FUNCTIONAL LEAF TRAITS

MORPHOLOGICAL ADAPTATIONS TO DIFFERENT LIGHT ENVIRONMENTS AND FUNCTIONAL GROUPS IN A BOLIVIAN DRY FOREST

BY

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Toborochi
Chorisia speciosa St. Hil. (Malvaceae)

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Summary

Niche-differentiation, with different species or groups of species specializing for different growth conditions, is possibly explanative to at least part of the high biological diversity found in many tropical forests. Still, while quite a bit is known from studies on temperate and tropical wet forests, only little information on plant adaptive responses to different growth environments in tropical dry forests is available.

This study evaluates morphological leaf trait adjustments of 41 dry forest tree species to different light environments and assesses leaf trait adaptations to drought- and shade-tolerance. Finally the possibility of trade-offs among functional groups based on trade-offs among these leaf characteristics is addressed. Traits included in this study are; adult stature (H_{max}), deciduousness (leaf habit), compoundness (leaf type), leaf length, width, shape index (LSI) and area; leaf mass per unit leaf area (LMA), leaf dry matter content (LDMC), leaf thickness, leaf toughness, petiole length, internode length, blade length fraction (BLF) and specific internode length (SIL).

The results showed that leaf characteristics varied greatly among species, light environments and individual trees. Sun-leaves were smaller than shade-leaves to promote cooling of the convective area; still they were not more slender, as wind-induced transpiration needs to be minimized. Sun-leaves are thicker to reduce heat-induced transpirational water loss, with higher LMA and LDMC. Consequently sun-leaves are tougher than shade-leaves, better protected against wind-induced damage and have greater herbivore resistance. Petioles are longer in the shade, as an adjustment to forage for light in the forest understory, where internodes are shorter, as they are more expensive to make because carbon assimilation is limited.

Shade-tolerance groups differed most in H_{max}, leaf habit and leaf type. Shade-tolerant species are small compared to light-demanding and intermediate shade-tolerant species. Light-demanding species are more often deciduous and harbor more compound leaved species. They have longer petioles, both absolute and in relation to the leaf blade. Still most of the morphological traits that I expected to differ between shade-tolerance groups did not contribute to their discrimination. As light availability is probably not a limiting factor in the relatively open dry forest habitat, the urge of species to adapt to a given strategy to tolerate shade is over ruled by adaptations that influence their ability to tolerate drought.

Drought tolerance groups differed most in leaf slenderness, LMA and length of the petiole.
Drought-tolerant species had the most slender leaves and are thus better equipped to reduce the heat load of the leaves by cooling of the convective area. Drought-intolerant species have a high LMA, which may reflect an adaptation to increase herbivore resistance, as these species grow in habitats within the dry forest with relatively high soil water availability, high densities of other trees and probably high densities of herbivorous insects. The deciduous leaf habit of drought-avoiding species emphasizes their need of efficient usage of the limited time they have to photosynthesize. Drought-avoiding species as such invested minimal biomass to their leaves, decreasing their payback time. Petiole tissue is relatively cheap compared to branch tissue. By forming relatively long petioles drought-avoiding species need to invest less in branch formation to increase light interception and thus optimize their carbon balance.

Possible trade-offs exists between drought-avoidance and the ability to persist in the shade, drought-intolerance and light-demand, and between drought-tolerance and light-demand.

Introduction

Semi-deciduous and deciduous dry forests in the tropics are typically found in transition zones between evergreen wet forests and drier savanna-like ecosystems. These forests often occur on soils relatively fertile in comparison to other tropical habitats. Consequently, the scale and rate of human settlement, and the with-coming deforestation and cultivation of these lands, exceeds that of humid forests (Hecht and Cockburn, 1989; Williams, 1989; Skole and Tucker, 1993; Hecht, 2001; Steininger *et al.*, 2001b). Large areas of intact (semi-) deciduous forest are becoming scarce (Maas, 1995) and although these forests are greatly effected by human development in countries as Brazil, Paraguay and Argentina, large areas are still found in the lowlands of eastern Bolivia, a region known as the Chiquitanía (Steininger *et al.*, 2001). The Chiquitano dry forest is a recognized refuge of a more widespread forest type found during the dry periods of the Pleistocene era (Killeen, 1997) and harbors some of the highest levels of biodiversity found among Neotropical dry forest formations (Gentry 1995; Killeen *et al.*, 1998). While deforestation of the Chiquitano dry forest used to be less severe than in the other areas mentioned, now-a-days low land prizes, infrastructural development and promotion of a commercial export economy have lead to a intensification of the private agricultural sector (Pacheco, 1998), that is threatening its existence. Deforestation and the overall lack of knowledge on the structure, function and diversity of dry forests have lead to increasing attention of biologists to the matter world-wide (Bullock *et al.* 1995).

The high biological diversity generally found in tropical forests has been suggested to result amongst others from different species specializing for different growth conditions, so-called niche-differentiation (Grubb, 1977). All plants need the same primary resources for their growth and survival, light, water and nutrients and consequently, species try to optimize morphological and physiological traits that increase their competitive success and thus their chance of survival in habitats where the availability of one or more of these primary resources is limiting. The optimization of one set of traits, though, leading to relative success in an associated growth environment by optimizing the uptake, use and / or conservation of a limiting resource, can negatively influence the species success in another environment by putting constraints on the optimization of other traits, influencing the species ability to compete for other limiting resources (Bongers and Popma, 1988).

Tropical forests prove to be very suitable to investigate plant responses to different resource levels, as one can study adaptations across a wide range of phylogenetic origins (Bongers and Popma, 1988) and across species of similar life form (Poorter, 1998).

Leaves can vary in a whole suite of morphological, anatomical, chemical and physiological characteristics. As such, leaf properties can vary within individual trees at any given time, with age of a leaf, age of a tree, and among trees of the same species due to genetic or environmental factors (Turner, 2001). Leaf characteristics are further known to vary along environmental gradients, such as latitude, altitude, soil fertility, salinity, rainfall and light availability (see e.g. Chapin 1980; Givnish, 1984; Turner, 2001; Wright *et al.*, 2001; Wright *et al.*, 2002; Wright and Westoby, 2003).

In this study I aim to analyze differences in leaf traits within and between tree species in relation to light availability in a Bolivian Chiquitano dry forest. I examine associations among leaf traits and identify traits of functional groups related to drought- and shade-tolerance. As functional groups of species may be expected not only to differ in leaf morphology in one environment but also in their leaf trait response (plasticity) when shifting between light levels I will further assess the differences in plasticity of the traits among functional groups. In order to do this I have asked myself the following main questions:

1. What are the biggest sources of variation in leaf characteristics?
   Differences among species, light levels, individual trees or differences among leaves within trees?
2. Do sun-leaves differ from shade-leaves?
3. Are leaf traits associated?
4. Do functional groups related to shade-tolerance differ in their leaf traits and in their plastic responses?
5. Do functional groups related to drought-tolerance differ in their leaf traits and in their plastic responses?

DIFFERENCES BETWEEN SUN- AND SHADE-LEAVES

I hypothesize that trees growing in high light conditions will form relatively small, thick leaves with a high leaf mass per unit area (LMA). Overheating is a severe problem in case of water scarcity (Smith, 1978), with temperatures in big leaves easily exceeding the photosynthetic optimum. Smaller leaves have a smaller boundary layer and are thus able to reduce excessive transpirational water loss through better convective cooling of the leaves (Parkhurst and Loucks, 1972; Givnish, 1984; Bongers and Popma 1988). This leaf area reduction can either result from a decrease in leaf width, leading to higher shape indices (length : width ratios) in sun-leaves, compared to shade-leaves (Bongers and Popma, 1988) or from a decrease of both leaf length and leaf width, leading to smaller areas. Evapotranspiration of sun-leaves is reduced by the formation of thick leaves with thick cuticles and a low surface to volume ratio. At the same time the photosynthetic capacity is enhanced by adding extra photosynthetically active parenchyma layers (Poorter *et al.*, 1995; Poorter, 1999). LMA is often related to leaf thickness and tissue density or leaf dry matter content (LDMC) (Wright and Cannon, 2001). I expect sun-leaves, next to being thicker, to be tougher, with relatively more biomass invested per unit fresh leaf weight (LDMC) and per unit leaf area (LMA), in comparison to shade-leaves.

Leaves from trees growing under shady conditions will need to increase light capture in an environment where carbon fixation is limited due to low light availability. Formation of bigger and thinner leaves can be one way to be more efficient in foraging for light in the forest understory, while limitations in carbon fixation might as well lead to the formation of smaller and thinner leaves. Foraging for light can also be improved by the formation of longer branches (e.g. Kempf and Pickett, 1981; Cornelissen, 1993) and thus wider crowns, to reduce self shading (Poorter,

1999; Bongers and Sterck, 1998). I hypothesize that petioles and internodial sections of shade-leaves are longer then those of sun-leaves as a result of light foraging. The proportional length of the leaf-blade over the length of the petiole will be smaller in shade leaves, as indicated by their smaller blade length fraction (BLF).

Finally, I hypothesize that internodes of shade-leaves are relatively thinner than those of sun-leaves, because they need to be less equipped to support the relatively lighter leaves in that environment.

FUNCTIONAL GROUPS

Shade-tolerance of a species is determined by its ability to persist in the shade and differences among species that differ in shade tolerance are often clear (Popma *et al.*, 1992). Pioneer or light-demanding species that establish in a high resource environment of gaps realize fast growth rates to compete with their neighbors and maintain a position in the top of the regrowing vegetation. They will establish high respiration rates and optimize their carbon balance to allocate more biomass to growth. To do so light-demanding species form short-lived leaves, which will have a low LDMC and LMA. Leaves will be large and relatively thin, optimizing for low construction costs (Popma *et al.*, 1992; Reich *et al.*, 2003; Lusk and Del Pozo, 2002). Shade-tolerant species establish in the low resource environment of the forest understory. As the investment in leaves is costly, because of the low carbon and nutrient uptake in this environment, shade-tolerant species will make long-lived leaves to pay back their construction cost. Their leaves will be tough and relatively thick, with a high LDMC and a high LMA, to prevent damage and herbivory.

Drought-tolerance of a species is determined by a suit of physiological and morphological characteristics to withstand periods of drought (Bullock *et al.*, 1995). Drought-avoiding species have a deciduous leaf habit, allowing them to avoid excessive water loss during the dry period. Expected leaf level adaptations of drought-tolerant species are small, thick leaves, with a high LDMC and high LMA. Leaves will be well protected against physical damage and herbivory because they are evergreen and live for a considerably longer time than the short-lived leaves of deciduous drought-avoiding species. With shorter petioles, and shorter and thicker internodes drought-tolerant species can reduce mechanical damage through better support of the leaves. At the other hand, deciduous trees will optimize their carbon investment given their limited leaf life span, leading to opposite expectations. Drought-intolerant species are not capable of reducing dry season water loss and are therefore limited to the lower, lesser-drained soils within the dry forest habitat. Drought-intolerant species will show a greater alikeness to rain forest leaves. Leaves of drought-intolerant species will be bigger and less slender than those of drought-tolerant and deciduous species. For a summary of the hypotheses I refer the reader to table 1.

The canopy of the Chiquitano dry forest is characterized by the dominant occurrence of deciduous drought avoiding tree species.

Trait	Differences between light environments	Shade-tolerance			Drought-tolerance		
		Light-demanding species	Intermediate shade-tolerant species	Shade-tolerant species	Drought-avoiding species	Drought-intolerant species	Drought-tolerant species
Leaf length	Sun < Shade	+	--	-	-	+	--
Leaf width	Sun < Shade	+	--	-	-	+	--
Leaf area	Sun < Shade	+	--	-	-	+	--
Thickness	Sun > Shade	--	-	+	--	-	+
Toughness	Sun > Shade	--	-	+	--	-	+
Leaf shape index	Sun >= Shade	+	-	--	-	--	+
Leaf dry matter content	Sun > Shade	--	-	+	--	-	+
Leaf mass per area	Sun > Shade	--	-	+	--	-	+
Petiole length	Sun < Shade	+	-	--	-	+	--
Internode length	Sun < Shade	+	-	--	-	+	--
Blade length fraction	Sun > Shade	+	-	--	-	+	--
Internode shape index	Sun > Shade	--	-	+	--	-	+

Table 1. **Summary of hypotheses.** Within tolerance classes symbols represent; **+** = biggest trait value; **-** = smaller trait value; **- -** = smallest trait value.

Material and Methods

STUDY AREA

During 4 months of fieldwork I gathered data concerning leaf characteristics in a semi-deciduous Chiquitano dry forest approximately 40 kilometers east of the town of Concepción in the province Ñuflo de Chávez, department of Santa Cruz, eastern Bolivia (16°07'S, 61°43'W; 458 m) (fig. 1).

The Chiquitanía region is situated in the lowlands of Bolivia, in the transition zone between the most southern limit of Amazonian moist forest in the north and the xerofitic matorral of the Gran Chaco, with its thorn shrub vegetation, in the south (Killeen *et al*, 1998; Jardim *et al.* 2003). The Chiquitano dry forest is characterized by deciduous and semi-deciduous vegetation types, of which the deciduous dry forest covers approximately 40% of the department Santa Cruz. Other important ecosystems in the region are cerrado savannas and pantanal wetlands at the border with Brazil.

Geomorphologically, the region is part of the Brazilian Shield. Low hills, composed of granite, gneiss and metamorphic rocks from Precambrian origin, dominate the landscape (Geobol, 1981). Soils are moderately acid (pH = 5,8 to 6,8 in the A horizon) and can be classified as inceptisols and alfisols (Killeen, 1990; Killeen *et al.*, 1998) and oxisols (Iporre, 1996). The study area is lacking main waterways, but on lower grounds there is evidence of seasonal creeks and streams (Schoonenberg *et al.*, 1999).

The region is characterized by a strong seasonality and the austral winter dry season occurs between April and September. Mean annual precipitation varies between 900 and 1200 mm, peaking around 175 mm per month in the January and getting as low as 25 mm in August. This great yearly amplitude in rainfall results in a mean annual evapotranspiration that has been reported to be approximately 1300 mm, leading to a deficit of 100 to 400 mm on a yearly basis (Montes de Oca, 1989, but see Killeen *et al*, 1998). The mean annual temperature at Concepción is 24.3 ºC, ranging from 3 ºC in July and 31 ºC in October.

The data gathering was carried out in a forest concession of approximately 30.000 ha, under

The field station at INPA, the dry forest research site managed by IBIF

exploitation of INPA Parket Ltda., in close cooperation with the Bolivian Forestry Research Institute (IBIF). This organization maintains several permanent sample plots in the area, laid out in a nested design and studies amongst others the impact of silvicultural practices on forest growth and development in order to come to a sustainable forest management plan for the region.

Although the vegetation of the Chiquitanía region may be variable it is mainly dominated by *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Anadenanthera macrocarpa* (Benth.) Brenan (Fabaceae), *Aspidosperma cylondrocarpon* Műll. Arg. (Apocynaceae), *Aspidosperma tomentosum* Mart. (Apocynaceae) and *Astronium urundeuva* (Allemão) Engl. (Anacardiaceae). Other abundant species are *Calycophyllum multiflorum* Griseb. (Rubiaceae), *Machaerium scleroxylum* Tul. (Fabaceae) and *Schinopsis brasiliensis* Engl. (Anacardiaceae) (Killeen *et al*, 1998; Jardim *et al.* 2003).

Commercially valuable timber species in the region are; *Cedrela fissilis* Vell. (Meliaceae), *Amburana cearensis* (Allemão) A.C. Smith (Fabaceae), *Machaerium scleroxylum* Tul. (Fabaceae), *Tabebuia impetiginosa* (Mart. Ex DC.) Standl. (Bignoniaceae), *Astronium urundeuva* (Allemão) Engl. (Anacardiaceae), *Centrolobium microchaete* (Mart. ex Benth.) Lima ex G. P. Lewis (Fabaceae), *Anadenanthera colubrine* (Vell.) Brenan (Fabaceae), *Aspidosperma cylondrocarpon* Műll. Arg. (Apocynaceae), *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae), *Guibourtia chodatiana* (Hassl.) J. Léonard (Fabaceae), *Schinopsis brasiliensis* Engl. (Anacardiaceae) and *Cariniana ianeirensis* R. Knuth (Lecythidiaceae).

In the dry climate of the Chiquitania plants with extreme adaptations to tolerate drought are prominently occurring in the vegetation as these Bromeliaceae and Cactaceae species. Some cacti even reach the forest canopy (right)

Bolivia: **Santa Cruz:**
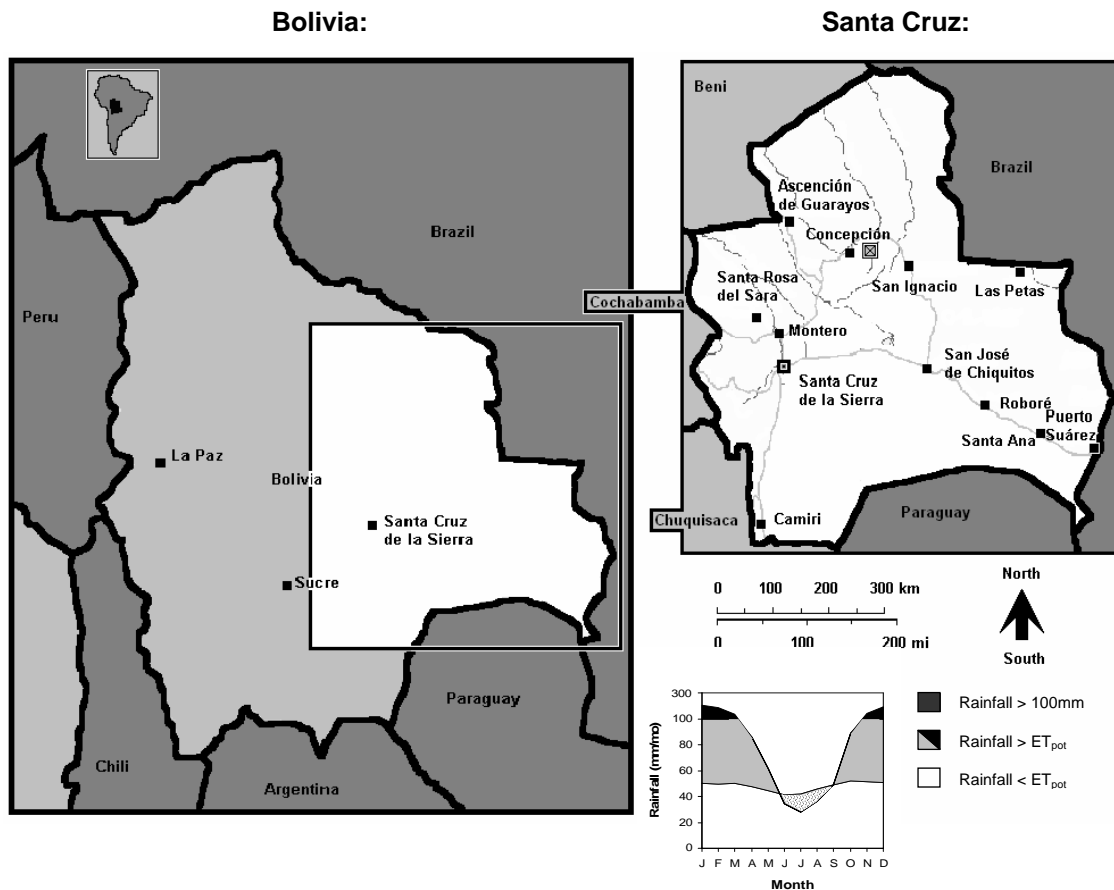
Figure 1.   **The study area.** The map shows the approximate location of the study area (⊠) near the town of Concepción, in the eastern lowlands of Bolivia and a climatic diagram, that indicates mean monthly precipitation and potential evapotranspiration (Et_{pot}) at the study site. The dry season is shown in the dotted area

SPECIES

I studied leaf characteristics of dry forest tree species varying greatly in phylogenetic origin, as the 41 species belong to 40 genera, 24 families and 19 orders. With six included species, Fabaceae is the biggest family in this study. This is in line with their dominance in the Chiquitano dry forest.

Species vary further in adult stature, leaf form and habit, shade-tolerance and drought-tolerance. I distinguish tree groups of shade-tolerance. Light-demanding species are long-lived pioneers that need full sunlight to establish and grow to their adult stature, intermediate shade-tolerant species are those that can establish under shady conditions, but need more light to grow and shade-tolerant species are species that can both establish and grow to adulthood in the shade. Drought-tolerance classifications were based on the species wilting index estimated for saplings during the dry season by dr. Poorter and the dominant occurrence of the species on either relatively dry elevated grounds (drought-tolerant species) or the more moist low areas, near creeks (drought-intolerant species) within the control plots. Species with a deciduous leaf habit were classified as drought-avoiding species. The expert opinion of forest engineers of the IBIF project, local field assistants and information from literature (Jardim *et al.*, 2003) added substantial information to these classifications.

Among the selected species are some of the most abundant species in this type of forest, as well as commercially valuable species (tab. 2). Especially *Tabebuia impetiginosa* is a highly valued timber species. Fruits of *Myrciaria cauliflora* and *Spondias mombin* are often for sale at local markets.

Species identification from the locally used species- and morpho-names, follow the identification presently used by IBIF and the former BOLFOR project. Identification was checked by an expert taxonomist and revised according to Jardim *et al.* (2003) and the nomenclature database of the Missouri Botanical Garden (W³TROPICOS) where necessary.

Scientfic species name	Local name / morphoname	Family	Adult stature (m)	Leaf form	Leaf habit	Shade-tolerance	Drought-tolerance	Use
Astronium uriundeuva	Cuchi	Anacardiaceae	27	C	D	LD	DA	Timber
Spondias mombin	Ocorocillo	Anacardiaceae	26	C	D	LD	DA	Edible fruit
Aspidosperma cylindrocarpon	Jichituriqui colorado	Apocynaceae	25	S	E	IS	DT	Timber
Aspidosperma tomentosum	Jichituriqui amarillo	Apocynaceae	23	S	D	IS	DA	Timber
Tabebuia impetiginosa	Tajibo negro	Bignoniaceae	30	C	D	LD	DA	Timber
Capparis prisca	Pacobillo	Capparaceae	15	S	E	ST	DI	Edible fruit
Jacaratia sp.	Chayote	Caricaceae	2	S	D	ST	DA	-
Combretum leprosum	Carne de toro	Combretaceae	19	S	E	ST	DT	-
Erithroxylum sp.	Coca don Israel	Erythroxylaceae	3	S	E	ST	DT	-
Actinostemon conceptionis	Don Concepcion	Euphorbiaceae	5	S	E	ST	DT	-
Manihot guaranitica subsp. guaranitica	Yucca	Euphorbiaceae	6	S	D	LD	DA	-
Phyllanthus sp. nov.	Maria pretina	Euphorbiaceae	4	S	E	ST	DT	-
Acosmium cardenasii	Tasaa	Fabaceae	24	C	E	IS	DT	-
Caesalpinia pluviosa	Momoqui	Fabaceae	29	C	E	LD	DT	Timber
Centrolobium microchaete	Tarara amarilla	Fabaceae	27	C	E	LD	DT	Timber
Guibourtia chodatiana	Sirari	Fabaceae	24	C	E	IS	DI	Timber
Platymiscium fragrans	Tarara colorada	Fabaceae	28	C	D	LD	DA	Timber
Sweetia fruticosa	Mani	Fabaceae	23	C	D	IS	DA	Timber
Casearia gossypiosperma	Cuse	Flacourtiaceae	18	S	D	IS	DA	-
Cariniana ianeirensis	Yesquero blanco	Lecythidaceae	31	S	D	IS	DA	Timber
Chorisia speciosa	Toborochi	Malvaceae	21	C	D	LD	DA	-
Eriotheca roseorum	Pequi blanco	Malvaceae	27	C	D	LD	DA	-
Trichilia elegans	Sama	Meliaceae	8	C	E	ST	DT	-
Myrciaria cauliflora	Guapuru	Myrtaceae	6	S	E	ST	DI	Edible fruit
Myrciaria floribunda	Sahuinto	Myrtaceae	26	S	E	IS	DT	-
Bougainvillea modesta	Comomosi	Nyctanginaceae	23	S	E	LD	DI	-
Neea hermafrodita	Mapabi	Nyctanginaceae	11	S	E	ST	DI	Timber
Ouratea sp.	Primo de guapomo	Ochnaceae	11	S	E	ST	DI	-
Gallesia integrifolia	Ajo ajo	Phytolaccaceae	22	S	E	IS	DI	-
Pogonopus tubulosus	Quina	Rubiaceae	10	S	D	ST	DA	-
Simira rubescens	Gabetillo blanco	Rubiaceae	16	S	D	ST	DA	-
Esenbeckia almawillia	Coca	Rutaceae	2	S	E	ST	DI	-
Galipea ciliata	Blanquillo falso	Rutaceae	12	C	E	ST	DT	-
Zanthoxylum monogynum	Naranjillo	Rutaceae	-	C	E	ST	DI	-
Talisia esculenta	Piton	Sapindaceae	16	C	E	ST	DT	-
Chrysophyllum gonocarpum	Aguai fruta chica	Sapotaceae	13	S	E	ST	DI	-
Pouteria gardneriana	Aguai fruta grande	Sapotaceae	-	S	E	ST	DI	-
Solanum cf. riparium	Tabacachi	Solanaceae	15	S	E	LD	DT	-
Ampelocera ruizii	Blanquillo	Ulmaceae	21	S	E	ST	DI	-
Phyllostylon rhamnoides	Cuta	Ulmaceae	26	S	E	IS	DI	-
Urera baccifera	Pica pica	Urticaceae	10	S	D	LD	DA	-

Table 2. **Species list.** The table shows taxonomical classification and common names of the 41 tree species from a Chiquitano dry forest in Santa Cruz, Bolivia. Shade tolerance (LD = light-demanding; IS = intermediate shade-tolerant; ST = shade-tolerant) and Drought-tolerance (DA = drought-avoiding; DI = drought-intolerant; DT = drought-tolerant) and are given per species, as well as the species adult stature, leaf form (S = simple; C = compound), leaf habit (E = evergreen; D = deciduous) and commercial product. Leaves of these species can be viewed in appendix III.

DATA COLLECTION

I sampled sun- and shade-leaves of these 41 species in the first half of the wet season (from October to January). Shade individuals were selected as much as possible in the permanent sample control plots, situated within the forest concession, while light individuals were selected along logging roads and in tree fall gaps in the, due to silvicultural management, more open permanent sample plots.

I selected 5 trees per species growing in full sunlight and 5 trees growing in shaded conditions. I tried to limit myself to sampling trees of comparable diameter and height (10 – 20 cm DBH, 10 – 20 m height); still some individuals of the less common species exceed these ranges. Species like *Manihot guaranitica* subsp*. guaranitica* and *Jacaratia* sp. are small treelets and do not attain these sizes. Of every individually selected tree I estimated DBH, total height and the percentage of canopy openness. Furthermore I classified the canopy position of every tree with the Dawkins index, ranging from 1 to 5. 1 was appointed to a tree in the absolute undergrowth of the forest, receiving no direct sunlight during the course of the day at all, 2 was

Cutting the selected leaves from a tree

 given to a tree above the undergrowth receiving no direct sunlight, 3 to a sub-canopy tree with some lateral illumination, 4 to a sub-canopy tree with full vertical light interception and 5 to an emergent tree fully illuminated for the entire day. Per individual 5 leaves were collected halfway the outer leaf layer of the crown with an extendable pruner and transported to the field laboratory in plastic bags.

A section of one of the five leaves per individual tree was stored for further anatomical analysis. The other four leaves per individual tree were included in this morphology study. I measured length and width of the total leaf and average foliole, in the case of compound leaves, length of the petiole and internode and internode diameter. Thickness of the laminae was measured with a micrometer in micro-inches. I determined the total leaf area and the area of the folioles and rachis by digitalizing the leaves with a desktop-scanner and analyzing the image with pixel-counting software. Furthermore I obtained leaf toughness by puncturing the leaves with a penetrometer (punch-head, ⌀ 3mm; $7mm^2$). Leaves were rehydrated overnight in wet paper in a dark refrigerator, superficially dried the next day and leaves, folioles and rachii were individually weighted to determine fully saturated leaf fresh weight with a balance (precision of 0,1 g). In Santa Cruz de la Sierra, the leaves, folioles and rachii were oven dried (65 ºC, 48 hours) at the IBIF laboratory and measured again to determine leaf dry weight (precision of 0,01 g). Leaf toughness was not determined for *Caesalpinia pluviosa* because of the impossibility to penetrate the tiny foliolels. I considered folioles to be functionally equivalent to simple leaves and will tread them accordingly in this study.
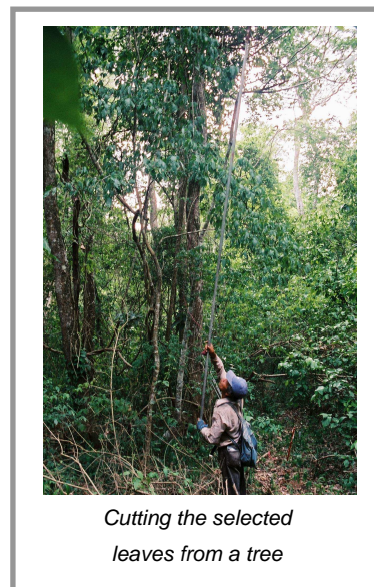
From these measurements I derived the following parameters: leaf shape index (LSI; leaf (foliole) length / leaf (foliole) width; cm cm^{-1}), Leaf mass per area (LMA; leaf dry weight / leaf area; g m^{-2}), leaf dry matter content (LDMC; leaf dry weight / fully saturated leaf fresh weight; g g^{-1}), blade length fraction (BLF; total leaf length / petiole length; cm cm^{-1}) and specific internode length (SIL; internode length / internode diameter; cm cm^{-1}).

Leaf toughness (in N cm^{-2}) is a functional indicator for the resistance of a plant to herbivory and the LSI for a plants ability to control overheating at the leaf level. LDMC, the amount of dry weight invested per unit fresh leaf weight and LMA, that indicates the amount of biomass a plant invests to produce a unit leaf surface for light capture are proxies for the construction costs of leaves.

Most time in the forest was spent taking measurements, from left to right; penetrating the leaf, digitalizing leaf areas, and determining the leaf thickness

DATA ANALYSIS

I preformed a four-way ANOVA on 1620 values per trait, testing differences in variance among light environments, species, individual trees and individual leaves nested within trees to determine the relative effect-size of these different factors. Eta-squared (η^2), which is analogous to r^2 in correlation analysis, was calculated to estimate the effect-size, expressed as the proportion of the total variance that is explained by the effect. η^2 is calculated from the models sum of squares (SS) with the formula: $\eta^2 = SS_{effect} / SS_{total}$.

To analyze within species differences between sun- and shade-leaves, shade-sun ratios (SHSU-ratios) for each trait were tested for significant deviation from unity with a One-Sample T test. SHSU-ratios are defined as a species mean shade value for a given trait divided by its mean sun-value and range from 0 to 1 when the sun-value is the bigger one and from 1 to ∞ when the shade-value is the larger one. Because these ratios have a non-linear response range, they were linearized with an arctangent transformation. Untransformed ratios response is non-linear as when e.g the mean leaf area of a given tree is 160 cm^2 in the sun and 80 cm^2 in the shade the ratio is 0,5 (deviating 0,5 from 1), while the other way around the ratio is 2 (deviating 1). After the following transformation; *SHSU(x) = ARCTAN(shade(x) / sun(x)) − ARTAN(1)*, these deviations are -0,77 and 0,78 respectively. As such the absolute deviation from unity remains the same whether the sun-value is *a* times bigger than the shade-value or

the shade-value is *a* times bigger than the sun-value. Using these transformed SHSU-ratios per species I tested the hypothesis; $H_0: SHSU(x) = 0$, against its alternative.

Leaf trait-values of sun-leaves and SHSU-ratios were correlated with Pearson product moment analyses, including adult stature as a variable and whether leaves were compound or not and deciduous or not as dummy-variables, to investigate bivariate associations. Here SHSU-ratios express the amount of plasticity when shifting from shade to sun. SHSU-ratios close to 1 imply small plasticity, as changes in the given leaf trait are small when shifting from shade to sun. SHSU-ratios that strongly deviate from 1 imply big plasticity, as changes in the given leaf trait are big when shifting from shade to sun.

Principal component analysis (PCA) was used to reduce the number of leaf traits (sun-values) and SHSU-ratio values into a smaller number of uncorrelated variables (principal components). In the analysis the first principal component accounted for as much of the variability in the data as possible, and each succeeding component accounted for as much of the remaining variability as possible. Principal component extraction was limited to three components. Leaf-traits that co-occur in trade-off with one another were identified as variables that have the highest amount of variation explained by a given principal component and were oppositely correlated to that principal component.

Finally, multivariate differences between and separation of functional groups related to drought- and shade-tolerance were tested with a Canonical Discriminant Analysis (CDA). I derived the separating power of the discriminant functions or canonical axes from their canonical correlation. Between functional group differences were evaluated using a one-way ANOVA in combination with a post-hoc Duncan's multiple range test. The different leaf traits were included as dependent variables and functional groups as fixed factors. To exclude variation in mean leaf trait values in the model resulting from the effect of differences in light environment, I implemented the latter analyses on mean leaf trait values of sun-leaves only. Additional CDA's on SHSU-ratios tested whether functional groups could be separated based on the amount of plasticity of the leaf trait when shifting from shade to sun.

Where necessary traits were log10-transformed to improve normality of its distribution or to minimize the effect of extreme and outlier values. An 0,05 criterion of statistical significance was used for all tests. Statistical analysis was carried out with SPSS 11.0.

Results

RELATIVE EFFECT SIZE OF LIGHT ENVIRONMENT, SPECIES, INDIVIDUAL TREE AND LEAF VARIATION

Leaves vary greatly in morphological traits among species (tab. 3.). Variation among individual trees accounts for some of the trait variation, but in most cases that is less important than the light environment- and species-effect. Variation among trees does not effect leaf length, LDMC, LMA, leaf toughness and blade length fraction at all. Leaves nested within individual trees are most alike and do not affect the mean trait values. The relative amount of variation that is explained by the variation among species is greatest for all traits, as indicated by their high η^2-values (0,43 – 0,91). The F-values of the light environment effect on LDMC, LMA, and leaf

thickness are bigger than the species effect (F = 48 – 190). Sun- and shade-leaves differ in LDMC, LMA and leaf thickness, but the actual amount of variation explained is modest (0,01-0,04). Variation among species explains 53%, 61% and 63% of the variance in LDMC, LMA and leaf thickness respectively.

In all cases leaf traits are affected by the interaction between light environment and species, indicating that different species adapt their morphological leaf properties in different ways when exposed to different light levels. The variation explained by this interaction effect is larger than the variation explained by the light environment alone.

Trait	Light environment			Species			Tree			Leaf			Light environment x species		
	F	Sig.	η^2	F	Sig.	η^2	F	Sig.	η^2	F	Sig.	η^2	F	Sig.	η^2
Leaf length (cm)	78	****	0,01	275	****	0,86	2	ns	0,00	1	ns	0,00	5	****	0,02
Leaf width (cm)	53	****	0,00	413	****	0,91	5	****	0,00	1	ns	0,00	5	****	0,01
Leaf shape index (cm cm^{-1}) [a]	4	ns	0,00	95	****	0,71	4	****	0,01	0	ns	0,00	3	****	0,02
Leaf area (cm^2)	74	****	0,00	339	****	0,88	4	***	0,00	1	ns	0,00	6	****	0,02
Leaf dry matter content (g g^{-1})	48	****	0,01	46	****	0,53	2	ns	0,00	1	ns	0,01	3	****	0,04
Leaf mass per area (g m^{-2})	190	****	0,04	70	****	0,61	1	ns	0,00	1	ns	0,00	5	****	0,04
Thickness (µm)	180	****	0,03	83	****	0,63	11	****	0,02	0	ns	0,00	6	****	0,05
Toughness (N cm^{-2})	26	****	0,01	85	****	0,68	2	ns	0,00	1	ns	0,00	4	****	0,03
Petiole length (cm)	37	****	0,00	514	****	0,93	4	***	0,00	1	ns	0,00	4	****	0,01
Internode length (cm)	11	**	0,00	33	****	0,45	3	***	0,01	1	ns	0,01	3	****	0,04
Blade length fraction (cm cm^{-1})	4	*	0,00	296	****	0,88	1	ns	0,00	1	ns	0,00	4	****	0,01
Specific internode length (cm cm^{-1}) [a]	1	ns	0,00	31	****	0,43	3	**	0,01	1	ns	0,01	3	****	0,05

Table 3. **Factor effects on leaf trait variation.** Outcome of a nested four-way ANOVA with light environment (*n = 2*) and species (*n = 41*) (leaf toughness; n = 40) as fixed factors and individual trees, (*n = 410*) and leaves nested within trees (*nested n = 4; total n = 1620*) as random factors. F-values, significance level (*Sig.*) and partial eta-squared (η^2) are given for the traits in the study; **ns**; p > 0,05; * p < 0,05; ** p < 0,01; *** p < 0,001; **** p < 0,0001. [a]; Traits were log_{10}-transformed, except for leaf shape index and specific internode length.

WITHIN SPECIES DIFFERENCES BETWEEN SUN- AND SHADE-LEAVES

SHSU-ratios of all traits except LSI, BLF and SIL deviated significantly from 1 (fig. 2). Shade-leaves are longer and broader than sun-leaves, leading to larger surface areas. While the absolute length and width of leaves differ between light environments, the leaf shape index (length : width) is not adjusted.

LDMC, LMA, thickness and toughness all differ between sun and shade-leaves. Sun-leaves have more dry weight invested per unit leaf weight and per unit photosynthetic area and they are thicker and tougher than shade-leaves. Petioles of sun-leaves are significantly shorter than shade leaves, but the BLF does not differ. The mean internode length differs within species; internodes are longer in sun trees. This increase of internode length corresponds with a proportional increase in thickness of the internodes, as the specific internode length (SIL) in both environments is similar. Traits with a significant deviation from unity are ranked from biggest to smallest in terms of this deviation; leaf area (with a deviation of 23%), LMA (15%), leaf length (10%), leaf thickness (10%), leaf width (9%) and petiole length (8%) LDMC (7%), internode length (6%) and toughness (6%).
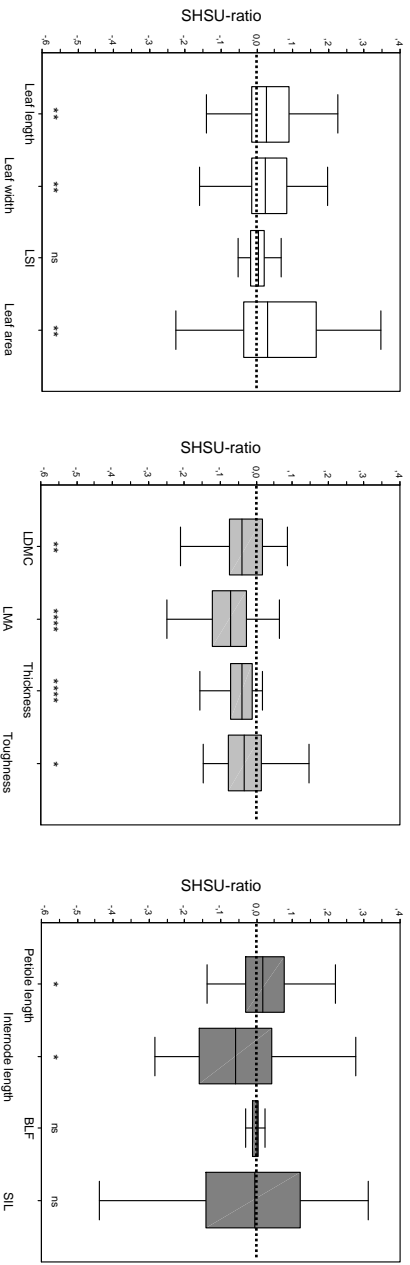
Figure 2. SHSU-ratios; deviation from unity. The upper and lower limits of the boxes indicate the 25 and 75 percentile of the shade – sun ratio-values (*arctangent transformed*) 41 species with their median value. Error bars represent the total range of shade – sun ratios. Significance of deviation from unity (·····= 0) are given per trait; **ns**; non significant. *; p < 0,05. **; p <0,01. ***; p < 0,001. ****; p < 0,0001. For the untransformed SHSU-ratios per species see appendix I.

ASSOCIATIONS AND TRADE-OFFS AMONG LEAF TRAITS

Bivariate correlations among leaf traits and among SHSU-ratios are summarized in table 4.

	Specific internode length (cm cm⁻¹)	Blade length fraction (cm cm⁻¹)	Internode length (cm)	Petiole length (cm)	Toughness (N cm⁻²)	Thickness (µm)	Leaf mass per area (g m⁻²)	Leaf dry matter content (g g⁻¹)	Leaf area (cm²)	Leaf shape index (cm cm⁻¹)	Leaf width (cm)	Leaf length (cm)	Adult stature (m)	Deciduous leaves
Compound leaves	-0,15*	-0,32****	0,06	0,28****	0,02	-0,05	0,14*	0,14*	-0,39****	0,27****	-0,33****	-0,32****	0,45****	0,15*
Decidous leaves	-0,17**	-0,32****	0,25***	0,45****	-0,16*	-0,02	-0,09	-0,20**	0,26****	-0,38****	0,43****	0,26***	0,21**	
Adult stature (m)	0,00	0,13*	0,06	0,00	0,04	-0,08	0,21**	0,17**	-0,18**	0,16*	-0,23***	-0,08		
Leaf length (cm)	-0,19**	-0,25***	0,26****	0,44****	0,29****	0,20**	0,02	-0,19**	0,92****	-0,16*	0,78****		-0,12	
Leaf width (cm)	-0,14*	-0,56****	0,44****	0,68****	0,00	0,14*	-0,18**	-0,35****	0,86****	-0,59****		0,87****	-0,20	
Leaf shape index (cm cm⁻¹)	0,03	0,38****	-0,22***	-0,34****	0,22**	-0,15*	0,19**	0,35****	-0,33****		-0,20	0,28*	0,13	
Leaf area (cm²)	-0,13*	-0,33****	0,30****	0,48****	0,16*	0,20**	-0,01	-0,22***		0,10	0,89****	0,93****	-0,22	
Leaf dry matter content (g g⁻¹)	0,17**	0,28****	-0,06	-0,26****	0,35****	-0,27****	0,56****		-0,16	-0,06	-0,11	-0,12	0,00	
Leaf mass per area (g m⁻²)	-0,03	0,14*	-0,02	-0,12*	0,45****	0,34****		0,63****	-0,25	-0,09	-0,17	-0,21	0,07	
Thickness (µm)	-0,26***	-0,12*	-0,02	0,06	0,19**		0,40**	0,19	-0,52***	0,02	-0,52***	-0,50***	0,25	
Toughness (N cm⁻²)	0,04	0,11	0,04	-0,05		0,51***	0,21	-0,07	-0,18	0,12	-0,20	-0,14	0,12	
Petiole length (cm)	-0,23***	-0,86****	0,46****		-0,14	-0,14	-0,32*	-0,14	0,52***	-0,16	0,53***	0,46**	-0,04	
Internode length (cm)	0,41****	-0,34****		0,19	0,00	-0,08	-0,19	-0,15	0,24	0,04	0,33*	0,32*	-0,10	
Blade length fraction (cm cm⁻¹)	0,24***		-0,06	-0,70****	0,08	-0,07	0,22	0,14	-0,04	0,31*	-0,09	0,06	-0,08	
Specific internode length (cm cm⁻¹)		0,13	0,78****	0,04	0,07	-0,08	-0,05	-0,20	0,05	0,01	0,20	0,19	-0,08	

Table 4. Leaf trait associations. Outcome of a Pearson product moment correlation analysis on leaf trait sun-values (n = 203; white, upper part of the table) and transformed SHSU-ratios (n = 41; grey, lower part of the graph). **ns**; p > 0,05; * p < 0,05; ** p < 0,01; *** p < 0,001; **** p < 0,0001.

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Associations amongst leaf characteristics, were analyzed with a principal component analysis. Three principal components (PC´s) were extracted, together explaining as much as 58% of the total variation (tab. 5a). The first axis is mainly correlated with blade- and entire leaf-size dimensions and their shape (fig. 3a, b). Whether leaves are deciduous or not and LDMC are other correlates of the 1st PC. Traits correlating to the 2nd PC are related to the investment of biomass per unit leaf-area. A high LMA leads to a higher toughness of the leaves. The 3rd PC is mainly related to adult stature and whether leaves are compound or not. A high adult stature trees more frequently have a compound leaf habit. The PC's reveal several interesting trade-offs that were not priory expected. The 1st PC shows the strong trade-off between leaf area and LSI, which implies bigger leaves to be less slender than smaller ones. Leaf area and LDMC are also in trade-off, as bigger leaves have less biomass invested per unit leaf weight (tab. 4). Deciduous leaves also have a lower LDMC. Deciduous leaves are less slender, with relatively shorter leaf blades.

With a PCA on SHSU-ratios (tab. 5b, fig. 3c, d), three PC´s are extracted that correlate with changes in area and size of leaves and leaf thickness (1st PC), proportional relation between the length of the leaf-blade and that of the petiole (2nd PC) and internode dimensions (3rd PC). Together the extracted PC's explain up to 59% of the total variation. While plasticity of the response among leaf dimensions and petiole length are logically related along the 1st PC, a trade-off is found with the responses and that of leaf thickness. This relation implies that species with a big plasticity in leaf area dimensions to changing light environment have a smaller plastic response in leaf thickness.

Sun-leaves	Principal Component		
	1	2	3
Eigen-value	4,52	2,15	2,07
% variance explained	30	14	14
Cumulative % variance explained	30	44	58
Leaf width (cm)	**0,95**	0,15	-0,10
Leaf area (cm^2)	**0,81**	0,44	-0,14
Petiole length (cm)	**0,79**	-0,19	0,44
Leaf length (cm)	**0,74**	0,52	-0,05
Blade length fraction (cm cm^{-1})	**-0,69**	0,29	-0,38
Leaf shape index (cm cm^{-1})	**-0,60**	0,22	0,20
Decidous leaves	**0,52**	-0,26	0,32
Leaf dry matter content (g g^{-1})	**-0,48**	0,43	0,35
Toughness (N cm^{-2})	-0,06	**0,75**	0,26
Leaf mass per area (g m^{-2})	-0,23	**0,65**	0,47
Compound leaves	-0,18	-0,35	**0,83**
Adult stature (m)	-0,20	-0,07	**0,61**
Specific internode length (cm cm^{-1})	-0,21	0,04	-0,17
Internode length (cm)	0,46	0,01	0,25
Thickness (µm)	0,22	0,35	0,05

a

SHSU-ratios	Principal Component		
	1	2	3
Eigen-value	4,03	1,86	1,72
% variance explained	31	14	13
Cumulative % variance explained	31	45	59
Leaf width (cm)	**0,89**	0,02	-0,18
Leaf area (cm^2)	**0,89**	0,06	-0,27
Leaf length (cm)	**0,87**	0,25	-0,23
Thickness (µm)	**-0,65**	-0,03	0,34
Petiole length (cm)	**0,64**	-0,54	0,22
Blade length fraction (cm cm^{-1})	-0,20	**0,79**	-0,40
Specific internode length (cm cm^{-1})	0,29	0,57	**0,58**
Internode length (cm)	0,45	0,45	**0,58**
Leaf mass per area (g m^{-2})	-0,48	0,21	-0,35
Leaf dry matter content (g g^{-1})	-0,33	0,05	-0,52
Leaf shape index (cm cm^{-1})	-0,01	0,49	-0,08
Adult stature (m)	-0,27	-0,10	0,18
Toughness (N cm^{-2})	-0,33	0,24	0,34

b

Table 5. **Principal component analysis.** The tables show the correlation of the species values for sun-leaves (**a**) and transformed SHSU-ratios (**b**) with the principal components. Numbers in **bolt** indicate the main assessors of the components, based on their correlation to the components .

Eigen-values and percentages of variation explained by the separate and cumulative components are given at the top of each sub-table.
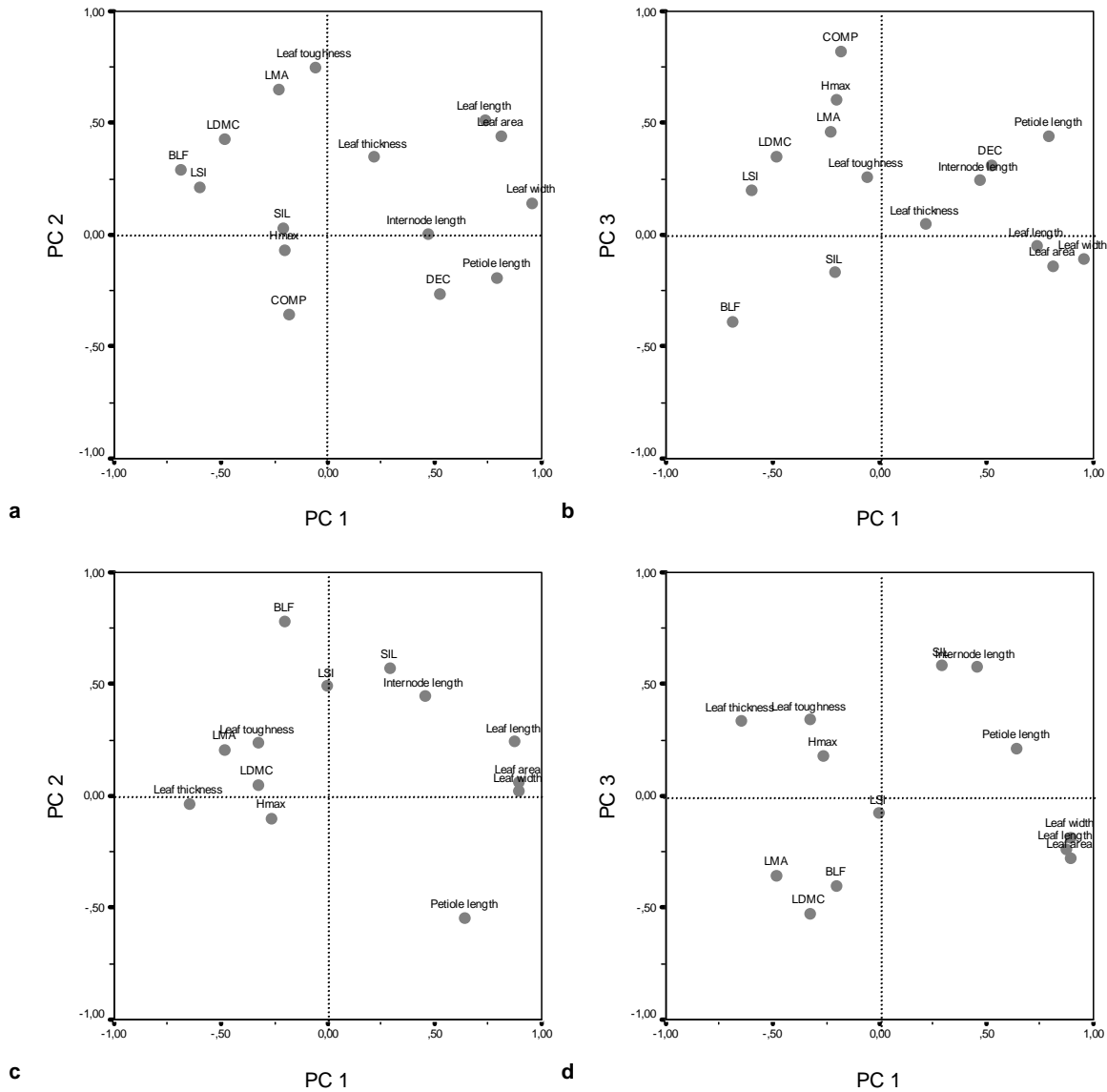
Figure 3. **Leaf trait associations.** The figures show correlations (**a, b**) among the mean sun-leaf trait–values (DEC = deciduous leaves; COMP = compound leaves) and (**c, d**) among SHSU-ratio-values of 5 trees per species (n =41; n = 40 for leaf toughness) and correlation with the first three principal components (PC1 – PC3). Adult stature (H_{max}) is included.

FUNCTIONAL GROUPS, SHADE-TOLERANCE

The Canonical Discriminant Analysis (CDA) on mean sun-leaf characteristics significantly separates the three a priori-defined shade-tolerance groups along the first canonical axis (CA 1) (p < 0,001) (fig. 4a). Along the 2nd axis the separation is marginal (0,5 < p < 0,1) Boundaries between the group territories as indicated in the graph are not completely discrete, but slightly diffuse, especially between light-demanding and intermediate shade-tolerant species. The 1st canonical axis explains as much as 71% of variation and mainly discriminates between shade-tolerant (at the left) and intermediate shade-tolerant and light-demanding species (right), while the 2nd axis, explaining 27%, separates trees of light-demanding (bottom) and intermediate shade-tolerant species (top). Not all traits included in the analysis contribute to group

discrimination. Traits that do discriminate between groups are adult stature, petiole length, blade-length fraction and whether species have compound or simple leaves and whether they are deciduous or evergreen. Differences in leaf length and width, leaf thickness and length of the internode between functional groups marginally contribute to the separation.

Along the 1st CA species are separated on their tall adult stature at the right, while at the left species are characterized by their smaller full grown height. Along the 2nd axis species separate in the top part of the graph mainly because of their relatively longer leaf blades (high BLF) and thick leaves. At the bottom part of the graph species have more frequently compound leaves and a deciduous leaf habit, petioles are longer and leaves are longer and broader with longer internodes. Based on this model, a-priory selected functional groups are for 90% correctly classified.

Light-demanding species have a high adult stature and the longest petioles and smallest BLF (tab. 6). Leaves of light-demanding species are marginally bigger than those of intermediate shade-tolerant species. Internodes are longest among groups, still their specific internode length is relatively small. Intermediate shade-tolerant species have short petioles and a big BLF, while leaves are comparatively small. Internodes are short, while the specific internode length is biggest among groups. Shade-tolerant species have the shortest adult stature. Their leaf size and internode dimensions do not differ from those of light-demanding and intermediate shade-tolerant species.

Figure 4.   **Shade tolerance.** The figures show the separation of functional groups related to shade tolerance based on mean trait values of sun-leaves (**a**) and SHSU-ratios of 41 species along two canonical axis. Symbols represent; ●, shade-tolerant species (n = 19); ●, intermediate shade-tolerant species (n = 10) and; ○, light-demanding species (n = 12). Circular shapes are rough interprets of the functional group territories.

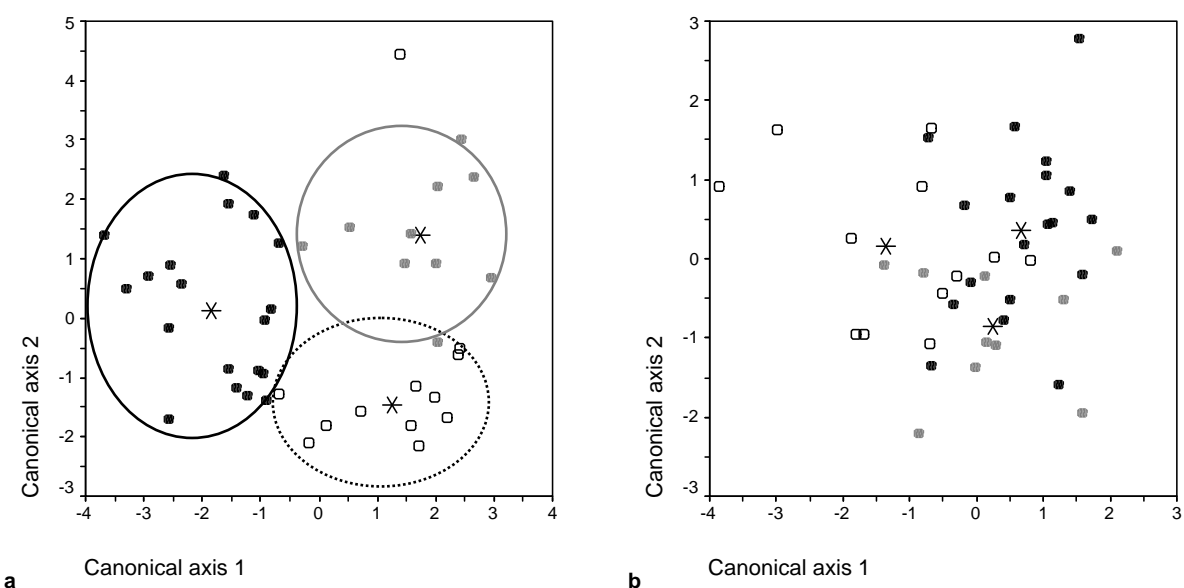| Trait	n	mean		se	n	mean		se	n	mean		se	p	1	2
		Light-demanding species				Intermediate shade-tolerant species				Shade-tolerant species				Canonical structure [1]	
Adult stature (m) [2]	11	22,30	b	2,24	10	24,27	b	1,05	17	10,21	a	1,41	****	0,64	0,04
Leaf length (cm)	11	10,87		1,36	10	6,78		1,18	17	9,72		1,31	ns	-0,06	-0,35
Leaf width (cm)	11	5,74		1,42	10	3,22		0,62	17	4,64		0,82	ns	-0,03	-0,38
Leaf shape index (cm cm^{-1}) [2]	11	2,03		0,21	10	2,16		0,14	17	2,19		0,12	ns	-0,05	0,23
Leaf area (cm^2)	11	37,01		13,90	10	15,79		6,77	17	30,75		10,14	ns	-0,06	-0,32
Leaf dry matter content (g g^{-1})	11	0,27		0,02	10	0,31		0,02	17	0,29		0,02	ns	-0,05	0,29
Leaf mass per area (g m^{-2})	11	60,37		4,06	10	61,68		5,03	17	56,20		5,24	ns	0,08	0,02
Thickness (µm)	11	205,16		19,03	10	169,03		8,76	17	182,82		11,77	ns	0,04	-0,34
Toughness (N cm^{-2})	11	28,21		2,42	10	25,95		2,44	17	31,69		3,94	ns	-0,10	-0,06
Petiole length (cm)	11	5,31	b	1,31	10	0,91	a	0,24	17	1,43	a	0,65	***	0,13	-0,71
Internode length (cm)	11	2,44		0,59	10	1,35		0,25	17	1,61		0,18	ns	0,05	-0,36
Blade length fraction (cm cm^{-1})	11	0,77	a	0,03	10	0,90	b	0,02	17	0,85	b	0,02	*	-0,05	0,47
Specific internode length (cm cm^{-1}) [2]	11	6,04		1,12	10	9,82		1,60	17	8,63		1,16	ns	-0,06	0,32

Table 6. **Shade-tolerance.** The table shows differences in traits of sun-leaf among functional groups resulting from a one-way ANOVA and (1) Pearson correlation coefficients of the separate variables to each of the two canonical axis in the CDA. (2) Traits were log$_{10}$-transformed, except adult stature, LSI and ISI

When we investigate shade-tolerance group classification based on the plasticity of leaf trait adjustments to different light environments (SHSU-ratios), neither one of the CA's significantly separates groups. The functional groups differ only in plasticity of BLF and marginally in plasticity of their leaf area (tab. 7). Light-demanding species show the greatest plasticity in leaf area, Light-demanding and shade-tolerant species have opposite SHSU-ratios of BLF. The proportional length of the leaf-blade to the petiole in light-demanding species becomes bigger, while shade-tolerant species leaf-blades become relatively shorter.

SHSU-ratio	n	mean		se	n	mean		se	n	mean		se	p	1	2
		Light-demanding species				Intermediate shade-tolerant species				Shade-tolerant species				Canonical structure [1]	
Leaf length (cm)	11	1,15		0,05	10	1,03		0,03	19	1,10		0,04	ns	-0,23	0,35
Leaf width (cm)	11	1,14		0,05	10	1,01		0,03	19	1,09		0,04	ns	-0,22	0,46
Leaf shape index (cm cm^{-1})	11	1,01		0,02	10	1,02		0,01	19	1,01		0,02	ns	-0,03	-0,13
Leaf area (cm^2)	11	1,41		0,14	10	1,04		0,07	19	1,22		0,09	ns	-0,30	0,48
Leaf dry matter content (g g^{-1})	11	0,88		0,03	10	0,99		0,02	19	0,93		0,04	ns	0,22	-0,43
Leaf mass per area (g m^{-2})	11	0,82		0,05	10	0,90		0,05	19	0,85		0,03	ns	0,19	-0,26
Thickness (µm)	11	0,88		0,04	10	0,95		0,02	19	0,90		0,02	ns	0,15	-0,46
Toughness (N cm^{-2})	11	0,90		0,06	10	0,95		0,06	19	0,96		0,03	ns	0,21	0,03
Petiole length (cm)	11	1,18		0,08	10	1,03		0,04	19	1,04		0,05	ns	-0,34	0,14
Internode length (cm)	11	0,93		0,09	10	0,93		0,10	19	0,95		0,08	ns	-0,03	0,04
Blade length fraction (cm cm^{-1})	11	0,97	a	0,01	10	1,00	b	0,00	19	1,01	b	0,01	**	0,61	0,11
Specific internode length (cm cm^{-1})	11	0,93		0,10	10	0,95		0,10	19	1,10		0,09	ns	0,15	0,25

Table 7. **Shade-tolerance.** The table show differences in mean arctangent transformed SHSU-ratios among functional groups resulting from a one-way ANOVA and (1) Pearson correlation coefficients of the separate variables to each of the two canonical axis in the CDA, of which none are significant.

FUNCTIONAL GROUPS, DROUGHT-TOLERANCE

The CDA on mean sun-leaf characteristics does not significantly separate the three a priory classified functional groups related to drought-tolerance (fig. 5a). Only a marginal separation occurs along the 1st CA (0,05 < p < 0,1).

Boundaries between the group territories as indicated in the graph are not discrete, but diffuse (fig. 5a). The 1st canonical axis explains as much as 58% of variation and mainly discriminates between Drought-avoiding and drought-intolerant species, while the 2nd axis, explaining 42%, mainly separates drought-tolerant and drought-avoiding species. Only leaf width, LSI, LMA and petiole length significantly contribute to this group separation. Along the 1st axis separation occurs mainly between species with long petioles at the right and trees with relatively slender leaf-blades, with a high LMA at the left. Along the 2nd axis species with broad, big leaves, at the top are separated from those at the down end.

Leaves of drought-avoiding species are least slender among groups. Their leaves are broad, and big and have less biomass invested per unit photosynthetic area than drought-intolerant species. Drought-tolerant species have smallest leaf-size dimensions and a low LMA, while drought-intolerant trees have the highest LMA. Their leaf area is average and in-between that of the other two groups (tab. 8).

a   b

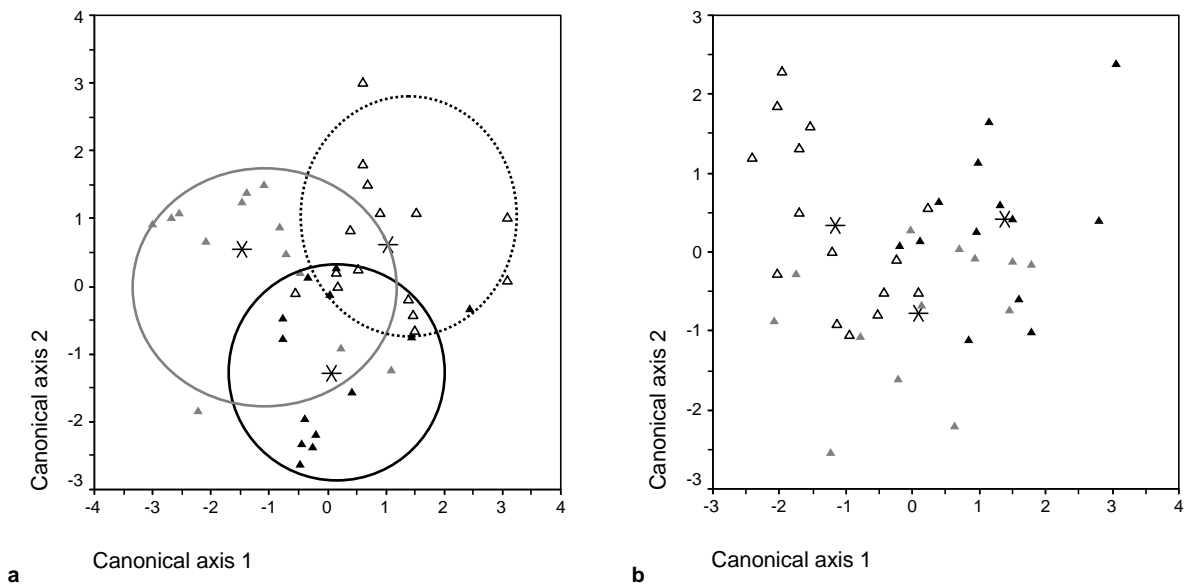**Figure 5.**   **Drought tolerance.** The figures show the separation of functional groups related to drought tolerance based on mean trait values of sun-leaves (**a**) and SHSU-ratios of 41 species along two canonical axis. Symbols represent; ▲, drought-tolerant species (n = 13); ▲, drought-intolerant species (n = 13) and; △, drought-avoiding species (n = 15). Circular shapes are rough interprets of the functional group territories.

Trait	Drought-avoiding species			Drought-intolerant species			Drought-tolerant species				Canonical structure [1]	
	n	mean	se	n	mean	se	n	mean	se	p	1	2
Adult stature (m) [2]	15	19,85	2,34	11	15,79	2,38	12	16,34	2,57	ns	0,18	0,18
Leaf length (cm)	15	11,16	1,15	11	9,42	1,73	12	7,19	1,11	ns	0,15	0,37
Leaf width (cm)	15	6,42 b	1,28	11	4,23 ab	0,60	12	3,22 a	0,65	*	0,26	0,42
Leaf shape index (cm cm^{-1}) [2]	15	1,82 a	0,12	11	2,30 b	0,13	12	2,33 b	0,17	*	-0,33	-0,29
Leaf area (cm^2)	15	42,58	11,49	11	28,94	12,31	12	15,94	8,44	ns	0,14	0,38
Leaf dry matter content (g g^{-1})	15	0,27	0,02	11	0,32	0,02	12	0,30	0,02	ns	-0,32	0,01
Leaf mass per area (g m^{-2})	15	55,26 a	5,00	11	69,90 b	5,25	12	52,87 a	3,70	*	-0,36	0,30
Thickness (µm)	15	186,76	9,55	11	198,11	12,40	12	172,38	20,65	ns	-0,09	0,15
Toughness (N cm^{-2})	15	26,53	2,36	11	34,59	5,37	12	27,38	1,80	ns	-0,24	0,08
Petiole length (cm)	15	3,35 b	1,31	11	1,17 a	0,42	12	1,56 ab	0,57	*	0,42	0,16
Internode length (cm)	15	2,00	0,51	11	1,75	0,16	12	1,48	0,23	ns	0,08	0,25
Blade length fraction (cm cm^{-1})	15	0,79	0,04	11	0,88	0,02	12	0,86	0,02	ns	-0,31	-0,15
Specific internode length (cm cm^{-1}) [2]	15	6,69	1,08	11	9,91	1,41	12	8,11	1,41	ns	-0,32	0,03

Table 8. **Drought-tolerance.** The table shows differences in traits of sun-leaf among functional groups resulting from a one-way ANOVA and (1) Pearson correlation coefficients of the separate variables to each of the two canonical axis in the CDA. (2) Traits were $\log_{10}$-transformed, except adult stature, LSI and SIL

When I investigate drought-tolerance group classification on the bases of their SHSU-ratios, groups do not significantly separate along the CA's. Plasticity of leaf length and specific internode length are significant contributors, while leaf width, leaf area, internode length and BLF are marginally discriminate. The 1st axis explains 79% of the total variation and separates trees with a large plasticity in specific internode length and BLF at the right. The variability of these traits thus discriminates mainly between trees of drought-tolerant and drought-avoiding species (fig. 5b).

Table 9 shows that trees of drought-tolerant species are most plastic in their changes in leaf length dimensions. Drought-avoiding and drought-tolerant species do not differ in leaf length plasticity.

The strongest differences among functional groups in terms of plasticity are found for the specific internode length, not in terms of the size of the plastic response but in the direction. Internodes of sun-leaves of drought-avoiding species are relatively short and thick, compared to those of shade leaves, while internodes of the other two groups are relatively long and thin in comparison to those of their shade leaves.

SHSU-ratio	Drought-avoiding species			Drought-intolerant species			Drought-tolerant species				Canonical structure [1]	
	n	mean	se	n	mean	se	n	mean	se	p	1	2
Leaf length (cm)	15	1,07 a	0,03	13	1,04 a	0,04	12	1,19 b	0,06	*	0,30	0,51
Leaf width (cm)	15	1,05	0,04	13	1,05	0,04	12	1,16	0,04	ns	0,31	0,36
Leaf shape index (cm cm^{-1})	15	1,02	0,02	13	1,00	0,02	12	1,02	0,02	ns	0,00	0,32
Leaf area (cm^2)	15	1,21	0,10	13	1,09	0,09	12	1,40	0,12	ns	0,21	0,54
Leaf dry matter content (g g^{-1})	15	0,93	0,03	13	0,92	0,04	12	0,95	0,05	ns	0,03	0,15
Leaf mass per area (g m^{-2})	15	0,82	0,03	13	0,89	0,04	12	0,85	0,05	ns	0,09	-0,34
Thickness (µm)	15	0,90	0,02	13	0,94	0,02	12	0,87	0,04	ns	-0,11	-0,41
Toughness (N cm^{-2})	15	0,91	0,03	13	0,96	0,04	12	0,96	0,07	ns	0,08	-0,20
Petiole length (cm)	15	1,08	0,07	13	1,03	0,04	12	1,12	0,06	ns	0,09	0,26
Internode length (cm)	15	0,84	0,06	13	0,90	0,07	12	1,08	0,11	ns	0,33	0,17
Blade length fraction (cm cm^{-1})	15	0,98	0,01	13	1,00	0,00	12	1,01	0,01	ns	0,35	-0,01
Specific internode length (cm cm^{-1})	15	0,80 a	0,06	13	1,10 b	0,10	12	1,17 b	0,11	**	0,48	-0,27

Table 9.   **Drought-tolerance.** The table show differences in mean SHSU-ratios among functional groups resulting from a one-way ANOVA and (1) Pearson correlation coefficients of the separate variables to each of the two canonical axis in the CDA, of which non are significant.

Discussion

DIFFERENCES BETWEEN SUN AND SHADE LEAVES

I found leaf area dimensions to differ between sun and shade leaves, both among and within species. In line with my hypotheses, the sun-leaves are shorter and less broad, with a bigger surface area than shade leaves. This reduction of the leaf area is frequently mentioned in literature as an adaptation to the high light environment (e.g. Fisher, 1986; Bongers and Popma, 1988; Turner, 2001; Kuroki *et al.*, 2002) To my knowledge Bongers and Popma (1988) have conducted the most detailed study of tropical leaf form variation and they found sun-leaves from 61 Mexican rain forest species to be smaller than shade-leaves, both among and within species. Sun-leaves are smaller to allow a more effective convective cooling (Parkhurst an Louks, 1972; Givnish, 1984), while large leaves are mentioned to have a high boundary-layer resistance that reduces the rate of heat transfer between the leaf and the atmosphere. As a consequence, bigger leaves might easily reach lethal temperatures and must there for be able to maintain rapid transpiration to prevent overheating (Smith, 1978; Turner , 2001).

I hypothesized that, in addition to reducing total leaf area, sun-leaves would have a higher length-width ratio, to facilitate convective cooling. Yet, the sun- and shade-leaves do not differ in slenderness, whereas it was increased in a Mexican rain forest (Bongers and Popma 1988). To make this result even more contrasting, a negative relation was found between leaf area and slenderness in sun-leaves (tab. 4). Seemingly slenderness is not a favored adaptation to reduce leaf level temperature in the dry forest habitat. In comparison to wet forests, dry forest species function and survival is to a greater extent influenced by their ability to conserve water. It might be that increasing the leaf slenderness negatively influences the species water use efficiency through increased wind–induced transpiration. Leaf slenderness might therefore be an adaptation to reduce leaf level temperature in habitats where water stress is not that pronounced.

Sun-leaves were thicker than shade-leaves (fig. 2). This is again a commonly found adjustment to light. Thicker leaves have been found for sun and shade leaves from one tree (Wylie, 1951) or for trees growing in different light environments (McClendon and McMillen, 1980; Fisher, 1986; Bongers and Popma, 1988) Under fully illuminated conditions light is better capable of penetrating several cell layers in the leaf lamina. Sun grown species can therefore produce more chloroplast bearing palisade parenchyma, in order to increase light interception and photosynthesis (Bongers and Popma, 1988; Turner 2001). Thicker leaves are furthermore better equipped to endure water stress, as carbon-fixation rates show a stronger increase with thickness than the rate of water loss (Turner 2001). Thicker leaves have a lower surface to volume ratio and therefore less evapotranspiration. Thicker leaves are may be less likely to wilt during the hours at the day with highest radiation and can maintain a vertical leaf angle to

secure high light interception. Still light-demanding species are actually found to wilt in order to reduce light intercepted (Chariello *et al.*, 1987). This suggests that increasing leaf thickness is an adjustment to reduce water loss, rather than to increase light interception.

In line with my hypotheses sun-leaves have both a higher LDMC and LMA than shade-leaves. Sun grown species have a high photosynthetic capacity and high respiration rates. They maintain a positive carbon balance and can as such afford to invest a lot of biomass to the leaf. The LDMC and leaf toughness are strongly associated (tab. 4). Sun-leaves are therefore tougher than shade leaves. This might be favorable in the open habitat where these trees are growing. Well protected leaves are less vulnerable to weather induced leaf damage. Tougher leaves also imply better defense against herbivory. Herbivory rates by insects in tropical forests are much higher than those in temperate forests (Coley and Barone, 1996) and leaves of tree species in the canopy of tropical forests have been found to endure much higher herbivory rates than in the sun-canopy environment, due to the high insect densities found in this stratum (Sterck *et al.*, 1992). Although sun-leaves in this study were not all collected from canopy positions, a with coming effect of the greater toughness of sun-leaves could be better defense against herbivore damage.

It is the amount of biomass investment per unit leaf area (LMA) that should be considered to be the functional trait determining natural selection in the shade (Turner, 2001). As light availability is low, shade trees have a low photosynthetic capacity, low respiration rates and thus a low carbon uptake. In order to optimize their carbon balance shade trees ideally will invest a minimum of carbon to a maximum photosynthetic area and thus have low LMA and low LDMC.

Petioles of shade leaves are longer than those of sun-leaves. This is in line with my hypothesis, as I expected petioles in the shade to be longer, as an result of light foraging and to occur in combination with longer internodes. However internodes of shade leaves were shorter in the shade. And although the absolute petiole length and internode length are positively related, their plastic response to different light environments (SHSU-ratios) is not related (tab. 4). In stead SHSU-ratios of petiole length and those of leaf length, width and area are strongly related. This suggests that the petiole, in combination with the leaf blade, is an extendable unit that can be adjusted for light-foraging in the forest understory. Internodes are expensive, and as carbon investment in the shade is limited, petioles are cheaper to make than the relatively thick internodes. Internodes as such do not seem to have light foraging capacity.

In conclusion, differences in characteristics of sun and shade leaves result from different constraints and pressures the leaves have to endure in these habitats. In the sun leaf morphology is mostly determined by the struggle to reduce negative heat effects at the leaf level and the need to maintain a high water use efficiency. The latter of course is especially important in dry forest ecosystems. In the shade leaf morphology is guided by competition for light and optimization of the carbon balance.

FUNCTIONAL GROUPS, SHADE-TOLERANCE

The three shade-tolerance groups I studied could be discriminated based on the traits I included in the analysis. Still the separation of species depended most on differences in adult stature among species in stead of leaf morphological trait differences. Significant differences in absolute length of the petiole, and marginal differences in leaf size dimensions were the only morphological traits contributing to group separation (fig. 4, tab. 6). Deciduousness and whether leaves were compound or simple further assessed group discrimination.

In line with Popma *et al.* (1992) boundaries between groups were distinct (fig. 4), although an outlying light-demanding species disturbs them somewhat between light-demanding and intermediate shade-tolerant species. The outlying species is *Urera baccifera* (Urticaceae), with its, in proportion to the petiole, relatively long leaf blades and simple leaf habit, it distinguishes itself from the other light-demanding species, which more often employ a compound leaf habit and have relatively long petioles. Small individuals of this species were also frequently observed in the forest understory (Markesteijn, pers. obs.), where e.g. other, at first glance similar simple leaved light-demanding species, as *Solanum cf. riparium* (Solanaceae) were not encountered. This suggests the possible need to reevaluation of the level of shade-tolerance of *Urera baccifera.*

My findings on leaf morphological characteristics of shade-tolerance groups are overall neither in line with my hypothesis nor with findings from other studies. Differences between shade-tolerance groups are often quite distinct. In various climates, light-demanding species have been found to differ from shade-tolerant species in e.g. leaf area (Popma *et al.*, 1992; Kappelle and Leal, 1996), thickness (Jackson, 1967; Popma *et al*, 1992;), slenderness (Popma *et al.*, 1992), LMA (Popma *et al.* 1992; Veneklaas and Poorter, 1998; Walter and Reich, 1999; Reich *et al.,* 2003). Light-demanding species from other studies are known to optimize growth rates by increasing carbon assimilation in the high light environment. Leaves can be big or small with low biomass investment per unit leaf area (LMA) and per unit leaf weight (LDMC). Leaves of shade-tolerant species are often small and relatively thick (high LMA) and costly (high LDMC). Shade-tolerant species are suggested to protect their initially expensive biomass investment to the leaves. Their leaves are expensive as carbon assimilation in the shade is limited by low light availability, low photosynthetic rates and low respiration rates. The payback time for leaves of shade-tolerant species is thus often much longer than that of light-demanding species.

A possible explanation of why I did not find differences between functional groups in LMA, LDMC and the related leaf toughness, could be the fact that the a-priori shade-tolerance group classification included both long-lived pioneers and early successional pioneers as light-demanding species and compared them with shade-tolerant species, whereas other studies frequently compare ´true´ early pioneers with ´true´ shade-tolerant species, from the extremes of the light gradient. As shade-tolerance groups are probably less profound because of the deciduous character of the Chiquitano dry forest, these extremes of the light gradient are not found. During the dry season the forest canopy harbors virtually no leaves (Poorter, pers. comm.), because of the many drought-avoiding, deciduous species that dominate it (tab. 2.) and

although limited information is available on this specific forest type, relatively low leaf area indices (LAR) and high percentages of daylight penetration have also been reported in semi-deciduous dry forests during the wet season (review in Coomes and Grubb, 2000). Mean yearly light availability may thus not be so distinct and important in this ecosystem as I initially anticipated, down weighting the need for species to specialize for a certain strategy to tolerate shade. Plastic morphological adjustments to the light regime a species encounters at any given time during the year are probably more important than long term morphological adaptations.

In line with my hypotheses, deciduousness and whether leaves were simple or compound significantly contributed to shade-tolerance group separation. Out of 12 light-demanding species 8 exhibit a deciduous leaf habit and 4 out of 10 intermediate shade-tolerant species and only 3 out of 19 shade-tolerant species were deciduous (χ^2 = 8,27, df = 2, p < 0,05) (fig. aA, app. II). A deciduous leaf habit minimizes water loss during the dry season (Chabot and Hicks, 1982). Popma *et al.* (1992) also reported a high frequency of deciduousness among light-demanding species in a tropical wet forest. Light-demanding species typically grow in the more open and drier habitats within the dry forest ecosystem and are better adapted to avoid drought stress during the dry season than do shade-tolerant species. Differences in leaf characteristics between deciduous an evergreen leaves can be viewed in appendix II, table aA.

Out of 12 light-demanding species 8 had a compound leaf type, 3 out of 10 intermediate shade-tolerant species and only 4 out of 19 shade-tolerant species were have a compound leaf type (χ^2 = 6,84, df = 2, p < 0,05) (fig. aB, app. II). Givnish (1978) suggested that compound-leaved taxa are early-successional light-demanders and this hypothesis was later verified and tested (Niinemets, 1998). The latter research compilation found few late-successional or very shade-tolerant temperate trees with compound leaves, though many mid-successional ones.

Dissection and lobbing of a single leaf into individual leaflets was found to be adaptive in environments where evaporative demand is high, because it diminishes effective leaf size and increases leaf slenderness (Niinemets, 1998). This is in line with my results that show that compound leaflets are significantly smaller that simple leaves. However I did not find an increased slenderness. Reduction of wind-induced transpirational water loss in the dry forest habitat may explain this. I did not find significant differences between simple and compound leaves in terms of biomass investment either (tab. aB).

Finally I think that the blade length fraction, although it significantly contributed to shade-tolerance group classification, is not a good functional trait to be used. I derived BLF by dividing the total length of the entire leaf by the length of the petiole. Its values are probably too much dependent upon genotypic differences between entire compound and simple leaved species and species classification relies thus too much upon the biased spread of compound leaves among functional groups (cf. above).

FUNCTIONAL GROUPS, DROUGHT-TOLERANCE

Drought-tolerance groups could not significantly be separated based on the characteristics I included in the CDA. Boundaries between the group territories (fig. 5a) are not discrete. Leaf width, slenderness, LMA and petiole length significantly differed among groups.

Leaves of drought-avoiding species were broadest and least slender and had the longest petioles. Their leaves had a lower LMA than drought-intolerant species. Drought-tolerant species had the smallest width and a low LMA while drought-intolerant species had the highest LMA. Their leaf area was average and in-between that of the other two groups (tab. 8).

The slender leaves of drought-tolerant species are in line with my hypotheses. Overheating is a severe risk when water for transpiration is scarce (Smith, 1978). Smaller and more slender leaves increase drought-tolerance, as they decrease the amount of heat induced transpirational water loss through convective cooling. Still this reduction of heat induced transpiration may be in trade-off with wind induced transpiration (cf. above, shade-tolerance). Although models of leaf size have predicted decreasing sizes with increasing temperature and decreasing water availability (e.g Parkhurst and Louks, 1972) and found empirical evidence for this decrease (Werger and Ellenbroek, 1978) or found a decrease in the area to volume ratio of leaves (Roderick *et al.*, 2000), I did not find significant leaf area differences among species groups.

Drought-intolerant species were expected to have bigger leaf sizes than drought-avoiding species, because they grow in habitats within the dry forest with a higher soil water availability, allowing drought-intolerant species to maintain relatively high transpiration rates. My results imply an opposite picture, drought-avoiding species had marginally the biggest leaf sizes.

As all drought-avoiding species in this study have a deciduous leaf habit it may well be that they need not to be extremely cautious with their water use. Leaves are deployed during the wet season and they need to make optimal use of the limited time they have to photosynthesize. Big leaves, combined with a low LMA, are better adapted to increase light intercept, establish high photosynthetic rates, optimize carbon balance and as such reduce the pay back time of their leaves. By the time that water becomes scarce again, drought-avoiding species shed the leaves. Strong relations between LMA and leaf life span are reported for Australian woody species from dry habitats (Wright and Cannon, 2001; Wright and Westoby, 2002; Wright *et al.*, 2002). Low LMA, high photosynthetic capacity and faster turnover of plant parts permits a more flexible response to the spatial patchiness of light and soil nutrient resources, giving low LMA species short term advantages over high LMA species (Wright *et al.*, 2002).

Drought-avoiding species had the longest petioles and drought-intolerant species the shortest. This is not in line with my hypothesis, where I expected drought-intolerant species to have the longest petioles, in order to forage for light in their relatively wetter habitats with greater tree densities, and the shortest petioles in drought-tolerant species.

The fact that petioles are relatively cheap in terms of carbon and mineral nutrient investments required, compared to durable branches, but at the same time functionally equivalent (Niinemets, 1998), may explain why they are longer in drought-avoiding species. As discussed above, drought-avoiding species need to make optimal use of the limited time they have to photosynthesize. Investing heavily in branching in order to secure light interception may as such be an unfavorable strategy. Instead drought-avoiding species invest relatively more in petioles to establish their crown.

One might argue that the longer petioles found in the drought-avoiding species group are the results of the high proportion of compound leaved species in this group (fig. b, app. II). Still leaf type distribution did not significantly differ among the three drought-tolerance groups (χ^2 = 3,69, df = 2, p > 0,1) (fig. b, app. II), as a relatively large proportion of compound leaved species is also found within the drought-tolerant group. Petioles of drought-avoiding and drought-tolerant species do significantly differ, still the trend of shorter petioles in the latter group is eminent (tab. 8).

Two examples of simple leaved drought-avoiding species with exceptionally long petioles are *Jacaratia sp.* and *Manihot guaranitica* subsp. *guaranitica*, I personally observed in the field that these species hardly show any branching until later during their life cycle. Future measurements of biomass investment to the petiole in relation to that of the leaf blade or folioles could shed more light on this matter.

SHADE-TOLERANCE VERSUS DROUGHT-TOLERANCE

Is it true that species that seemingly choose to follow a certain strategy to tolerate shade put restrictions on their capacity to tolerate drought? The design of my study can not answer this question, still the distribution of shade-tolerance groups among drought-tolerance groups may give some insight on this important topic in the continuum of the project.

Shade-tolerance tends to be associated with the drought-tolerance groups, although the P-levels are at the edge of significance (χ^2 = 3,69, df = 2, 0, p = 0,058). As much as 53% of the drought-avoiding species were also light-demanding, while large proportions of both drought-intolerant and drought-tolerant species were shade-tolerant, 69% and 54% respectively The lowest percentage of light-demanding species (8%) was found within the drought-intolerant species group (fig. b, app. II). This suggests that possible trade-offs exists between (1) drought-avoidance and the ability to persist in the shade, (2) drought-intolerance and light-demand, but also between (3) drought-tolerance and light-demand. Especially the deciduous leaf habit of drought-avoiding species lures them from the shade where durable leaves are needed to pay back initial construction costs. Drought-intolerant species grow in relatively moist and densely occupied habitats, were species that need a lot of light to grow and function can not survive. The ability to tolerate drought is favored by maintaining low transpiration rates, light-demanding species need relatively high transpiration to increase their carbon assimilation. As many light-demanding species in the Chiquitano dry forest have a deciduous leaf habit they can maintain relatively high transpiration, because their leaves are deployed during the wet season, when water is not a limited resource.

Conclusions

- Leaves of tree species are found to vary greatly under influence of different factors. Variability in morphological leaf characteristics is explained most by differences among species. Still different light availability and individual differences among trees also explain some of the variation. Leaves within individual trees do not differ from on and other.

- Sun-leaves are smaller than shade-leaves to promote cooling of the convective area, still they are not more slender as wind-induced transpiration needs to be minimal. Sun-leaves are thicker to reduce heat-induced transpirational water loss, with higher biomass invested per unit photosynthetic area and per unit leaf weight. Consequently sun-leaves are tougher than shade-leaves, better protected against wind-induced damage and have greater herbivore resistance. Petioles are longer in the shade, as an adjustment to forage for light in the forest understory, where internodes are shorter, as they are more expensive to make because carbon assimilation is limited.

- Shade-tolerance groups differ most in adult stature, leaf habit and leaf type. Shade-tolerant species are small compared to light-demanding and intermediate shade-tolerant species. Light-demanding species harbor a greater proportion of species with deciduous and compound leaves. They have longer petioles, both absolute and in relation to the leaf blade.

- Most of the morphological traits that I expected to differ between shade-tolerance groups did not contribute to their discrimination. As light availability is probably not a limiting factor in the relatively open dry forest habitat, the urge of species to adapt to a given strategy to tolerate shade is over ruled by adaptations that influence their ability to tolerate drought.

- Drought tolerance groups differed most in their leaf slenderness, LMA and length of the petiole. Drought-tolerant species had the most slender and marginally the smallest leaves and are thus better equipped to reduce the heat load of the leaves by cooling of the convective area. The unexpected high LMA of drought-intolerant species may reflect an adaptation to increase herbivore resistance, as these species grow in habitats within the dry forest with relatively high soil water availability, high densities of other trees and probably high densities of herbivorous insects.

- The deciduous leaf habit of drought-avoiding species puts emphasis on their need of efficient usage of the limited time they have to photosynthesize. Drought-avoiding species as such invested minimal biomass to their leaves, decreasing their payback time. Petiole tissue is relatively cheap compared to branch tissue. By forming relatively long petioles drought-avoiding species have to invest less in branch formation to increase light interception and optimize carbon balance.

- Possible trade-offs exists between drought-avoidance and the ability to persist in the shade, drought-intolerance and light-demand, and between drought-tolerance and light-demand.

Acknowledgements

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Appendix I

Species	Family	Shade-tolerance	Drought-tolerance	Value	a	b	c	d	e	f	g	h	i	j	k	l
Astronium uriundeuva	Anacardiaceae	LD	DA	Sun	6,60	3,53	16,42	195,99	19,46	1,88	0,39	92,80	3,73	1,86	0,82	5,32
				Shade	6,50	3,59	15,24	194,56	17,94	1,84	0,37	81,13	3,76	1,65	0,81	5,54
				SHSU-ratio	0,99	1,02	0,93	0,99	0,92	0,98	0,95	0,87	1,01	0,89	0,99	1,04
Spondias mombin	Anacardiaceae	LD	DA	Sun	10,84	3,99	24,68	223,90	35,75	2,72	0,23	57,80	6,14	3,12	0,85	3,57
				Shade	10,84	4,31	24,86	205,23	34,92	2,54	0,23	56,77	6,31	0,96	0,84	1,29
				SHSU-ratio	1,00	1,08	1,01	0,92	0,98	0,94	0,97	0,98	1,03	0,31	0,99	0,36
Aspidosperma cylindrocarpon	Apocynaceae	IS	DT	Sun	10,75	4,61	35,56	193,29	30,14	2,32	0,32	64,37	1,64	1,11	0,90	5,54
				Shade	12,92	5,58	49,78	191,90	36,39	2,34	0,34	70,92	1,97	1,02	0,87	4,77
				SHSU-ratio	1,20	1,21	1,40	0,99	1,21	1,01	1,08	1,10	1,20	0,92	0,97	0,86
Aspidosperma tomentosum	Apocynaceae	IS	DA	Sun	9,42	5,23	32,34	193,80	25,04	1,82	0,31	77,52	0,41	0,49	0,98	1,95
				Shade	11,47	6,22	48,65	172,72	24,07	1,86	0,30	68,99	0,39	0,32	0,97	1,12
				SHSU-ratio	1,22	1,19	1,50	0,89	0,96	1,02	0,98	0,89	0,95	0,65	0,99	0,57
Tabebuia impetiginosa	Bignoniaceae	LD	DA	Sun	14,06	7,09	58,29	219,08	39,96	2,04	0,31	78,68	8,86	4,15	0,74	8,54
				Shade	15,40	6,79	58,68	189,10	35,35	2,27	0,25	53,40	10,00	3,18	0,71	8,21
				SHSU-ratio	1,10	0,96	1,01	0,86	0,88	1,12	0,82	0,68	1,13	0,77	0,96	0,96
Capparis prisca	Capparaceae	ST	DI	Sun	20,25	8,55	144,52	250,57	50,64	2,43	0,39	106,10	5,84	1,49	0,79	3,31
				Shade	21,35	8,79	132,59	219,84	49,22	2,46	0,35	86,61	7,20	1,95	0,75	5,03
				SHSU-ratio	1,05	1,03	0,92	0,88	0,97	1,01	0,90	0,82	1,23	1,31	0,95	1,52
Jacaratia sp.	Caricaceae	ST	DA	Sun	15,01	16,08	98,84	158,12	15,33	0,94	0,14	20,56	11,56	2,41	0,57	4,85
				Shade	13,86	14,27	88,24	159,64	15,45	0,98	0,16	16,42	10,18	1,73	0,58	2,34
				SHSU-ratio	0,92	0,89	0,89	1,01	1,01	1,04	1,14	0,80	0,88	0,72	1,02	0,48
Combretum leprosum	Combretaceae	ST	DT	Sun	13,28	8,65	89,62	178,82	36,19	1,50	0,34	59,93	1,44	3,30	0,88	13,08
				Shade	16,53	10,12	122,51	164,21	31,87	1,65	0,29	52,69	1,40	5,92	0,92	25,40
				SHSU-ratio	1,24	1,17	1,37	0,92	0,88	1,10	0,87	0,88	0,98	1,80	1,05	1,94
Erithroxylum sp.	Erythroxylaceae	ST	DT	Sun	5,66	2,68	10,97	125,22	25,68	2,12	0,33	40,78	0,29	0,63	0,95	8,33
				Shade	6,38	3,16	14,31	121,29	23,09	2,03	0,38	37,57	0,31	0,96	0,95	13,75
				SHSU-ratio	1,13	1,18	1,31	0,97	0,90	0,96	1,15	0,92	1,10	1,53	1,00	1,65
Actinostemon conceptionis	Euphorbiaceae	ST	DT	Sun	6,97	3,74	19,73	137,54	27,01	1,87	0,29	35,87	1,10	1,58	0,86	16,57
				Shade	7,35	3,92	21,98	122,81	24,34	1,99	0,26	31,19	1,16	1,31	0,87	11,01
				SHSU-ratio	1,05	1,05	1,11	0,89	0,90	1,07	0,90	0,92	1,05	0,83	1,01	0,66
Manihot guaranitica subsp. *guaranitica*	Euphorbiaceae	LD	DA	Sun	16,37	19,01	132,36	196,72	25,56	0,86	0,26	50,71	16,28	7,84	0,52	9,32
				Shade	18,51	20,95	225,10	149,23	22,44	0,88	0,21	39,74	19,48	6,52	0,49	7,28
				SHSU-ratio	1,13	1,10	1,70	0,76	0,88	1,02	0,83	0,78	1,20	0,83	0,94	0,78
Phyllanthus sp. nov.	Euphorbiaceae	ST	DT	Sun	6,42	3,20	16,28	116,21	29,06	2,17	0,29	35,87	0,63	1,94	0,92	8,45
				Shade	6,53	3,40	17,24	114,94	21,97	1,98	0,34	34,70	1,00	1,39	0,87	8,96
				SHSU-ratio	1,02	1,06	1,06	0,99	0,76	0,92	1,19	0,97	1,58	0,72	0,95	1,06
Acosmium cardenasii	Fabaceae	IS	DT	Sun	2,41	0,76	1,44	134,11	19,47	3,22	0,33	59,14	1,64	0,81	0,88	4,76
				Shade	2,34	0,73	1,20	124,71	23,82	3,22	0,30	40,18	1,49	1,39	0,89	6,20
				SHSU-ratio	0,97	0,96	0,83	0,93	1,22	1,00	0,90	0,68	0,91	1,72	1,01	1,30
Caesalpinia pluviosa	Fabaceae	LD	DT	Sun	6,84	1,82	7,47	121,79		3,87	0,45	68,69	2,08	2,55	0,90	10,72
				Shade	6,59	1,84	7,53	99,57		3,64	0,42	55,14	2,43	1,55	0,88	6,88
				SHSU-ratio	0,96	1,01	1,01	0,82		0,94	0,92	0,80	1,17	0,61	0,98	0,64
Centrolobium microchaete	Fabaceae	LD	DT	Sun	8,05	4,05	20,59	135,13	19,84	2,00	0,27	46,07	6,08	2,90	0,84	4,93
				Shade	11,35	5,24	38,43	140,08	26,80	2,17	0,19	27,40	8,45	3,41	0,82	6,98
				SHSU-ratio	1,41	1,29	1,87	1,04	1,35	1,09	0,69	0,59	1,39	1,18	0,98	1,42
Guibourtia chodatiana	Fabaceae	IS	DI	Sun	6,43	3,28	16,33	169,29	37,05	1,97	0,42	79,13	1,63	2,08	0,81	15,89
				Shade	6,07	2,97	13,19	173,90	39,76	2,06	0,41	78,81	1,48	1,50	0,81	13,12
				SHSU-ratio	0,94	0,91	0,81	1,03	1,07	1,05	0,97	1,00	0,91	0,72	1,00	0,83
Platymiscium fragrans	Fabaceae	LD	DA	Sun	7,32	3,75	17,95	199,14	31,73	2,01	0,32	63,74	3,28	5,56	0,87	14,37
				Shade	9,56	4,83	30,62	191,52	30,13	1,99	0,28	55,91	4,29	5,62	0,84	12,29
				SHSU-ratio	1,31	1,29	1,71	0,96	0,95	0,99	0,89	0,88	1,31	1,01	0,97	0,86
Sweetia fruticosa	Fabaceae	IS	DA	Sun	3,54	1,83	4,56	172,85	36,26	1,96	0,37	90,09	1,96	1,50	0,87	8,71
				Shade	3,57	1,78	4,46	149,48	20,17	2,02	0,39	58,52	1,82	1,21	0,88	5,99
				SHSU-ratio	1,01	0,97	0,98	0,86	0,56	1,03	1,05	0,65	0,93	0,80	1,01	0,69
Casearia gossypiosperma	Flacourtiaceae	IS	DA	Sun	9,64	4,39	29,42	123,06	31,55	2,22	0,37	50,99	0,75	1,47	0,93	11,43
				Shade	9,35	4,08	27,02	119,38	25,95	2,30	0,34	44,23	0,74	1,33	0,93	11,00
				SHSU-ratio	0,97	0,93	0,92	0,97	0,82	1,04	0,92	0,87	0,99	0,90	1,00	0,96
Cariniana ianeirensis	Lecythidaceae	IS	DA	Sun	13,14	7,32	70,56	145,67	33,84	1,79	0,31	48,50	1,14	3,36	0,92	13,22
				Shade	13,94	7,09	70,65	136,02	31,85	1,97	0,30	45,88	1,08	2,98	0,93	15,68
				SHSU-ratio	1,06	0,97	1,00	0,93	0,94	1,10	0,98	0,95	0,94	0,89	1,01	1,19
Chorisia speciosa	Malvaceae	LD	DA	Sun	8,91	3,96	19,67	191,64	26,72	2,26	0,26	57,60	7,79	1,43	0,66	4,07
				Shade	10,20	4,10	35,28	176,91	22,09	2,46	0,22	39,99	9,71	1,27	0,64	2,38
				SHSU-ratio	1,14	1,04	1,79	0,92	0,83	1,09	0,85	0,69	1,25	0,89	0,97	0,58

Data summary.   The appendix shows functional group classification and mean leaf trait-values for sun and shade leaves and (untransformed) SHSU-ratios per species. Shade-tolerance; LD = light-demanding species; IS = intermediate shade-tolerant species; S = shade-tolerant species. Drought-tolerance; DA = drought-avoiding species; DI = drought-intolerant DT = drought-tolerant species. Leaf traits; **a**, leaf length (cm); **b**, leaf width (cm); **c**, leaf area (cm^2); **d**, leaf thickness (µm)**; e**, leaf toughness (N cm^{-2}) ; **f**, leaf shape index (cm cm^{-1}); **g**, leaf dry matter content (g g^{-1}); **h**, leaf mass per area (g m^{-2}); **i**, petiole length (cm)**; j**, internode length (cm); **k**, blade length fraction (cm cm^{-1}); **l**, Specific internode length (cm cm^{-1}). Parameters are mean trait-values from 5 individual trees per species per light environment.

Species	Family	Shade-tolerance	Drought-tolerance	Value	a	b	c	d	e	f	g	h	i	j	k	l
Eriotheca roseorum	Malvaceae	LD	DA	Sun	18,18	10,38	84,76	191,90	42,27	1,76	0,26	54,99	13,56	1,11	0,71	1,58
				Shade	17,71	9,98	75,42	188,98	42,20	1,83	0,22	52,95	12,48	1,47	0,70	1,88
				SHSU-ratio	0,97	0,96	0,89	0,98	1,00	1,04	0,84	0,96	0,92	1,32	0,99	1,19
Trichilia elegans	Meliaceae	ST	DT	Sun	7,15	2,90	12,27	223,52	32,88	2,48	0,35	70,50	3,91	1,45	0,78	4,57
				Shade	7,62	3,38	15,50	166,62	27,60	2,31	0,23	46,49	4,03	1,05	0,79	4,61
				SHSU-ratio	1,07	1,17	1,26	0,75	0,84	0,93	0,65	0,66	1,03	0,72	1,01	1,01
Myrciaria cauliflora	Myrtaceae	ST	DI	Sun	3,11	1,44	3,43	174,37	22,68	2,18	0,34	71,30	0,19	1,17	0,94	19,39
				Shade	3,63	1,69	4,45	139,70	18,31	2,15	0,19	48,36	0,19	1,20	0,95	34,45
				SHSU-ratio	1,17	1,17	1,30	0,80	0,81	0,99	0,58	0,68	0,99	1,02	1,01	1,78
Myrciaria floribunda	Myrtaceae	IS	DT	Sun	4,49	1,97	6,12	200,03	17,82	2,31	0,20	40,94	0,21	1,75	0,96	17,96
				Shade	4,46	2,05	6,30	193,29	16,77	2,18	0,21	46,57	0,23	1,91	0,95	23,06
				SHSU-ratio	0,99	1,04	1,03	0,97	0,94	0,94	1,07	1,14	1,10	1,09	0,99	1,28
Bougainvillea modesta	Nyctanginaceae	LD	DI	Sun	8,19	5,74	33,23	230,51	28,04	1,45	0,25	56,68	2,41	1,63	0,79	4,42
				Shade	8,18	5,71	32,78	224,79	23,38	1,45	0,26	64,44	2,27	1,26	0,79	4,79
				SHSU-ratio	1,00	0,99	0,99	0,98	0,83	1,00	1,03	1,14	0,94	0,77	1,00	1,08
Neea hermafrodita	Nyctanginaceae	ST	DI	Sun	8,61	4,10	23,79	245,87	26,11	2,12	0,24	71,59	1,12	2,80	0,89	9,27
				Shade	9,97	4,77	32,17	218,95	26,72	2,10	0,25	60,79	1,23	2,38	0,89	11,88
				SHSU-ratio	1,16	1,16	1,35	0,89	1,02	0,99	1,01	0,85	1,10	0,85	1,00	1,28
Ouratea sp.	Ochnaceae	ST	DI	Sun	13,20	5,94	60,90	293,24	84,95	2,29	0,37	109,27	0,95	3,10	0,93	15,23
				Shade	14,80	7,29	81,97	281,31	78,49	2,09	0,42	114,74	0,94	3,24	0,94	13,62
				SHSU-ratio	1,12	1,23	1,35	0,96	0,92	0,92	1,12	1,05	1,00	1,05	1,01	0,89
Gallesia integrifolia	Phytolaccaceae	IS	DI	Sun	11,86	5,33	43,41	187,83	17,56	2,25	0,23	51,64	2,44	1,48	0,83	7,83
				Shade	12,08	5,34	45,51	191,39	12,98	2,26	0,21	42,68	2,80	0,89	0,81	3,36
				SHSU-ratio	1,02	1,00	1,05	1,02	0,74	1,00	0,89	0,83	1,15	0,60	0,98	0,43
Pogonopus tubulosus	Rubiaceae	ST	DA	Sun	16,51	9,72	101,22	196,47	10,44	1,72	0,20	41,41	1,71	2,54	0,91	8,01
				Shade	15,77	9,75	99,66	171,32	11,16	1,66	0,20	35,46	1,41	1,72	0,92	6,01
				SHSU-ratio	0,96	1,00	0,98	0,87	1,07	0,96	0,98	0,86	0,82	0,68	1,01	0,75
Simira rubescens	Rubiaceae	ST	DA	Sun	14,20	7,39	66,20	161,29	29,37	1,94	0,29	49,63	0,70	0,40	0,95	1,51
				Shade	13,67	6,88	60,37	141,73	31,45	2,00	0,30	43,08	0,68	0,29	0,95	1,22
				SHSU-ratio	0,96	0,93	0,91	0,88	1,07	1,03	1,04	0,87	0,97	0,74	1,00	0,81
Esenbeckia almawillia	Rutaceae	ST	DI	Sun	5,90	2,07	8,70	216,92	25,59	2,86	0,36	66,63	0,60	1,48	0,91	8,84
				Shade	7,72	2,66	15,11	201,80	30,89	2,91	0,31	65,74	0,64	1,90	0,92	11,66
				SHSU-ratio	1,31	1,29	1,74	0,93	1,21	1,02	0,88	0,99	1,06	1,28	1,01	1,32
Galipea ciliata	Rutaceae	ST	DT	Sun	5,02	2,57	10,27	275,72	31,29	1,96	0,23	63,58	2,86	0,78	0,74	3,49
				Shade	8,03	3,56	21,95	196,34	27,20	2,24	0,21	42,82	3,78	0,85	0,76	4,25
				SHSU-ratio	1,60	1,39	2,14	0,71	0,87	1,14	0,92	0,67	1,32	1,09	1,03	1,22
Zanthoxylum monogynum	Rutaceae	ST	DI	Sun	6,52	2,69	10,56	202,18	31,85	2,49	0,20	44,16	2,74	1,97	0,81	8,45
				Shade	7,99	3,25	14,52	175,26	28,66	2,51	0,21	42,60	3,02	1,11	0,82	5,09
				SHSU-ratio	1,23	1,21	1,38	0,87	0,90	1,01	1,08	0,96	1,10	0,56	1,01	0,60
Talisia esculenta	Sapindaceae	ST	DT	Sun	10,15	4,56	23,46	167,64	35,08	2,38	0,34	55,27	6,59	2,03	0,73	5,26
				Shade	13,16	4,92	41,38	135,26	38,27	2,68	0,31	50,45	5,60	1,11	0,80	3,68
				SHSU-ratio	1,30	1,08	1,76	0,81	1,09	1,13	0,92	0,91	0,85	0,55	1,10	0,70
Chrysophyllum gonocarpum	Sapotaceae	ST	DI	Sun	19,49	7,31	101,38	150,75	52,20	2,69	0,35	68,09	1,69	1,58	0,92	5,45
				Shade	16,38	5,27	63,19	149,23	52,33	3,18	0,30	59,83	1,34	1,16	0,92	5,39
				SHSU-ratio	0,84	0,72	0,62	0,99	1,00	1,18	0,86	0,88	0,79	0,73	1,00	0,99
Pouteria gardneriana	Sapotaceae	ST	DI	Sun	22,38	6,73	106,24	193,04	61,58	3,33	0,36	80,25	1,77	1,75	0,93	4,66
				Shade	16,86	6,11	70,24	188,28	66,61	2,81	0,30	69,30	1,34	1,30	0,93	5,07
				SHSU-ratio	0,75	0,91	0,66	0,98	1,08	0,84	0,85	0,86	0,76	0,74	1,00	1,09
Solanum cf. riparium	Solanaceae	LD	DT	Sun	17,42	8,35	95,40	376,18	32,50	2,10	0,20	69,68	2,13	1,02	0,90	1,75
				Shade	25,78	12,52	198,73	212,22	16,35	2,07	0,22	57,49	2,01	1,36	0,93	2,55
				SHSU-ratio	1,48	1,50	2,08	0,56	0,50	0,99	1,08	0,83	0,94	1,34	1,03	1,46
Ampelocera ruizii	Ulmaceae	ST	DI	Sun	11,27	5,25	42,22	127,76	39,77	2,15	0,36	59,56	0,53	2,10	0,95	15,19
				Shade	11,30	5,69	47,24	122,94	35,65	1,99	0,27	41,40	0,62	2,18	0,95	17,63
				SHSU-ratio	1,00	1,08	1,12	0,96	0,90	0,93	0,73	0,70	1,17	1,04	1,00	1,16
Phyllostylon rhamnoides	Ulmaceae	IS	DI	Sun	5,49	3,21	14,12	192,28	20,97	1,73	0,33	72,51	0,26	1,15	0,95	10,91
				Shade	5,26	3,06	12,38	172,98	21,77	1,72	0,34	62,46	0,31	1,11	0,94	14,71
				SHSU-ratio	0,96	0,95	0,88	0,90	1,04	1,00	1,04	0,86	1,19	0,97	0,99	1,35
Urera baccifera	Urticaceae	LD	DA	Sun	17,86	12,37	144,77	281,31	19,55	1,45	0,15	43,36	6,86	2,22	0,73	3,89
				Shade	22,32	17,57	287,13	203,84	14,81	1,30	0,11	24,62	12,92	2,71	0,64	3,01
				SHSU-ratio	1,25	1,42	1,98	0,72	0,76	0,90	0,74	0,57	1,88	1,22	0,88	0,77

Data summary (continued). The appendix shows functional group classification and mean leaf trait-values for sun and shade leaves and (untransformed) SHSU-ratios per species. Shade-tolerance; LD = light-demanding species; IS = intermediate shade-tolerant species; S = shade-tolerant species. Drought-tolerance; DA = drought-avoiding species; DI = drought-intolerant DT = drought-tolerant species. Leaf traits; leaf length (cm); **b**, leaf width (cm); **c**, leaf area (cm^2); **d**, leaf thickness (µm); **e**, leaf toughness (N cm^{-2}) ; **f**, leaf shape index (cm cm^{-1}); **g**, leaf dry matter content (g g^{-1}); **h**, leaf mass per area (g m^{-2}); **i**, petiole length (cm); **j**, internode length (cm); **k**, blade length fraction (cm cm^{-1}); **l**, Specific internode length (cm cm^{-1}). Parameters are mean trait-values from 5 individual trees per species per light environment.
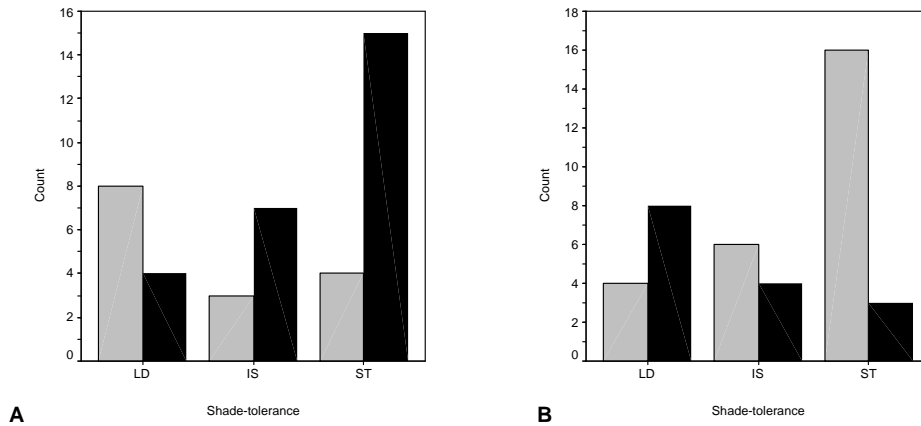
Appendix II

A

B

Figure a. **Leaf type and habit distribution among shade-tolerance groups.** The bars represent numbers of species in this study with (A) compound (●) or simple leaves (●) and (B) evergreen (●) or deciduous leaves (●); LD = light-demanding, IS = intermediate shade-tolerant, ST = shade-tolerant.

	ANOVA							
	Evergreen leaves			**Deciduous leaves**				
Trait	**n**	**mean**	**se**	**n**	**mean**	**se**	**F**	**Sig.**
Leaf length (cm) ^{2}	26	8,23 ±	1,11	15	11,16 ±	1,12	**3**	**ns**
Leaf width (cm) ^{2}	26	3,69 ±	1,12	15	6,42 ±	1,18	8	**
Leaf shape index (cm cm^{-1})	26	2,32 ±	0,11	15	1,82 ±	0,12	9	**
Leaf area (cm^2) ^{2}	26	21,48 ±	1,25	15	42,58 ±	1,28	4	ns
Petiole length (cm) ^{2}	26	1,35 ±	1,22	15	3,35 ±	1,36	7	*
Blade length fraction (cm cm^{-1})	26	0,87 ±	0,01	15	0,80 ±	0,04	5	*

A

	ANOVA							
	Simple leaves			**Compound leaves**				
Trait	**n**	**mean**	**se**	**n**	**mean**	**se**	**F**	**Sig.**
Leaf length (cm) ^{2}	26	10,53 ±	1,11	15	7,28 ±	1,14	5	*
Leaf width (cm) ^{2}	26	5,47 ±	1,13	15	3,25 ±	1,17	7	*
Leaf shape index (cm cm^{-1})	26	2,02 ±	0,11	15	2,33 ±	0,15	3	ns
Leaf area (cm^2) ^{2}	26	39,49 ±	1,23	15	14,82 ±	1,28	9	**
Petiole length (cm)	26	2,49 ±	0,74	15	4,86 ±	0,86	4	ns
Blade length fraction (cm cm^{-1})	26	0,87 ±	0,02	15	0,80 ±	0,02	5	*

B

Table a. **Leaf type and leaf habit.** The tables show significant and marginal (0,1 > p > 0,05) differences in mean leaf trait values between deciduous and evergreen leaves (A) and simple and compound leaves resulting from a one-way ANOVA; the petiole length and blade length fraction for compound leaves were not derived from the leaflets but from the whole leaf; ^{2} Traits were log_{10}-transformed to improve normality.
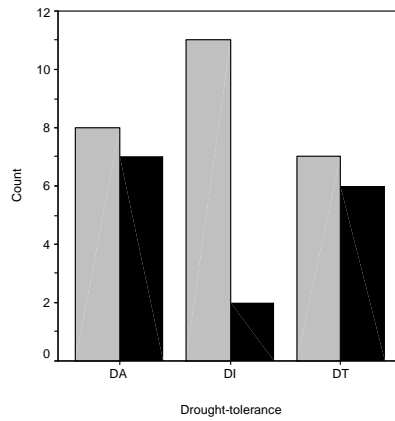
Figure b.   **Leaf type distribution among drought-tolerance groups.** The bars represent numbers of species in this study with simple (●) or compound leaves (●); DA = Drought-avoiding, DI = Drought-intolerant, DT = Drought-tolerant.
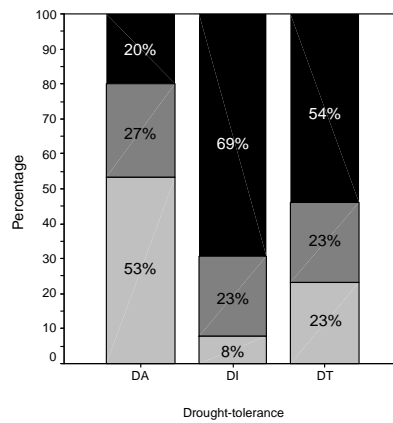

Figure c.   **Shade-tolerance distribution among drought-groups.** The bars represent percentages species within drought-tolerance groups that are either light-demanding (●); intermediate shade-tolerant (●) or shade-tolerant (●); DA = Drought-avoiding, DI = Drought-intolerant, DT = Drought-tolerant.

Appendix III

Cuchi
Astronium urundeuva

Ocorocillo
Spondias mombin

Jichituriqui colorado
Apidosperma cylindrocarpon

Jichituriqui amarillo
Apidosperma tomentosum

Tajibo negro
Tabebuia impetiginosa

Pacobillo
Capparis prisca

Chayote
Jacaratia sp.

Carne de toro
Combretum leprosum

Coca typo Don Israel
Erithroxylum sp.

Yucca
Manihot guaranitica subsp. *guaranitica*

Tasaa
Acosmium cardenasii

Momoqui
Caesalpinia pluviosa

Tarara amarilla
Centrolobium microcaete

Sirari
Guibourtia chodatiana

Tarara colorada
Platymiscium frafrans

Mani
Sweetia fruticosa

Cuse
Casearia gossypiosperma

Yesquero blanco
Cariniana ianeirensis

Toborochi
Chorisia speciosa

Pequi blanco
Eriotheca roseorum

Guapuru
Myrciaria cauliflora

Sahuinto
Myrciaria floribunda

Comomosi
Bourgainvillea modesta

Mapabi
Neea hermafrodita

Primo de Guapomo
Ouratea sp.

Quina
Pogonopus tubulosus

Gabetillo blanco
Simira rubescens

Coca
Esenbeckia almawillia

Blanquillo falso
Galipea ciliata

Naranjillo
Zanthoxylum monogynum

Piton
Talisia esculenta

Aguai fruta chica
Chrysophyllum gonocarpum

Aguai fruta grande
Pouteria gardneriana

Tabacachi
Solanum cf. riparium

Blanquillo
Ampelocera ruizii

Cuta
Phyllostylon rhamnoides

Pica pica
Urera baccifera