii) drought-avoiding species maximize resource capture during a limited growing season and then avoid stress with a deciduous leaf habit in the dry season; (iii) drought-intolerant species maximize both below- and above-ground resource capture to increase competitiveness for light, but are consequently precluded from dry habitats.

5. We found no direct trade-off between drought- and shade-tolerance, because they depend largely on different morphological adaptations. Drought-tolerance is supported by a high biomass investment to the root system, whereas shade-tolerance is mainly promoted by a low growth rate and low SLA.

6. *Synthesis*. We conclude that there are three general adaptation strategies of drought-tolerance, which seemingly hold true across biomes and for different life forms. Drought- and shade-tolerance are largely independent from one another, suggesting a high potential for niche differentiation, as species' specialization can occur at different combinations of water and light availability.

Key-words: Bolivia, biomass allocation, drought-tolerance, root morphology, shade-tolerance, seedlings, trade-offs, tropical dry and moist forest

Introduction

Species composition of tropical forests changes considerably with water availability (Bongers *et al*. 2004; Ter Steege *et al*. 2006): on a large scale, patterns of species' distribution change along rainfall gradients (Hall & Swaine 1981; Swaine 1996; Engelbrecht *et al*. 2007), as species vary in the annual precipitation, length of the dry period and cumulative water deficit at which they are most abundant (Bongers *et al*. 1999); on a smaller scale, species occurrence is affected by topographical variation in water availability, even in relatively wet ecosystems (Borchert 1994; Clark 1999; Valencia *et al*. 2004). Occurrence

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along these large- and small-scale gradients of water availability depends on a species' ability to resist drought. While drought-intolerant species are associated with relatively wet slopes and valleys, more drought-resistant species are associated with dry elevated areas (Harms *et al.* 2001; Engelbrecht & Kursar 2003). Under wet, shady conditions, drought-resistant species are probably out-competed by drought-intolerant ones.

Climate change scenarios predict a decrease in annual rainfall, an increase in dry season length and greater inter-annual rainfall variability for the tropics (Bawa & Markham 1995; Hulme & Viner 1998). If we want to assess how species will respond to these changes in water availability, we need to understand how they are adapted to drought. There is a longstanding interest in the effects of water deficit on basic plant processes, especially in the agricultural literature (reviewed in Iljin 1957; Vaadia *et al.* 1961; Hsiao 1973). Some early work also includes classifications of plants based on their physiological response to water stress and ability to survive water shortages (e.g. Milthorpe & Spencer 1957; De Wit 1959). Nowadays two major strategies of species' adaptation to drought can be identified, each with its specific suite of functional traits: (i) tolerating drought stress and (ii) delaying drought stress. Drought-tolerance is promoted by a plant's continued physiological functioning at low water availability. Drought-tolerant species reduce the probability of xylem cavitation and maintain gas exchange, hydraulic conductance and cell survival at low water potentials (Engelbrecht & Kursar 2003; Tyree *et al.* 2003). Delaying drought stress can be achieved by deciduousness, that is, shedding leaves in the dry season (Reich & Borchert 1984; Borchert 1994). Deciduousness is a strong predictor of seedling survival during drought (Poorter & Markesteijn 2008), but comes at the expense of a shorter growing season and regular biomass loss. Deciduous species are therefore often light-demanding (Eamus & Prior 2001) and highly efficient in reabsorbing nutrients before shedding their leaves (Aerts 1996; H. Paz, pers. comm.), which are cheap because of a low biomass investment per unit leaf area, but costly in terms of nutrient or carbon loss (Givnish 2002). Evergreen species can delay drought stress by maximizing their access to water, whereas minimizing transpirational water loss. Traits associated with this form of drought-delay include high biomass investments to the root system; high specific root lengths, small leaf area and strong stomatal control (cf. Paz 2003; Slot & Poorter 2007; Poorter & Markesteijn 2008).

Species are most susceptible to drought in the early phase of their life cycle (Gerhardt 1996) when seedlings have limited access to water as their small root system is confined to the drier upper soil layers (Kobe *et al.* 1995; Poorter & Hayashida-Oliver 2000; Gilbert 2001). As seedling mortality rates increase exponentially with a decrease in rainfall (Marod *et al.* 2004; Poorter 2005), seedling size at the onset of the dry season is therefore an important, though often neglected, characteristic of species' differentiation in response to drought.

Water and light availability are often negatively correlated across environmental gradients: when water availability increases along rainfall or topographical gradients, primary production increases, vegetation becomes denser and light availability thus decreases. Species' distribution along this combined water and light availability gradient is therefore largely determined by the species' ability to tolerate drought and shade. A trade-off between drought- and shade-tolerance can exist when the adaptations of a species to tolerate drought constrain its survival in the shade or vice versa. Smith & Huston (1989) hypothesized the existence of a trade-off between drought- and shade-tolerance as a consequence of a trade-off between below- and above-ground biomass allocation. This hypothesis postulates that drought-tolerant species allocate more biomass to their root system to augment water acquisition, thus limiting biomass allocation to the shoot system, and ultimately their capacity to forage for light. A meta-analysis on 806 woody species from the Northern Hemisphere indeed confirmed this negative relation between drought- and shade-tolerance (Niinemets & Valladares 2006) although it only explained 8% of the variation. Experimental evidence suggests that drought- and shade-tolerance are largely unrelated (Holmgren 2000; Sack & Grubb 2002; Sack 2004).

In this study we evaluate variation in morphological seedling traits of 62 tropical dry and moist forest tree species. Twenty-one traits were selected based on their importance for water or light acquisition, water and carbon conservation or continued plant functioning during drought. We derive functional strategies of species from correlations among traits and relate seedling traits to independent axes of shade- and drought-tolerance. Shade-tolerance is inferred from the species' juvenile crown exposure, as the amount of light a species receives as a 2-m-tall juvenile (cf. Poorter & Kitajima 2007). Drought-tolerance is inferred from the species' distribution along the rainfall gradient, calculated from each species' relative abundance in the moist and dry forest (cf. Poorter & Markesteijn 2008). The following questions and corresponding predictions were addressed;

1. How do dry and moist forest tree species differ in root morphology and biomass allocation? The functional equilibrium hypothesis (Brouwer 1963) states that, under a given regime of stresses, plants maximize their surface area for intake of the most limiting resource (see also Poorter & Nagel 2000). In dry forests plant growth and survival will mainly be limited by water availability while in moist forests light availability will limit performance. We therefore predict that dry forest seedlings are characterized by traits that allow them to maximize water capture and/or conservation, while minimizing transpirational water loss. Moist forest seedlings will show adaptations that enhance their light interception.

2. How are species' traits associated, and can we distinguish functional groups of species related to drought-tolerance? We expect that drought-tolerance and drought-delay are largely determined by different suites of adaptations and that our species will follow one of these two major strategies.

3. Is there a trade-off between drought- and shade-tolerance, and if so, what is the functional basis? We predict drought-

tolerance to be related to traits that maximise water capture (high root mass fraction, high root length per unit leaf area) and reduce transpiration (small total leaf area). Shade-tolerance will be related to traits that maximize light capture efficiency (high leaf mass fraction, high specific leaf area and leaf area ratio). In line with the hypothesis of Smith and Huston (1989) we predict a trade-off between drought- and shade-tolerance because of a trade-off between biomass allocation to roots and leaves.

Methods

FOREST SITES

Fieldwork was carried out in a dry and in a moist forest in the Department of Santa Cruz, in the eastern lowlands of Bolivia. Both forests are situated on the Precambrian Brazilian Shield at the transition zone between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Killeen 1998; Jardim *et al.* 2003). The forests are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF) and differ strikingly in structure, diversity and species composition (M. Peña-Claros, unpublished data).

The dry site (Inpa; 16°07′ S, 61°43′ W) can be classified as a tropical lowland dry deciduous forest. It has a mean annual temperature of 24.3 °C, a mean annual precipitation of 1160 mm (meteorological data from 1943 to 2005 for nearby Concepción at 40 km distance) with a period of 3 months (June–September) when the potential evapotranspiration exceeds precipitation. The study area has generally poor soils that can be classified as oxisols (M. Peña-Claros, unpublished data). The forest has a density of 420 stems ha^{-1}, a basal area of 18.3 m^2 ha^{-1}, and a species richness of 34 ha^{-1} (trees ≥ 10 cm d.b.h; Villegas *et al.*, in revision.). Average canopy height is 20 m and all canopy trees are deciduous in the dry season, as are most sub-canopy trees. The most dominant species are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), Casearia gossypiosperma *Briquet* (*Flacourtiaceae*), and Caesalpinia pluviosa *DC* (*Fabaceae*).

The moist site (La Chonta; 15°47′ S, 62°55′ W), classified as a tropical lowland semi-evergreen moist forest, has a mean annual temperature of 25.3 °C and an annual precipitation of 1580 mm (meteorological data from 2000 to 2007 at La Chonta) with a dry period of one month (July). Soils at la Chonta are described as fertile inceptisols; they have a high CEC and are especially rich in P and Ca (M. Peña-Claros, unpublished data). The La Chonta forest has a stem density of 367 trees ha^{-1}, a basal area of 19.3 m^2 ha^{-1}, and a species richness of 59 ha^{-1} (Peña-Claros *et al.*, in press). The canopy has an average height of 27 m and *c.* 30% of the canopy trees are deciduous in the dry season. The most common species are Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr. (*Moraceae*), Ampelocera ruizii *Klotzsch* (*Ulmaceae*) and Hirtella triandra *Sw.* (*Chrysobalanaceae*).

Water availability in our dry and moist forest was quantified during the dry period of 2007 and we found that soil water potentials in August (at the height of the dry season) were substantially lower in the dry site (−4.6 ± 0.37 MPa) than in the moist site (−1.8 ± 0.14 MPa) (*t*-test; *t* = 6.4, d.f. = 52, *P* < 0.001) (Markesteijn, unpublished data).

SPECIES AND SEEDLING SELECTION

We selected a total of 62 species from 30 families; 34 species from the dry forest and 37 species from the moist forest, with 9 species in common between both sites (Table 2). The selection of the species was based on their relative abundance in each forest and together they represent more than 75% of all trees ≥ 10 cm d.b.h (M. Peña-Claros, unpublished data).

Ten first year seedlings per species were excavated at the onset of the dry season (April–May 2006) to evaluate seedling morphology just before they were exposed to drought for the first time. To reduce the probability of seedlings being older than one growing season we used several selection criteria. Seedling height varied among species (mean overall seedling height = 14 cm, range mean seedling height of species = 5–29 cm), but never exceeded 40 cm. The presence of seed remnants or cotyledons was used as an indicator for recent establishment and if not present, seedlings showing bud or leaf scars as morphological markers of first year height extension were excluded. Additionally, we consulted local experts for their opinion. Seedlings were selected that grew in high light conditions, that is, in big tree fall gaps or along logging roads. All selected seedlings had a crown position of 4 (cf. Dawkins & Field 1978), meaning they received full direct overhead light. Under these conditions seedlings were most likely to experience the largest vapour pressure deficits and the greatest water stress. Moreover, it is virtually impossible to find short-lived pioneers under shady conditions. By sampling at full overhead light we are able to compare pioneers and shade-tolerants under similar growth conditions, thus reducing effect of phenotypic variation in response to light. Never more than three seedlings of a species were collected near a mother tree to assure the genetic independence of our observations.

Excavation was done with a shovel and the soil around the roots was then carefully loosened avoiding loss of fine roots as much as possible. To standardize soil conditions we only sampled seedlings from sandy loam soils relatively rich in organic matter. The maximum rooting depth (RD) and rooting width were measured in the field. The sampled seedlings were put into plastic bags, labelled and transported to the field station for further processing.

SEEDLING TRAITS

Seedlings were dissected into roots, stems, leaves and, if present, cotyledons. Root fresh mass was measured. The number of leaves was counted and leaves were digitized with a desktop-scanner (Canon Lide 30). Total leaf area (LA; cm^2) was determined with the help of pixel-counting software (Van Berloo 1998). We measured stem length and diameter at the top and base of the stem, including bark, and calculated stem volume using a formula for a cone: $V = (\pi L/12)(D_{top}^2 + D_{top}D_{base} + D_{base}^2)$, where V is stem volume (cm^3), L is stem length (cm), D_{top} is the diameter at the top of the stem (cm) just under the growth meristem, and D_{base} the diameter at the base of the stem (cm) just above the root. Total root length (RL; cm) was determined using the line intersect method of Newman (1966). Roots were placed in a transparent water bath over paper with a 1 × 1 cm grid and the number of intersects between the roots and the grid were counted in two directions. Subsequently, total root length was estimated as $R = \pi NA/2H$, where R is the total length of the root (cm), N is the number of intersections between root and gridlines, A is the area of the rectangle (cm^2) and H is the total length of the straight lines of the grid (cm) (Newman 1966). Afterwards seedlings were oven-dried for 48 h at 65 °C and measured again for their dry mass.

With these measurements we calculated average leaf size (LS; cm^2), root water content (RWC; amount of water per unit root mass; g g^{-1}), leaf, stem and root mass fractions (LMF, SMF, RMF; dry mass per unit dry plant mass; g g^{-1}) and rooting area and volume

(RA, RV; in cm^2 and cm^3). We calculated the specific leaf area (SLA; leaf area per unit dry leaf mass; cm^2 g^{-1}), leaf area ratio (LAR; leaf area per unit dry plant mass; cm^2 g^{-1}), specific root length (SRL; root length per unit dry root mass; cm g^{-1}), root length per unit plant mass (RLPM; cm g^{-1}), root length per unit leaf area (RLLA; cm cm^{-2}), the secondary-to-primary-root-mass ratio (SPRMR; secondary root mass per unit primary root mass; g g^{-1}), and leaf area per unit cross-sectional stem area (LASA; cm^2 mm^{-2}), which is the inverse of the Huber-value. Stem density (SD) was determined as dry stem mass per unit stem volume (g cm^{-3}). Finally we scored whether species had simple or compound leaves.

The 21 traits presented are functionally important for the following reasons: seedling biomass serves as a proxy for relative growth rate over the first year. Leaf area and leaf mass fraction describe the plant level biomass investment in light intercepting tissue, while leaf size is important for the regulation of heat load. The specific leaf area and leaf area ratio indicate how efficiently plants display their leaves to intercept light. Stem density is an indicator of the stem vulnerability to cavitation (Preston *et al.* 2006), and the stem mass fraction and leaf area per unit stem area are important for biomechanical and hydraulic support. Rooting depth, area and volume indicate how much and what part of the soil volume is explored for nutrients and water. The root mass fraction indicates the biomass investment in below-ground foraging, and the specific root length and secondary-to-primary-root-mass ratio indicate how efficient this biomass is used to create a large absorptive area. Root length, and root length per unit leaf area and per unit plant mass indicate the relative amount of hydraulic support. Root water content is an indicator for the construction costs of roots (how much root 'volume' is created per unit of root dry mass), and the potential for water storage in the roots. Seedling traits and their abbreviations are summarized in Table 1.

SPECIES DROUGHT- AND SHADE-TOLERANCE

The 62 study species were ranked along independent axes of drought- and shade-tolerance. We used a 'drought index' (DI) as an ecological indicator of a species' drought-tolerance (cf. Poorter & Markesteijn 2008). The DI corresponds to the species' distribution along the rainfall gradient and was derived from the relative abundance of a species in the dry and the moist forest. The DI is calculated as: DI = $100(D_{dry}/D_{dry} + D_{moist})$, where D_{dry} and D_{moist} are the mean stem densities (trees ha^{-1}) of a given species in the dry and the moist forest site, respectively. Stem densities were calculated from the number of trees ($\geq$ 10 cm d.b.h.), for 32 one-hectare plots in the dry and 48 one-hectare plots in the moist forest (Peña-Claro *et al.*, in prep.). It is important to keep in mind that the DI provides a simplified description of the actual species' distribution, as it resulted from an analysis including two forests only. The DI thus provides a rough estimate of the actual species' position along the rainfall gradient, as the species' occurrence further up or down the gradient (in wetter or drier systems) could not be assessed. The DI among species varies from 0 to 100, where 0 indicates that a species is only found in the moist forest, and 100 indicates that the species is only found in the dry forest, while the remainders occur at both sites (0 < DI < 100) (Table 2). The DI is positively correlated with the seedling drought survival of evergreen species, as determined under standardized experimental conditions (Poorter & Markesteijn 2008).

Poorter & Kitajima (2007) provided an independent, objective and continuous measure of the regeneration light requirements of the species (i.e. the inverse of shade-tolerance). On average 523 individuals (range 16–9064) per species were measured over their whole size range for their height and crown exposure (cf. Dawkins and Field 1978). Crown exposure (CE) varies from 1 if a the tree does not receive any direct light, to 2 if it receives lateral light, 3 if it receives overhead light on 10–90% of the vertical projection of the crown surface, 4 when it receives full overhead light on > 90% of the vertical projection of the crown, and 5 when it has an emergent crown. CE measurements are repeatable (average difference between two independent observers is 0.1 ± 0.01 SE), and there is a good relation between CE and both canopy openness and incident radiation (Clark *et al.* 1993; Keeling & Phillips 2007). For each species CE was related to tree height, using a multinomial regression analysis (cf. Poorter *et al.* 2005; Sheil *et al.* 2006). Using the regression equation, the average population-level CE at a standardized height of two meters (juvenile crown exposure) was calculated. Similar-sized individuals of the same species can be found under a wide range of crown exposures, but what counts from an evolutionary point of view is the average population-level CE of the species (Poorter *et al.* 2005). Species with a low juvenile CE mainly regenerate in the shaded understorey (shade-tolerant species), whereas species with a high juvenile CE mainly regenerate in the high-light conditions of gaps (light-demanding pioneer species). In line with this assumption, functional shade-tolerance groups in both the moist and the dry forest differed in the mean juvenile CE of their species (Rozendaal *et al.* 2006; Markesteijn *et al.* 2007). The juvenile CE is also negatively correlated with sapling survival of the species in the shade (Poorter & Bongers 2006).

Table 1. Seedling traits investigated in this study with abbreviations used in the text and the units of expression. Pearson correlation coefficients describe the relation between several morphological seedling traits under field conditions (this study) and under standardized experimental conditions (Poorter and Markesteijn, 2008) for a subset of species collected (n = 31). Coefficients are significant at: *: P < 0.05; **: P < 0.01; ***: P < 0.001

Trait	Abbreviation	Unit	Pearson correlation coefficients
Total seedling biomass	BIOM	g	
Leaf area	LA	cm^2	0.32
Leaf size	LS	cm^2	0.53**
Specific leaf area	SLA	cm^2 g^{-1}	0.87***
Leaf mass fraction	LMF	g g^{-1}	0.43*
Leaf area ratio	LAR	cm^2 g^{-1}	0.24
Stem density	SD	g cm^{-3}	0.76***
Stem mass fraction	SMF	g g^{-1}	0.46**
Root length	RL	cm	0.41*
Rooting depth	RD	cm	
Rooting area	RA	cm^2	
Rooting volume	RV	cm^3	
Specific root length	SRL	cm g^{-1}	0.78***
Root water content	RWC	g g^{-1}	0.73***
Root mass fraction	RMF	g g^{-1}	0.78***
Root length per unit leaf area	RLLA	cm cm^{-2}	0.60***
Root length per unit plant biomass	RLPM	cm g^{-1}	0.76***
Secondary to primary root mass ratio	SPRMR	g g^{-1}	
Leaf area per unit stem area	LASA	cm^2 mm^2	
Deciduousness	DEC		
Compoundness	COMP		

Table 2. List of 62 species with scientific and family names and abbreviations as used in the graphs. The species' drought index (relative distribution of species along the rainfall gradient) (DI) is given, as well as their juvenile crown exposure (CE). Values presented are the back-transformed species' means of seedling biomass at harvest (BIOM) and seedling traits included in this study. Trait values were calculated at a standardized seedling size of 4.7 g (see Table 1 for the abbreviations)

Species	Family	Code	DI	CE	BIOM (g)	LA (cm²)	LS (cm²)	SLA (cm² g⁻¹)	LMF (g g⁻¹)	LAR (cm² g⁻¹)	SD (g cm⁻³)	SMF (g g⁻¹)	RD (cm)	RA (cm²)	RV (cm³)	RL (cm)	SRL (cm g⁻¹)	RWC (g g⁻¹)	RMF (g g⁻¹)	RLLA (cm cm⁻¹)	RLPM (cm g⁻¹)	SPRMR (g g⁻¹)	LASA (cm² mm⁻²)
Dry forest																							
Acosmium cardenasii	Fabaceae	Aco.c	100	1.44	8	19	6	182	0.23	42	0.71	0.18	7	0.35	1.02	42	166	0.38	0.56	2.19	91	1.05	8
Ampelocera ruizii	Ulmaceae	Amp.r	2	1.59	4	58	12	269	0.43	115	0.47	0.23	7	3.47	11.22	102	832	0.58	0.25	1.78	204	1.23	16
Anadenanthera colubrina	Fabaceae	Ana.c	100	1.75	3	13	4	191	0.16	28	0.68	0.19	3	1.07	1.82	33	115	0.43	0.64	2.57	72	1.02	8
Aspidosperma cylindrocarpon	Apocynaceae	Asp.c	82	1.31	3	40	5	182	0.41	74	0.44	0.22	4	0.00	0.00	37	324	0.74	0.22	0.93	69	1.51	10
Aspidosperma tomentosum	Apocynaceae	Asp.t	100	1.31	14	26	6	302	0.19	59	0.58	0.25	9	0.12	0.71	20	79	0.51	0.56	0.76	45	1.02	12
Bougainvillea modesta	Nyctanginaceae	Bou.m	86	2.19	8	45	17	288	0.35	100	0.81	0.31	6	0.60	2.00	30	224	0.50	0.30	0.68	66	1.07	14
Caesalpinia pluviosa	Fabaceae	Cae.p	94	1.81	7	24	6	347	0.16	54	0.74	0.47	19	0.01	0.04	14	89	0.62	0.36	0.58	31	1.00	7
Capparis prisca	Capparaceae	Cap.p	100	1.59	7	27	6	245	0.25	59	0.54	0.28	6	0.54	0.65	30	148	0.56	0.46	1.12	66	1.05	7
Casearia gossypiosperma	Flacourtiaceae	Cas.g	93	1.71	2	46	9	302	0.35	100	0.79	0.27	8	0.56	1.38	65	398	0.42	0.36	1.41	141	1.17	19
Ceiba samaura	Bombacaeae	Cei.s	65	2.45	10	186	178	550	0.29	417	0.20	0.34	2	0.01	0.01	7	41	0.80	0.33	0.04	15	0.95	31
Ceiba speciosa	Bombacaeae	Cei.sp	96	1.64	7	28	6	479	0.14	60	0.17	0.36	8	1.45	2.04	32	151	0.83	0.47	1.15	69	1.10	2
Centrolobium microchaete	Fabaceae	Cen.m	95	1.93	3	35	8	339	0.25	78	0.71	0.34	7	0.05	0.10	19	115	0.45	0.37	0.54	43	1.05	11
Combretum leprosum	Combretaceae	Com.l	85		6	34	9	339	0.24	76	0.71	0.30	14	0.04	0.15	46	229	0.41	0.45	1.35	102	1.12	12
Copaifera chodatiana	Fabaceae	Cop.c	100	1.87	3	31	5	170	0.33	56	0.85	0.25	4	0.00	0.00	55	437	0.50	0.23	1.74	100	1.10	11
Erythroxylum daphnites	Erythroxylaceae	Ery.d	100	1.64	1	54	15	437	0.28	120	0.66	0.24	13	2.82	10.00	26	120	0.32	0.46	0.47	56	1.05	24
Gallesia integrifolia	Phytolaccaceae	Gal.i	58	1.81	3	43	10	339	0.29	93	0.47	0.39	5	1.26	3.09	132	977	0.61	0.31	3.09	288	1.15	9
Hymenaea courbaril	Fabaceae	Hym.c	74		17	54	10	234	0.37	85	0.20	0.19	10	1.20	8.13	35	309	0.72	0.24	0.68	58	1.05	10
Jacaratia sp.	Caricaceae	Jac.	100	2.12	14	28	12	676	0.11	62	0.11	0.29	13	4.57	21.88	26	98	0.94	0.59	0.93	58	1.05	2
Machaerium acutifolium	Fabaceae	Mac.a	100	1.39	4	28	5	309	0.20	62	0.62	0.31	6	4.07	11.75	26	126	0.60	0.48	0.95	59	1.05	10
Myrciaria cauliflora	Myrtaceae	Myr.c	100	1.70	2	23	10	155	0.33	52	1.02	0.30	11	0.02	0.03	28	174	0.26	0.34	1.15	60	1.02	11
Myrciaria sp.	Myrtaceae	Myr.	48	1.24	1	48	15	537	0.50	263	0.34	0.23	5	3.80	5.62	19	151	0.43	0.29	1.29	263	1.32	22
Neea cf. *steinbachii*	Nyctanginaceae	Nee.s	97	1.63	4	43	10	240	0.40	91	0.42	0.20	6	0.26	0.91	43	282	0.57	0.35	1.00	91	1.10	12
Phyllostylon rhamnoides	Ulmaceae	Phy.r	100	1.49	2	34	4	251	0.32	74	0.78	0.34	8	0.03	0.04	74	398	0.40	0.44	2.24	166	1.12	9
Pogonopus tubulosus	Rubiaceae	Pog.t	100	1.67	5	26	10	562	0.13	58	0.78	0.41	7	1.58	4.27	51	295	0.54	0.39	1.95	112	1.10	9
Pterogyne nitens	Fabaceae	Pte.n	78	2.00	3	56	14	288	0.41	117	0.74	0.13	10	0.05	0.19	34	204	0.57	0.36	0.60	71	1.07	35
Rollinia herzogii	Annonaceae	Rol.h	100		3	47	9	275	0.38	102	0.59	0.26	12	1.17	6.46	41	257	0.65	0.35	0.87	89	1.05	20
Simira rubescens	Rubiaceae	Sim.r	91	1.62	7	35	7	437	0.19	79	0.54	0.27	10	1.55	2.95	56	234	0.48	0.53	1.58	126	1.10	12
Solanum riparium	Solanaceae	Sol.r	100	3.00	13	162	42	550	0.66	363	0.19	0.16	6	1.12	2.57	89	1175	0.82	0.17	0.55	195	1.82	30
Spondias mombin	Anacardiaceae	Spo.m	48	2.40	13	95	4	324	0.39	123	0.66	0.23				93	537	0.52	0.34	1.41	178	2.09	7
Sweetia fruticosa	Fabaceae	Swe.f	78	1.70	5	46	10	417	0.27	100	0.71	0.18	13	1.86	8.13	16	68	0.51	0.56	0.36	36		30
Tabebuia impetiginosa	Bignoniaceae	Tab.i	100	2.42	9	24	3	372	0.15	52	0.60	0.24	8	5.89	27.54	78	295	0.48	0.60	3.24	174	1.12	8
Trichilia elegans	Meliaceae	Tri.e	100	1.64	1	66	55	302	0.48	148	0.81	0.23	6	0.04	0.05	60	589	0.61	0.23	0.91	135	1.12	30
Urera baccifera	Urticaceae	Ure.b	100	1.81	3	74	19	479	0.35	162	0.13	0.09	1	64.57	47.86	186	776	0.84	0.55	2.57	417	1.29	9
Zanthoxylum monogynum	Rutaceae	Zan.m	100	1.46	2	62	26	269	0.51	135	0.95	0.24	4	7.41	22.91	39	389	0.38	0.23	0.63	87	1.41	43
Moist forest																							
Alibertia verrucosa	Rubiaceae	Ali.v	1	1.35	2	50	16	214	0.51	112	0.72	0.27	14	0.56	1.66	22	269	0.64	0.19	0.45	50	1.15	25
Ampelocera ruizii	Ulmaceae	Amp.r	2	1.35	8	58	17	288	0.43	126	0.45	0.33	6	3.89	8.13	135	1288	0.57	0.22	2.34	295	1.48	17
Aspidosperma cylindrocarpon	Apocynaceae	Asp.c	82	1.75	4	42	10	174	0.45	79	0.48	0.24	4	0.72	2.09	26	309	0.61	0.17	0.63	50	1.29	13
Batocarpus amazonicus	Moraceae	Bat.a	6	1.35	4	49	13	302	0.36	100	0.36	0.32	10	0.16	0.46	30	282	0.67	0.25	0.60	60	1.10	17
Caesalpinia pluviosa	Fabaceae	Cae.p	94	1.87	5	23	5	339	0.16	52	0.74	0.38	8	0.89	2.04	28	141	0.46	0.44	1.17	62	1.07	7
Cariniana estrellensis	Lecythidaceae	Car.e	0	1.40	8	49	9	331	0.34	110	0.55	0.28	10	0.13	0.15	28	191	0.65	0.37	0.60	66	1.12	15
Cariniana ianeirensis	Lecythidaceae	Car.i	21	1.74	7	26	5	380	0.20	59	0.30	0.39	5	1.78	4.07	28	155	0.80	0.41	1.05	60	1.12	3
Casearia gossypiosperma	Flacourtiacae	Cas.g	93	1.83	7	59	11	316	0.43	132	0.66	0.23	9	0.21	0.62	69	513	0.59	0.31	1.17	155	1.35	25
Cavanillesia hylogeiton	Malvaceae	Cav.h	0	2.16	35	35	48	380	0.21	79	0.16	0.55	3	10.72	16.98	7	71	0.94	0.22	0.19	15	1.35	2

Table 2. *Continued*

Species	Family	Code	DI	CE	BIOM (g)	LA (cm²)	LS (cm²)	SLA (cm²g⁻¹)	LMF (gg⁻¹)	LAR (cm²g⁻¹)	SD (gcm⁻³)	SMF (gg⁻¹)	RD (cm)	RA (cm²)	RV (cm³)	RL (cm)	SRL (cmg⁻¹)	RWC (gg⁻¹)	RMF (gg⁻¹)	RLLA (cmcm⁻¹)	RLPM (cmg⁻¹)	SPRMR (gg⁻¹)	LASA (cm²mm⁻²)
Cecropia concolor	Cecropiaceae	Cec.c	30	2.44	7	93	13	331	0.63	204	0.30	0.13	3	3.39	4.47	76	794	0.72	0.23	0.81	170	2.34	15
Cedrela fissilis	Meliaceae	Ced.f	33	1.98	11	129	66	724	0.39	282	0.21	0.31	4	46.77	346.74	60	513	0.81	0.27	0.47	135	2.40	19
Centrolobium microchaete	Fabaceae	Cen.m	95	1.94	7	33	10	389	0.23	76	0.58	0.37	7	0.06	0.17	18	107	0.58	0.38	0.54	40	1.05	10
Ficus boliviana	Moraceae	Fic.b	2	1.93	7	31	6	380	0.19	69	0.27	0.33	7	3.47	3.63	79	389	0.74	0.46	2.57	178	1.51	6
Gallesia integrifolia	Phytolaccaceae	Gal.i	58	1.84	3	35	12	316	0.25	76	0.43	0.43	4	1.20	1.23	138	1000	0.53	0.31	3.98	302	1.41	6
Heliocarpus americanus	Malvaceae	Hel.a	46	2.36	3	93	22	417	0.50	204	0.19	0.31	5	1.58	2.19	62	851	0.77	0.16	0.66	135	1.45	15
Hirtella triandra	Chrysobalanaceae	Hir.t	0	1.28	1	58	28	282	0.46	126	0.74	0.31	9	0.09	0.20	42	490	0.59	0.22	0.72	91	1.17	23
Hura crepitans	Euphorbiaceae	Hur.c	0	1.62	6	69	11	537	0.29	151	0.15	0.40	5	1.66	4.68	49	380	0.82	0.29	0.71	107	1.38	5
Jacaratia spinosa	Caricaceae	Jac.s	0	2.02	2	110	24	708	0.37	245	0.13	0.40	10	4.17	10.96	32	372	0.90	0.20	0.29	71	1.17	6
Licaria triandra	Lauraceae	Lic.t	0	1.35	4	38	9	214	0.40	85	0.49	0.32	16	2.51	5.13	44	372	0.66	0.27	1.15	98	1.26	11
Myrciaria sp.	Myrtaceae	Myr.	48	1.45	2	49	16	295	0.37	110	0.74	0.31	8	0.41	0.52	63	490	0.37	0.29	1.29	138	1.35	22
Ocotea sp.	Lauraceae	Oco1	0	1.37	4	45	10	224	0.44	98	0.46	0.31	3	4.17	9.55	52	501	0.68	0.23	1.17	115	1.70	13
Ocotea sp.	Lauraceae	Oco2	0	1.34	4	41	9	209	0.43	89	0.55	0.31	17	2.14	7.59	42	389	0.60	0.24	1.02	91	1.20	14
Pourouma cecropiifolia	Cecropiaceae	Pou.c	0	1.38	1	63	6	309	0.45	141	0.44	0.25	8	0.23	0.27	30	251	0.47	0.26	0.46	65	1.20	21
Pouteria macrophylla	Sapotaceae	Pou.m	0	1.55	3	39	15	204	0.42	85	0.58	0.26	4	3.89	15.14	26	178	0.58	0.31	0.66	56	1.12	17
Pouteria nemorosa	Sapotaceae	Pou.n	0	1.57	8	19	4	331	0.13	41	0.47	0.29	9	0.06	0.11	35	135	0.53	0.57	1.91	78	1.10	4
Pseudolmedia laevis	Moraceae	Pse.l	0	1.32	3	49	14	240	0.46	107	0.46	0.23	8	1.15	4.47	45	468	0.55	0.22	0.93	100	1.07	15
Sapindus saponaria	Sapindaceae	Sap.s	2	2.23	10	72	25	468	0.35	162	0.28	0.31	9	3.09	9.33	63	447	0.67	0.32	0.87	138	1.48	13
Sapium glandulosum	Euphorbiaceae	Sap.g	8	1.63	8	35	8	437	0.32	78	0.37	0.34	8	0.04	0.12	91	603	0.60	0.34	2.57	200	1.58	7
Schizolobium parahyba	Fabaceae	Sch.p	0	2.39	8	63	16	372	0.38	141	0.31	0.29	10	10.72	20.89	105	871	0.80	0.28	1.62	229	2.04	10
Spondias mombin	Anacardiaceae	Spo.m	48	1.95	3	26	10	479	0.17	56	0.29	0.22	6	0.13	2.24	20	78	0.79	0.62	0.78	44	1.10	6
Stylogyne ambigua	Myrsinaceae	Sty.a	0	1.46	2	54	18	229	0.52	120	0.40	0.23	6	0.20	0.37	41	389	0.71	0.23	0.76	91	1.35	13
Sweetia fruticosa	Fabaceae	Swe.f	78	1.91	9	54	19	407	0.31	120	0.65	0.23	13	0.00	0.00	16	79	0.56	0.45	0.30	35	1.02	28
Swietenia macrophylla	Meliaceae	Swi.m	0	1.62	7	78	17	380	0.44	170	0.30	0.31	5	0.11	0.28	18	191	0.57	0.21	0.23	40	1.05	17
Terminalia oblonga	Combretaceae	Ter.o	0	1.88	11	68	9	324	0.49	151	0.71	0.28	3	0.26	0.29	100	1047	0.34	0.22	1.48	224	1.35	25
Trema micrantha	Ulmaceae	Tre.m	0	2.52	5	81	17	380	0.49	178	0.32	0.23	4	7.24	10.23	117	1023	0.65	0.26	1.45	257	3.31	26
Urera caracasana	Urticaceae	Ure.c	7	1.99	9	100	21	479	0.47	224	0.26	0.12	5	0.89	5.13	178	1122	0.80	0.38	1.78	398	1.62	19

Table 3. Two-way nested ANCOVA with the effect of forest ($n = 2$) and species nested within forest ($n = 71$) on seedling traits. Log-transformed seedling biomass was included as a covariate to test its effect on seedling traits and interaction with forest (forest × biomass) and species (species within forest × biomass). F-values, significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) and the amount of explained variation (η^2) of the effects are given. η^2 is an equivalent of R^2 and was calculated as the sum of squares of the effect relative to the total sum of squares (×100, in %). LMF, SMF, RMF and RWC arcsine transformed and the other traits were $\log_{10}$-transformed before analysis. The means of the absolute seedling trait values of dry and moist forest species ($n = 34$ and 37 respectively) are presented. See Table 1 for the trait abbreviations

Traits	Forest			Species within forest			Biomass			Forest * Biomass			Species within forest * Biomass			Means	
	F	P	η^2	F	P	η^2	F	P	η^2	F	P	η^2	F	P	η^2	Dry forest	Moist forest
Total seedling biomass (g)	7	**	1	9	***	52										4.20	4.85
LA (cm²)	156	***	3	17	***	19	3917	***	66	0	NS	0	2	***	3	34.8	54.0
LS (cm²)	22	***	1	3	***	13	916	***	50	5	*	0	2	***	7	8.01	12.1
SLA (cm² g⁻¹)	26	***	1	27	***	73	15	***	1	0	NS	0	2	***	5	309	333
LMF (g g⁻¹)	134	***	6	18	***	60	73	***	4	0	NS	0	2	**	5	0.30	0.37
LAR (cm² g⁻¹)	178	***	8	17	***	54	151	***	7	0	NS	0	2	***	7	80.4	111.0
SD (g cm⁻³)	224	***	7	29	***	67	114	***	4	1	NS	0	2	***	5	0.53	0.38
SMF (g g⁻¹)	53	***	3	13	***	56	7	**	0	18	***	1	2	***	8	0.27	0.30
RL (cm)	11	***	0	17	***	46	745	***	28	1	NS	0	2	***	5	39.4	47.7
RD (cm)	122	***	10	5	***	21	399	***	33	0	NS	0	1	NS	4	15.3	12.6
RA (cm²)	10	**	1	8	***	27	679	***	43	0	NS	0	1	*	5	12.3	17.8
RV (cm³)	0	NS	0	6	***	18	948	***	55	0	NS	0	1	*	4	189	223
SRL (cm g⁻¹)	130	***	4	23	***	47	984	***	30	5	*	0	2	***	4	253	354
RWC (g g⁻¹)	82	***	5	11	***	50	8	**	1	0	NS	0	3	***	11	0.59	0.67
RMF (g g⁻¹)	313	***	12	20	***	53	161	***	6	16	***	1	3	***	8	0.40	0.30
RLLA (cm cm⁻²)	25	***	1	11	***	44	271	***	16	0	NS	0	2	***	8	1.13	0.88
RLPM (cm g⁻¹)	16	***	1	18	***	45	827	***	30	0	NS	0	2	***	5	91.5	97.3
SPRMR (g g⁻¹)	137	***	9	12	***	52	0	NS	0	0	NS	0	2	**	7	1.14	1.32
LASA (cm² mm²)	3	NS	0	17	***	64	1	NS	0	2	NS	0	2	***	7	11.5	12.3

DO FIELD DATA REFLECT INHERENT SPECIES DIFFERENCES OR ENVIRONMENTAL DIFFERENCES?

When comparing functional seedling traits of species with data collected in the field, there is always the possibility that results are partly confounded by differences in environmental conditions under which seedlings were growing. To assess the magnitude of this problem we compared the species-specific trait values obtained for seedlings growing in the field with the values obtained from an independent common garden experiment, in which seedlings were grown at 10% of full irradiance (Poorter & Markesteijn 2008). For 31 species common to both studies we found that seedling trait values in the field and the greenhouse were highly correlated (Table 1): of the 13 traits compared 11 were positively correlated, 7 of which strongly ($0.60 \geq r \geq 0.87$; $P < 0.001$). Leaf area and leaf area ratio were unrelated between both studies, probably because they are strongly size-dependent and more prone to ontogenetic drift (no ontogenetic correction was done in the greenhouse study). The strong correlations between trait values obtained in the greenhouse and the field suggests that environmental heterogeneity in the field confounded the results only to a limited extent, and that sound generalizations can be made based upon this field study.

DATA ANALYSIS

Seedling biomass was used as an indicator of seedling size. Proportional traits (LMF, SMF, RMF and RWC) were arcsine-transformed and the remainder of the traits was $\log_{10}$-transformed before analyses to improve normality and homoscedasticity. We did not apply a phylogenetic correction to our data, as cross-species correlations of phylogenetically corrected and uncorrected data usually lead to very similar results and conclusions (Westoby *et al.* 2002; Poorter 2007). Also, we were mainly interested in the present day ecological consequences of seedling traits for species' distribution (cf. Westoby 1995).

We tested for the effect of forest type, species and seedling biomass on traits with a two-way nested ANCOVA, with forest as fixed factor, species nested within forest as a random factor and $\log_{10}$-transformed seedling biomass as a covariate. The amount of variation explained by the forest, species and seedling size was calculated as the sum of squares of the effect divided by the total sum of squares of the model ($\eta^2 * 100$%). η^2 is equivalent to R^2. The model showed that there was a strong effect of seedling biomass on most traits, and that sometimes the slopes were not homogeneous (Table 3). To correct for ontogenetic effects in further cross-species analyses, the trait values for each species were recalculated at a standardized seedling biomass of 4.7 g, using species-specific regression equations. 4.7 g is the grand mean biomass for all species and individuals lumped.

We used a principal component analysis (PCA) to evaluate associations among seedling traits. Seedling biomass and 18 seedling traits of all 62 species-site combinations were included as continuous variables, and deciduousness and compoundness of the leaves as dummy variables (present = 1, absent = 0). DI and juvenile CE were not included in the analysis, but later plotted in the graph based on their Pearson correlation with the species scores along the first and second PCA axis. Further univariate relations of seedling traits with DI and CE were analyzed with Pearson correlation analyses. All statistical analyses were done using SPSS 12.0.1 (SPSS Inc., Chicago).

Results

BETWEEN FORESTS AND AMONG SPECIES VARIATION

Variation in seedling traits between forests and among species was evaluated with a nested ANOVA, including seedling biomass as a covariate. All traits but RV and LASA differed significantly between dry and moist forests, but the amount of explained variation was low (0.4–12%) in comparison to among species variation (13–73%) (Table 3). Seedling biomass significantly explained variation in all traits but SPRMR and LASA (0.4–66%). There was a significant biomass-forest interaction effect on four traits, but the magnitude of this interaction effect was small (0.2–1.1%). A greater portion of the total variation was explained by the interaction between seedling biomass and species within forests (3–11%). The interaction was significant for all traits except RD (Table 3), indicating that species follow species-specific ontogenetic trajectories.

The strongest differences between dry and moist forest seedlings were found for RMF, RD, SPRMR, LAR and SD (Table 3). Seedlings of dry forest species had a higher biomass fraction in roots than moist forest species. Dry forest species had deeper root systems whereas moist forest species showed more secondary, lateral roots (higher SPRMR) covering a larger soil area (larger RA) and had a larger total root length. Dry forest species generally make a primary root with little to no lateral extensions that is relatively short and thick, with a low SRL. Dry forest species showed a lower RWC, but a higher SD than moist forest species, had smaller leaves and a higher root length per unit leaf area (Table 3). Total rooting volume (RV) did not differ between forests. Furthermore seedlings of moist forest species invested more of their total biomass into their leaves (they had high LMF and LAR, and a large LA) and their leaves were relatively thin (high SLA) in comparison to dry forest seedlings. Moist forest seedlings had a higher stem mass fraction and more root length per unit plant biomass.

TRAIT ASSOCIATIONS AND FUNCTIONAL GROUPS

We evaluated the associations among species traits with a principal component analysis (PCA). We included the 18 seedling traits together with seedling biomass, deciduousness and compoundness in the analysis. The first two axes together explained 48% of the variation, the first axis 28% (Fig. 1). Dry and moist forest species differed in their position along the first PCA axis (t-test; $t = 2.7$, d.f. = 66, $P = 0.009$), with moist forest species having higher axis scores. Species that invest biomass in above-ground light capture and have efficient root extension for below-ground resource capture (a high root length per unit biomass invested) are found towards the right. Seedlings of these species have a high LAR and LMF, while they show relatively long and thin roots (high SRL) with more lateral branching (high SPRMR). Most species on this side of the axis are found in the moist forest (Fig. 2) with a clear cluster of pioneers marking the end of the gradient (*Solanum riparium*; Sol.r, *Trema micrantha*; Tre.m, *Cecropia concolor*; Cec.c,
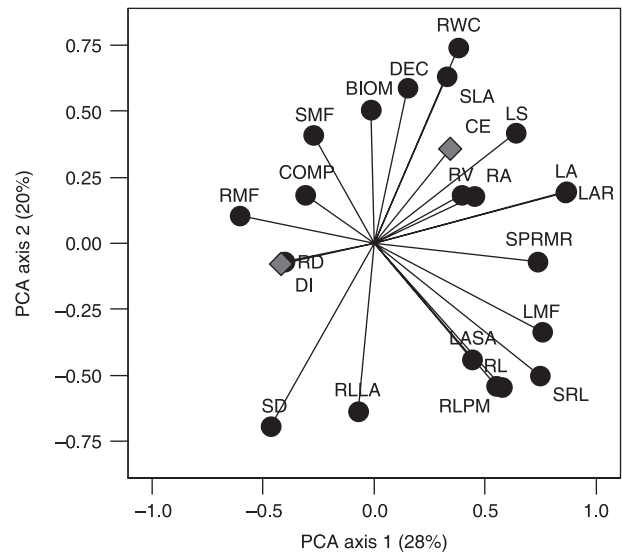
Fig. 1. Principal component analysis (PCA) with the mean values of the seedling traits, of 62 tree species. Trait values were calculated at a standardized seedling size of 4.7 grams. The first two PCA axes are shown with the percentages of explained variation. Total seedling biomass at the time of harvest (BIOM) was included in the analyses as a continuous variable and deciduousness (DEC) and compoundness (COMP) were included as dummy variables (0,1). Species' drought index (DI) and juvenile crown exposure (CE) were not included in the PCA, but plotted later based on their Pearson correlation coefficients with the first two axes.

Urera caracasana; Ure.c, *Heliocarpus americanus*; Hel.a, *Urera baccifera*; Ure.b and *Schizolobium parahyba*; Sch.p). Species on the left side of the axis invest a greater portion of their biomass in their root system (high RMF, large RD) and stem (high SD and SMF). These species have a compound leaf habit (Fig. 1) and are mainly dry forest species and shade-tolerant moist forest species (Fig. 2). This axis corresponds with 'persistence', as it ranks species that can persist under low resource conditions at the left to ephemeral, short-lived species with a high resource demand at the right.

The second PCA axis explains an additional 20% of the variation (Fig. 1). At the top of the axis are deciduous species with a high SLA and RWC and a large first year seedling biomass (Figs 1, 2). At the bottom of the axis are species with a greater stem density and LASA. They have a large root system with a high total root length, root length per unit leaf area (RLLA) and per unit plant biomass (RLPM). The majority of these species is evergreen. Evergreen and deciduous species significantly differ in their position along the second PCA axis (t-test; $t = -5.9$; d.f. = 19.3; $P < 0.001$) and this axis therefore corresponds to deciduousness.

SEEDLING TRAITS ASSOCIATED WITH DROUGHT- AND SHADE-TOLERANCE

The drought index (DI) ranks our species based on their relative abundance from moist to dry forests. The juvenile crown
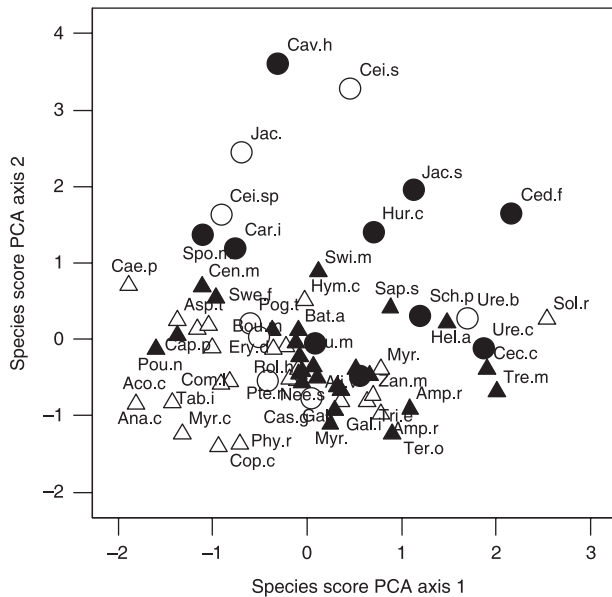
Fig. 2. Species scores along the first two principal components. Species names are given as abbreviations (see Table 2). Different symbols indicate forest type and deciduousness. Open symbols represent dry forest species, closed symbol represent moist forest species. Dots represent deciduous species and triangles represent evergreen species.

exposure (CE) ranks species based on their light requirements (or decreasing shade-tolerance). CE was positively related to the first and second PCA axes, whereas DI was negatively related to the first PCA axis only (Table 4, Fig. 1 and Fig. 4).

The DI was positively related to RMF, compoundness and SD, and negatively with LMF, LAR, LA, LS, SRL, SPRMR, RWC, RA and RV (Table 4, Fig. 3). With a forward multiple regression analysis we tested which combination of seedling traits could best predict the DI. The resulting model included two seedling traits, together explaining 57% of the variation: RMF (standardized regression coefficient $\beta = 0.39$, $P = 0.001$, 49% of variation explained), and SPRMR ($\beta = -0.30$, $P = 0.008$, 8% added).

CE was positively related to first year seedling biomass, SLA, LAR, LA, LS, SPRMR, and RWC, and negatively to SD. Following the same forward multiple regression procedure three seedling traits were included in a model that explained 64% of the variation in CE: seedling biomass at the onset of the dry season ($\beta = 0.32$, $P = 0.003$, 47% of variation explained), SLA ($\beta = 0.30$, $P = 0.006$, 10% added) and SPRMR ($\beta = 0.29$, $P = 0.005$, 7% added).

TRADE-OFFS BETWEEN DROUGHT- AND SHADE-TOLERANCE

The DI was not directly associated with CE ($r = 0.064$, $n = 62$, $P = 0.62$, Table 4). The DI and CE might be uncoupled, because they largely depend on a different suit of traits (Table 4). The DI and CE were both significantly associated with only six (LA, LS, LAR, SD, RWC and SPRMR) out of twenty-one

seedling traits. None of these correlations supported the proposed trade-off between the DI and the inverse of CE. The DI was in addition significantly related to six traits (LMF, RA, RV, SRL, RMF and compoundness) of which none showed a relationship with CE. CE was significantly related to two additional traits (seedling biomass and SLA), that did not vary significantly with the DI. Of the traits that best explained the DI (RMF, SPRMR) and CE (seedling biomass, SLA, SPRMR), only SPRMR was related to both the DI (negatively) and CE (positively), in each case explaining a minor portion of additional variation (8% and 7% respectively). SPRMR did not support a trade-off between drought- and shade-tolerance, but rather supported a positive relation between both gradients.

Discussion

DO DRY AND MOIST FOREST SPECIES DIFFER IN THEIR SEEDLING TRAITS?

Root morphology and biomass allocation of seedlings differed between dry and moist forests, but the explained variation was generally low (average 4%, range 1–12%, Table 3). This low explained variation is partly intrinsic to field studies, where environmental heterogeneity leads to additional noise (Møller & Jennions 2002). However, given the fact that our field data and experimental data were strongly correlated (see Methods), this may also indicate that other factors than first year seedling morphology (e.g. seedling physiology, Engelbrecht et al. 2007) determine the assembly of dry and moist tropical forest communities. Within each forest, there was a surprisingly large inter-specific variation in seedling traits (average explained variation is 45%, range 13–73%, Table 3). This large variation may be important, because it possibly allows coexisting species to sort out along smaller scale environmental gradients within each forest. Seedling size at the onset of the dry season had a strong effect on 16 out of 18 seedling traits and explained on average 23% of the variation (range 1–66%, Table 3). This strong ontogenetic drift indicates that many traits change when plants increase in size, and indicates that ontogenetic corrections, as done in this study, are important to avoid erroneous conclusions (cf. Evans 1972; Poorter & Pothmann 1992).

Overall, seedling morphology of dry and moist forest species differed in line with the hypothesis of Brouwer (1963) which predicts that, under a given regime of stresses, plants maximize their surface area for intake of the most limiting resource. In tropical dry deciduous forests water is the most limiting resource for plant growth and survival. Consequently, seedlings of dry forest species enhance water uptake through an increased RMF, a higher root length per unit leaf area and a greater RD, which allows them to forage more efficiently in deeper soil layers, where more water is available, especially in the dry season (Engelbrecht et al. 2005). Rooting volumes did not differ significantly between dry and wet forest seedlings. Foraging deeper underground, rather than increasing the volume of exploited soil, appears to be the preferred strategy

Table 4. Correlation among species traits. Traits were calculated at a standardized seedling size of 4.7 g, the drought index (DI), juvenile crown exposure (CE) and the first two PCA axes of 62 tropical tree species. Pearson correlation coefficients are shown (two-tailed; *n* = 62) at (*Italic*) *P* < 0.05; (**Bold**) *P* < 0.01; (***Bold Italic***) *P* < 0.001. See Table 1 for trait abbreviations

|	BIOM	LA	LS	SLA	LMF	LAR	SD	SMF	RD	RA	RV	RL	SRL	RWC	RMF	RLLA	RLPM	SPRMR	LASA	DEC	COMP	DI	CE
LA	0.04																						
LS	0.03	***0.71***																					
SLA	*0.28*	**0.39**	**0.38**																				
LMF	*−0.25*	***0.71***	**0.44**	−0.19																			
LAR	−0.05	***0.96***	***0.75***	***0.45***	***0.71***																		
SD	**−0.35**	**−0.40**	**−0.37**	***−0.59***	−0.04	***−0.41***																	
SMF	0.15	−0.23	0.02	0.20	***−0.44***	−0.21	−0.09																
RD	−0.04	*−0.27*	*−0.26*	−0.04	−0.22	*−0.26*	**0.31**	0.13															
RA	0.13	0.17	0.18	**0.33**	0.07	0.22	*−0.40*	0.02	−0.17														
RV	0.15	0.13	0.15	**0.33**	0.04	0.16	**−0.36**	−0.02	−0.06	***0.98***													
RL	−0.04	*0.24*	−0.10	0.01	**0.32**	0.19	−0.05	*−0.28*	−0.24	0.29	0.25												
SRL	−0.11	***0.46***	0.12	−0.06	***0.61***	***0.41***	−0.11	−0.20	−0.27	0.27	0.22	***0.90***											
RWC	**0.39**	**0.34**	**0.40**	**0.49**	0.03	**0.31**	***−0.86***	0.17	−0.21	*0.28*	*0.27*	−0.04	0.05										
RMF	0.17	***−0.60***	***−0.46***	0.18	***−0.77***	***−0.57***	0.09	−0.14	0.15	0.02	0.07	−0.13	***−0.53***	−0.14									
RLLA	−0.11	***−0.45***	***−0.58***	−0.22	−0.16	***−0.44***	0.21	−0.13	−0.05	0.17	0.16	***0.74***	***0.51***	−0.29	*0.27*								
RLPM	−0.14	*0.24*	−0.07	0.09	**0.35**	*0.26*	−0.07	*−0.29*	−0.25	**0.34**	*0.29*	***0.95***	***0.86***	−0.08	−0.13	***0.75***							
SPRMR	0.17	***0.50***	0.22	0.20	***0.49***	***0.48***	*−0.30*	−0.17	**−0.37**	**0.37**	*0.32*	***0.55***	***0.64***	**0.27**	**−0.38**	0.18	***0.56***						
LASA	**−0.36**	***0.54***	**0.42**	−0.15	***0.66***	***0.57***	**0.40**	***−0.49***	−0.01	−0.12	−0.12	0.09	*0.24*	**−0.41**	**−0.39**	−0.27	0.13	0.14					
DEC	*0.25*	0.18	0.15	**0.43**	−0.20	0.14	**−0.47**	0.11	−0.22	0.15	0.15	0.01	−0.04	**0.55**	0.09	−0.12	−0.02	0.16	**−0.36**				
COMP	0.19	−0.10	−0.03	0.08	*−0.28*	−0.15	0.14	−0.05	0.02	−0.21	−0.16	*−0.26*	**−0.34**	−0.08	*0.26*	−0.17	*−0.30*	−0.13	−0.01	−0.02			
DI	−0.06	***−0.41***	*−0.30*	−0.18	***−0.44***	***−0.42***	**0.39**	−0.16	0.02	*−0.29*	*−0.28*	−0.16	**−0.37**	**−0.36**	***0.50***	0.11	−0.18	***−0.44***	−0.06	0.00	**0.39**		
CE	***0.47***	**0.40**	*0.29*	**0.45**	0.06	**0.34**	**−0.37**	−0.06	−0.23	0.16	0.14	0.16	0.14	**0.37**	−0.01	−0.15	0.10	**0.41**	−0.06	0.23	0.20	0.06	
PCA axis 1	−0.02	***0.87***	***0.64***	**0.33**	***0.76***	***0.86***	***−0.47***	**−0.27**	**−0.40**	***0.45***	**0.39**	***0.55***	***0.75***	**0.38**	***−0.61***	−0.07	***0.58***	***0.74***	***0.44***	0.15	*−0.31*	***−0.42***	**0.35**
PCA axis 2	***0.50***	0.20	**0.42**	***0.63***	**−0.33**	0.19	***−0.69***	**0.41**	−0.07	0.18	0.18	***−0.54***	**−0.50**	***0.74***	0.10	***−0.64***	**−0.54**	−0.07	***−0.44***	***0.59***	0.18	−0.13	**0.36**
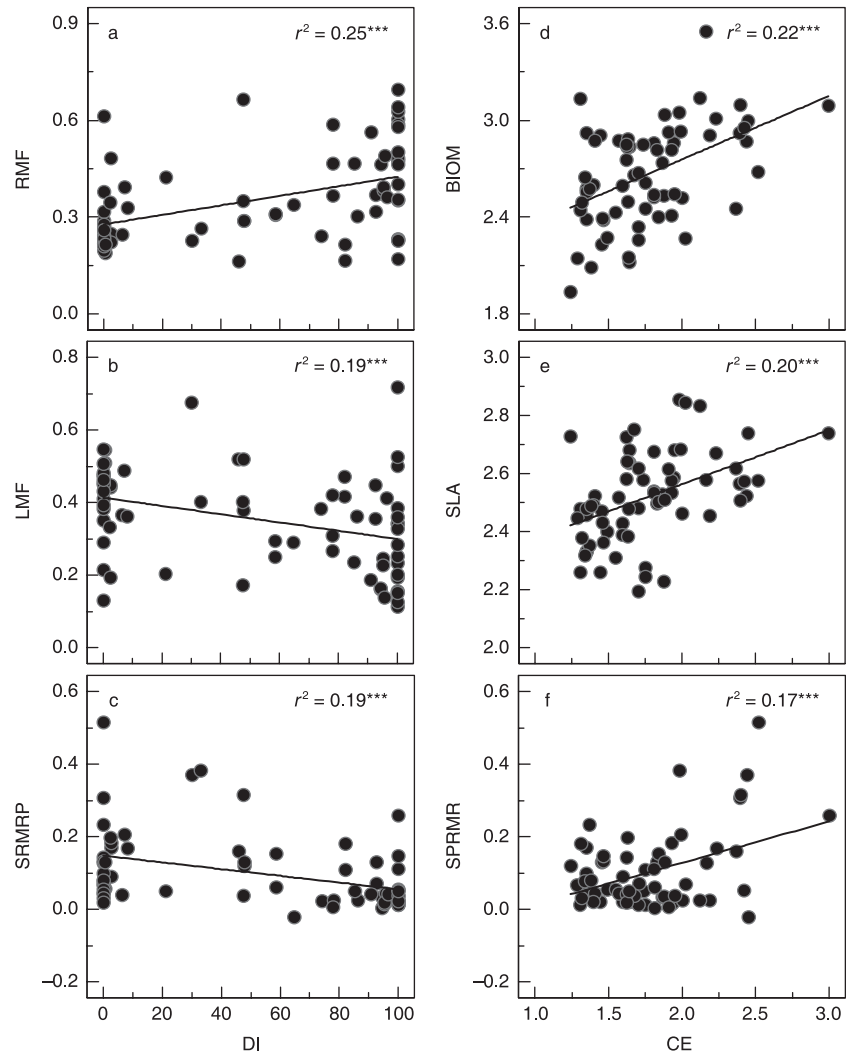
Fig. 3. Associations between species' drought index (DI; $n = 56$), juvenile crown exposure (CE; $n = 59$) and functional seedling traits. Trait values were calculated at a standardized seedling size of 4.7 grams. Not all 62 species were included in the analyses as we were unable to calculate the DI for six and CE for three species. a) root mass fraction (RMF; g g^{-1}), b) leaf mass fraction (LMF; g g^{-1}), and c) secondary to primary root mass ratio (SPRMR; g g^{-1}) with the DI, and d) seedling biomass (BIOM; g), e) specific leaf area (SLA; cm^2 g^{-1}), and f) secondary to primary root mass ratio (SPRMR; g g^{-1}) with CE. Regression lines, coefficients of determination, and significance levels are shown. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

when it comes to water acquisition in dry ecosystems. Rooting depths were indeed found to be greater in vegetations from dry ecosystems (Canadell *et al.* 1996; but see Schenk & Jackson 2002), in seedlings from forests with a long dry period (Paz 2003) and in species from dry sandy soils (Yamada *et al.* 2005). Dry forest seedlings had a smaller SRL, SPRMR, root length and rooting area than moist forest seedlings, in contrast to our hypothesis. In terms of water availability, dry forest species grow in a poorer resource environment than moist forest species. This may call for a conservative, rather than an acquisitive resource strategy. Dry forest species reduce water loss through a reduction of the amount of transpirational tissue (low LS, LA, SLA and LAR) and their seedlings have higher stem densities, which makes them less vulnerable to xylem cavitation. High stem densities mainly result from smaller vessels that have a higher resistance to embolism (Castro-Díez 1998; Hacke *et al.* 2001; Tyree & Zimmermann 2002). Cavitation reduces hydraulic conductance as vessels become (partly) dysfunctional once an embolism has formed (Tyree & Sperry 1989; Tyree & Zimmermann 2002). Such reduced hydraulic conductance limits

photosynthesis (Santiago *et al.* 2004) and can ultimately result in the loss of entire stem sections.

We hypothesized that moist forest seedlings should show characteristics related to acquisition of light rather than water as denser vegetation casts deeper shades and reduces light availability, thus making light the most limiting resource. Moist forest species indeed increased their light interception by investing a large portion of their biomass in leaf tissue (high LMF) by making larger leaves, having a larger total seedling leaf area, and having higher SLA and LAR. The bigger seedling size of moist forest species at the onset of the dry season may both be the result of a longer growing season and of a higher relative growth rate, and can be advantageous to dry season survival as bigger seedlings are less susceptible to drought (Kobe *et al.* 1995; Poorter & Hayashida-Oliver 2000; Gilbert 2001). Moist forest species increased below-ground resource capture by producing long, branched root systems (high SPRMR), which at first sight seems in contradiction with our hypothesis. However, moist forest species may be more nutrient and water demanding, because of their greater photosynthetic capacity and higher inherent growth rates.
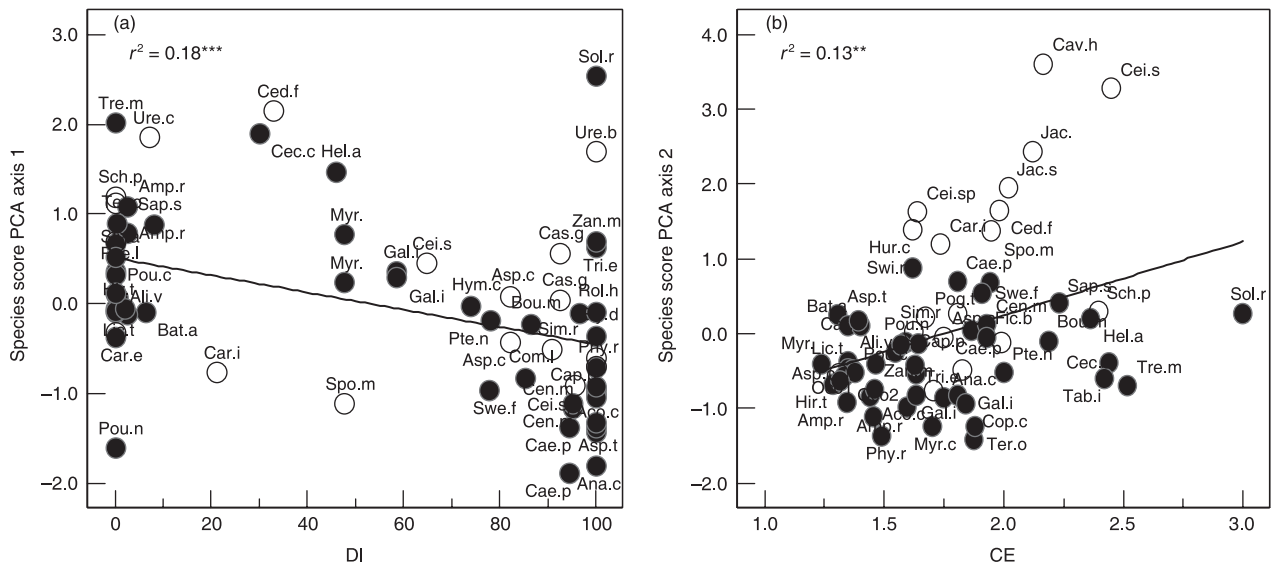
Fig. 4. Association between species' drought index (DI), juvenile crown exposure (CE) and the species scores along the first two principal components. a) DI with the species' scores along the first principal component axis and b) CE with the species scores along the second principal component axis. Regression lines with coefficients of determination and significance levels are shown.

Unexpectedly, we found high water contents in the root systems of moist forest species, which is usually associated with species in dry ecosystems (e.g. Borchert 1994). As carbon assimilation in moist forests is limited by low light availability, species seem to store water to bulk up their root system rather than spending precious carbon for constructing root tissue.

TRAIT ASSOCIATIONS AND FUNCTIONAL GROUPS

Species separated along two major trait axes that reflected species variation in persistence and deciduousness, respectively. The persistence axis separated drought- and shade-tolerant species from water- and light-demanding species (Fig. 1 and Fig. 2). Persistent species show a conservative resource use strategy with high biomass investment in enduring plant organs (roots and stem) and little in leaf tissue. These species are generally slow-growing and forage for water in deeper soil layers. Their high stem densities suggest a lower risk of cavitation (Tyree & Sperry 1989; Tyree & Zimmermann 2002), a higher structural stability and smaller chance of damage by falling debris or herbivory. The water- and light-demanding species at the other end of the gradient allocate more biomass to their leaves, resulting in a larger total leaf area, which allows for increased light foraging, and thus more photosynthesis. In addition, they have long and branched root systems (cf. Huante *et al.* 1992) which increase the probability to encounter and exploit high nutrient pockets (Fitter 1985; Craine 2002; Raynaud & Leadley 2004) and fuel onward growth. These drought-intolerant species therefore follow an acquisitive resource strategy, maximizing resource uptake to increase their competitiveness in relatively wet microhabitats.

The deciduousness axis was mainly related to high root water content, high SLA, a large stem mass fraction and a

large seedling size at the onset of the dry season. Deciduous species have high growth rates during the wet season and so may compensate for their short growing season, mainly through a more efficient light capture per unit leaf mass (Antuñez *et al.* 2001; Eamus & Prior 2001; Ruiz-Robleto & Villar 2005). Deciduous species have a high root water content, and such water storage in roots has been found to increase the drought survival of seedlings (Poorter & Markesteijn 2008). Deciduousness was related to a low stem density and LASA, which indicates that deciduous species have highly conductive sapwood with wide xylem vessels (Santiago *et al.* 2004). Low density wood is not very strong or stiff, which, in combination with a large seedling size, may increase the probability of buckling (cf. Van Gelder *et al.* 2006). Deciduous species may augment their stability by increasing their basal area which leads to a low LASA. A low LASA has also been reported for drought-tolerant evergreen shrub species (Preston & Ackerly 1990).

The two PCA axes combined thus show that tropical tree species follow three major strategies in relation to drought; species either avoid drought by shedding their leaves, persist during drought by having enduring plant tissues or are intolerant to drought, but realize fast growth rates in more productive environments. These strategies were also found in an experimental study (Poorter & Markesteijn 2008) and are in line with the conceptual model of Ackerly (2004), who suggests similar functional strategies among Californian Chaparral shrub species, based upon variation in leaf life span (deciduousness) and ability to tolerate water deficit (persistence). Although more multispecies studies are needed to further test this model, the similarities between the two studies suggest that there may be general pathways of plant adaptations to drought, which hold true for different woody life forms and different biomes (cf. Eamus & Prior 2001).

IS THERE A TRADE-OFF BETWEEN DROUGHT- AND SHADE-TOLERANCE? THE UNDERLYING MECHANISMS REVISITED

Smith and Huston (1989) predicted a trade-off between drought- and shade-tolerance based on a trade-off in biomass allocation to roots versus shoot. We indeed found a strong trade-off between RMF and LMF ($r = 0.77$, $P < 0.001$). Still no trade-off between drought- and shade-tolerance was found, neither when all species were taken into account ($r = 0.06$, $P > 0.05$) (Table 4, Fig. 1), nor when analyzing evergreen species ($r = 0.26$, $P > 0.05$) and deciduous species ($r = -0.39$, $P > 0.05$) separately.

Evidence for the proposed biomass allocation trade-off is equivocal and the underlying mechanisms are not well understood. Root and leaf mass fraction affect below- and above-ground foraging capacity only to a minor extent (cf. Poorter & Nagel 2000). Moreover, a small biomass investment in roots (low RMF) can be compensated for by making cheap roots with a large root length per unit biomass invested (i.e. a high SRL). Likewise, a low biomass investment in leaves (low LMF) can be compensated for by realizing a large leaf area per unit leaf biomass invested (i.e. high SLA) (Poorter 2005), through the formation of thin or low density leaves (Witkowski & Lamont 1991). Our results partly support the latter idea. RMF and SRL are indeed negatively correlated ($r = -0.53$, $P < 0.001$), which leads to an uncoupling of RMF and root length per unit plant mass ($r = -0.13$, $P > 0.05$). However, LMF is only marginally negatively correlated with SLA ($r = -0.19$, $P > 0.05$), and therefore there is still a positive association between LMF and LAR at the whole-plant level ($r = 0.71$, $P < 0.001$) (Table 4, Fig. 1). Because of the compensation by SRL, and to a lesser extent SLA, this means that at the whole plant level there is no trade-off between the surface area for below-ground (RLPM) and above-ground (LAR) resource capture per unit plant mass ($r = 0.26$, $P < 0.05$), and hence no trade-off between drought- and shade-tolerance (Table 4, Fig. 1).

The multiple regression analyses further showed that drought- and shade-tolerance were mainly determined by different suites of traits (see also Fig. 4). Our results thus support the idea that drought- and shade-tolerance are uncoupled and vary independently. This implies a high potential for species niche differentiation, because adaptations that favour drought-tolerance do not necessarily restrain species performance in the shade, nor do adaptations that favour shade-tolerance automatically imply that species are drought-intolerant (Coomes & Grubb 2000; Sack & Grubb 2002; Sanchez-Gomez *et al.* 2006).

We also reported on the correlations of morphological seedling traits with a DI in an experimental study (Poorter & Markesteijn 2008) and overall we found the same trends in the current study. RMF and compoundness were positively related and LAR, LMF and SMF were negatively related to the DI. Still a multiple regression analysis on that experimental data showed that the DI was mainly explained by different traits than in the current field study. Both studies have a large

number of species in common ($n = 31$), but nine of the experimental species were not studied in the field and 31 species from this field study were not assessed in the experiment. Additionally, not all traits measured in the experiment were measured in the field, and several new traits that were not measured in the experiment were added in the field study. These methodological differences probably explain some discrepancies in results between both studies.

Conclusions

This study shows that dry and moist forest species vary substantially in their first year seedling morphology, in line with the functional equilibrium hypothesis of Brouwer. Dry forest species enhance their access to water in deeper soil layers and increase water conservation. Moist forest species enhance their light foraging capacity and increase nutrient and water acquisition. Based upon the trait associations, three major drought strategies can be distinguished; species are either drought-avoiding, drought-tolerant or drought-intolerant. Drought-avoiders delay drought stress through a deciduous leaf habit, whereas drought-tolerant species probably include both the physiological drought-tolerators and the evergreen drought-delayers (see introduction). Drought- and shade-tolerance are associated with different suites of traits. As a consequence both strategies are largely independent from each other, suggesting great potential for niche differentiation across a vast array of water and light availability combinations, which may potentially contribute to the high diversity of tropical forests.

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