DROUGHT TOLERANCE OF TROPICAL TREE SPECIES

Functional Traits, Trade-offs and Species Distribution

Lars Markesteijn

THESIS COMMITEE

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Wageningen University

THESIS CO-SUPERVISOR

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To my parents for giving me life
To Estrella for giving it meaning
To Jacqueline for giving it a motto

Geniet van het leven
Enjoy life
Disfrute la vida

Abstract

Tropical forests occur under rainfall regimes that vary greatly in the rainfall pattern and frequency and intensity of drought. Consequently water availability is one of the most important environmental factors influencing community structure, species composition, and plant functioning across large-scale rainfall gradients and small-scale topographic gradients within forests. The relative success of tree species to establish along these gradients of water availability and their success in dealing with future changes in water availability will depend on how they are adapted to tolerate drought.

In this dissertation I applied a multi-species, multi-trait approach in field studies and a controlled experiment to give detailed information on the mechanisms of drought-tolerance of a large set of tropical dry and moist forest tree species. The following research questions were addressed; 1) How do dry and moist forests differ in soil water availability? 2) How are dry and moist forest species adapted to drought and what different drought-strategies can be distinguished? 3) Is there a trade-off between drought- and shade-tolerance? and 4) How do drought- and shade-tolerance determine local and regional tree species distribution?

Dry season soil water availability is clearly lower in the dry forest than in the moist forest. Especially in the dry forest there is a lot of temporal and spatial variation in soil water availability. Temporal variation depends on the annual cycle of precipitation. Spatial heterogeneity is two-dimensional; 1) water availability varies with topography of the landscape; elevated crests are dry in comparison to slopes and low valleys, and 2) soil water is vertically redistributed with soil depth; in the dry season more water is available in deep soil layers while in the wet season most water is found in the top soil. When combining temporal and spatial dimensions, a complex mosaic of soil water availability emerges that shows great potential for niche partitioning among species at various levels, if species are adapted to exploit this variation.

Seedlings of dry forest species have evolved mechanisms that enhance their access to water in deep soil layers, increase drought-induced cavitation resistance and increase water conservation. Seedlings of moist forest species show adaptations that improve their light foraging capacity and increase nutrient and water acquisition. Associations among functional traits show that there are three major drought strategies among tropical tree species, 1) physiological drought-tolerance, 2) drought-intolerance and 3) drought-avoidance.

No conclusive evidence for a direct trade-off between species drought- and shade-tolerance was found, and the association between drought- and shade-tolerance is mainly subject to the scale of observation. On small scales, within the dry forest, drought- and shade-tolerance are positively related, as species hydraulic properties are integrally linked with niche differentiation for both light and water. This implies that in their distribution, light-demanding species will be restricted to habitats that combine high light and high moisture availability, while shade-tolerant species will be the better competitors in drier and shadier habitats. On larger scales a strong trade-off between above and belowground biomass allocation was found, which should in theory have resulted in a trade-off between drought- and shade-tolerance, but in practice it did not. Plants can compensate for a low root mass fraction by producing relatively cheap roots with a large specific root length and compensate for a low leaf mass fraction by making cheap leaves with a large specific leaf area. Drought- and shade-tolerance thus depend largely on different suites of morphological traits and can be uncoupled.

Species distribution along the rainfall gradient was not directly explained by species drought survival, mainly because deciduousness was the most important factor contributing to survival and deciduous species are well represented in both dry and moist forests. The occurrence of evergreen species at the dry end of the rainfall gradient largely depends on drought related traits as a high wood density and a large biomass allocation to deep roots. Species occurrence at the moist end of the rainfall gradient was mainly determined by traits related to light-demand, as a high leaf mass fraction and long, branched root systems. In conclusion, I propose that at small scales, within forests, species distribution along water gradients depends on the interaction between species drought- and shade-tolerance while at larger scales distribution of (evergreen) species is mainly determined by their drought-tolerance.

Sweetia fruticosa
(Fabaceae)

Contents

Solanum riparium
(Solanaceae)

Chapter 1

General introduction

DROUGHT IN TROPICAL FORESTS

Tropical forests are found under rainfall regimes that vary greatly in rainfall pattern, as well as the frequency of occurrence and intensity of drought (Walsh 1996, Walsh and Newberry 1999). Most tropical forests have a pronounced seasonality with dry periods of 15-30 days occurring every other year in tropical wet forests (Walsh and Newbery 1999, Veenendaal *et al.* 1996) and up to 8 months per year in tropical dry monsoon forests (Walter 1985, Walsh 1996). Even in hyper-wet forests, known for not having a clear annual seasonality, droughts occur typically every three to six years triggered by El Niño Southern Oscillation (ENSO) events (Allan *et al.* 1996).

Water availability is one of the most important environmental factors in tropical forests and the variation in community structure, composition and plant functioning that distinguish different tropical forest types is to great extent determined by the variation in rainfall (Medina 1999, Poorter *et al.* 2004). Continuous and gradual changes in species richness (Gentry 1988, Ter Steege *et al.* 2006), species composition (Hall and Swaine 1981, Bongers *et al.* 1999, Engelbrecht *et al.* 2007) and species abundance (Bongers *et al.* 2004) are observed along the rainfall gradient, while within forests species tend to sort out along slope gradients in water availability (Van Rompaey 1993, Webb and Peart 2000).

Climate change models for the tropics show that water availability in the tropics is going to be of even greater importance as considerable shifts in precipitation patterns are predicted involving both reductions in the total amount of annual precipitation and longer dry seasons, with a greater year to year variability (Bawa and Markham 1995, Hulme and Viner 1998, Margin *et al.* 2007). The question in need of answering is how this will affect the occurrence and distribution of species in the tropics.

A logical corollary would be that that the relative success of species to establish along small and large scale gradients of water availability will depend on how species are adapted to drought, but studies that examine drought-tolerance across many tropical tree species are rare. Existing studies tend to focus on only few species of distinct groups e.g. species that differ clearly in leaf phenology (deciduous vs. evergreen species) or on species at the extremes of the shade-tolerance continuum (pioneers vs. shade-tolerant species). This implies that generalization of results and the up-scaling of species-specific processes to the level of the forest community are difficult to make. In this dissertation we applied a multi-species, multi-trait gradient approach to overcome this dilemma and give detailed information on the mechanisms of drought-tolerance on a large set of species. New insights into the drivers that shape species distribution should be of great value as they can help explain patterns of local and regional biodiversity in the present as well as help predict the vulnerability of communities to current and future environmental change.

DROUGHT AND PLANT PERFORMANCE

Drought negatively affects plant performance by reducing recruitment, growth and survival. In Amazonia, Malaysia and Central America severe droughts (related to El Niño–Southern Oscillation) increased both seedling and adult tree mortality (Condit 1995, 2004, Delissio and Primack 2003, Williamson et al. 2000) and experimental rainfall reduction of ~60% increased mortality of trees in the Brazilian Amazon with nearly 38% (Nepstad et al. 2007). In Panama and Peru dry season irrigation positively affected growth, survival, density and diversity of seedlings (Engelbrecht et al. 2005, Paine et al. 2009).

When a soil dries out the energy state of the water in the soil matrix is affected and the soil water potential decreases. In response to this drop in soil water potential a decrease of the leaf water potential of the plant is observed (Tobin et al. 1999, Cao 2000). According to the cohesion-tension theory of the ascent of sap (Dixon 1894), lower leaf water potentials are needed to maintain a sufficiently negative pressure gradient between soil and leaf to continue whole plant conductivity and photosynthesis (Tyree 1997, Angeles 2004). The drop in leaf water potential is mainly a passive process that results from the negative water balance of the plant created by excessive transpiration, but plants can also actively lower their leaf water potential by changes in the cell modulus of elasticity or by lowering the leaf osmotic potential (Zimmermann 1978, Monson and Smith 1982). A decrease in leaf water potential triggers a reduction in stomatal conductance. In turn this enables the plant to reduce excessive transpiration and recover the leaf water potential to avoid desiccation damage to the leaf tissue (Brodribb 2009). An increased stomatal conductance will not only reduce transpiration but also decrease carbon assimilation through a reduced gas exchange. When dry spells are short and do not occur too often no real harm is done to the plant and reduced stomatal conductance will only temporally reduce carbon assimilation (Hsiao 1973). In case of severe or prolonged drought, however, a series of events may be triggered that will results in a continued decline of assimilation and thus a noticeable growth reduction and eventually reduced survival.

Under extreme or prolonged drought the potential gradient between soil and leaf can become so negative that an increased number of xylem vessels run the risk of cavitation (the formation of an embolism under negative pressure), as a result of air-seeding or vessel implosion. Air-seeding occurs when air is being sucked into the vessel through the pit pores under high pressure (Zimmermann 1983, Sperry and Tyree 1988, Jarbeau et al. 1995). Vessel implosion can occur when negative xylem pressure induces cell wall collapse (Hacke et al. 2001). In both cases cavitation leads to embolisation which can lead to vessels becoming completely dysfunctional, a loss of plant hydraulic conductivity, stomatal closure and eventually the abscission of leaves, shoots, and branches, and finally plant death (Tyree and Sperry 1988, Davis et al. 2002, Engelbrecht et al. 2005). Although many other factors affect plant functioning during drought (e.g. hormonal regulation of hydraulics; Pons et al.

2001), in theory the above holds for any given plant, though in reality plants have evolved to cope with these drought-induced problems in different ways (Fitter and Hay 2002).

DROUGHT-TOLERANCE STRATEGIES

Drought-tolerance can be defined as the ability of species to survive desiccation while minimizing reductions in growth and fitness (Larcher 2003, Engelbrecht and Kursar 2003). At present we recognize two different strategies to deal with desiccation across species; species can either secure growth and survival by resisting desiccation or by delaying desiccation.

Desiccation resistance is supported by a continued plant functioning during drought, through continued hydraulic conductance, increased resistance to xylem cavitation, sustained gas exchange, and cell survival at low leaf water contents and low leaf water potentials (Engelbrecht and Kursar 2003, Tyree et al. 2003). Desiccation delay is promoted by an increased accessibility to water and/or increase water conservation. Species desiccation resistance and desiccation delay will depend on different suites of functional traits.

FUNCTIONAL PLANT TRAITS

Functional plant traits are physical plant attributes caused by genetic expression, which serve as indicators or estimators of plant responses to environmental factors (Lavorel and Garnier 2002, Cornelissen et al. 2003). Functional traits are as such usually divided into hard traits and soft traits. Hard traits are precise estimators of plant functions, but difficult to measure, whereas soft traits are relatively quick and easy to measure and good estimators of hard traits. This makes soft traits especially efficient when assessing large numbers of individuals or species (Cornelissen et al. 2003). Most species traits addressed in this dissertation are soft traits and an example is the specific root length (SRL) that expresses the root length produced per gram root biomass. SRL serves as an estimator of the efficiency of belowground resource foraging (hard trait). In figure 1.1 other examples of functional traits are presented that will be explained in detail in the following chapters of this dissertation.

Desiccation resistance and desiccation delay, mentioned earlier, will largely depend on different suites of functional traits. Desiccation tolerance is related to an increased leaf tissue density (notably a high leaf dry matter content (LDMC) and/or low specific leaf area (SLA)), because dense leaves have smaller cells with thicker and more rigid cell walls that restrict the leaf modulus of elasticity and help avoid the loss of turgor at low leaf water potentials (Cheung 1975, Zimmermann 1978, Monson and Smith 1982). Another example of a typical desiccation tolerance trait is a high wood density (WD) that facilitates cavitation resistance and is associated with a suite of anatomical adaptations, including thin and short xylem vessels, thick cell walls, a decreased total lumen area and small pit-pores (Hacke et al. 2001, Zanne et al. 2006, Sperry et al. 2008). All of these adaptations potentially limit conductivity by increasing the hydraulic resistance of the flow path way (Hacke 2001; Jacobsen et al. 2005, 2007). Species traits that increase the accessibility to water are for example an increased root biomass, and extensive or deep root systems. Species traits that facilitate water conservation are for example a reduced leaf area per unit plant mass, early stomatal closure, water storage in plant organs, and a deciduous leaf habit.

A TRADE-OFF BETWEEN DROUGHT- AND SHADE-TOLERANCE?

Environmental factors are often negatively associated. With an increase in rainfall net primary production increases (Field et al. 1998) and forests become denser and more complex in structure (Medina 1999, Toledo et al. submitted). As a result tropical wet forests cast deeper shades than dry forests (cf. Coomes and Grubb 2000, Parker et al. 2005). In tropical dry forests water may be the ´most important' limiting factor to plant growth and survival, but it is not the ´only´ limiting factor. In the wet season the vegetation of dry forests is often very lush, forest canopies are closed and understory plants experience deep shade. As such over the year combined water and light gradients exist within dry forests and species distribution along these gradients will largely depend on their ability to tolerate both drought and shade.

A trade-off between drought- and shade-tolerance can exist if adaptations that enhance species drought-tolerance constrain the species´ survival under low light conditions and vice versa. An example of this situation is given by Smith and Huston (1989) who argued that a trade-off between drought- and shade-tolerance would result from a trade-off in biomass allocation to roots versus shoot. The idea behind this hypothesis is that a plant can only invest its carbon once. Extra biomass investment in the root system gives the plant a competitive advantage in foraging for water, but it results in a reduced above ground biomass and a limited light foraging capacity. According to their principle no woody plant could thus simultaneously tolerate low levels of water and light availability.

A trade-off between drought- and shade-tolerance would imply that drought-tolerant species are per definition more light-demanding and that drought-intolerant species are per definition more shade-tolerant. Under wet, shady conditions, drought-tolerant species will be out-competed by shade-tolerant species, which are intolerant to drought. In dry forests the distribution of those drought-intolerant species will be restricted to relatively wet and shady habitats (e.g. slopes or valley bottoms) (Harms et al. 2001; Engelbrecht and Kursar 2003).

While the hypothesised trade-off between drought and shade-tolerance has been confirmed in a meta-study across 806 woody species from the Northern Hemisphere

(Niinemets and Valladares 2006), it remains a controversial theory as other studies find them to be largely unrelated (Holmgren 2000, Sack and Grubb 2002, Sack 2004). The ecological consequence of an uncoupling or independence of drought- and shade-tolerance will be that there no direct constraints on niche differentiation and species coexistence. Ecological niches can be as many as the possible combinations of water and light availability in the forest.

OBJECTIVE AND RESEARCH QUESTIONS

In this dissertation I study soil water availability in a dry and moist tropical forest and identify the basic morphological and physiological adaptations to drought of a large number of coexisting tropical tree species. A multi-trait, multi-species gradient approach is used to identify drought-tolerance strategies and to address how trade-offs among functional traits affect the interaction between species drought and shade-tolerance. The final objective is to examine how species adaptations affect their drought survival and how they determine the local and regional distribution of species along gradients of water availability. A conceptual framework of this dissertation is given in figure 1.1. The following questions are addressed:

1) How do dry and moist forests differ in soil water availability?
2) How are dry and moist forest species adapted to drought and what different drought-strategies can be distinguished?
3) Is there a trade-off between drought- and shade-tolerance?
4) How do drought- and shade-tolerance determine local and regional tree species distribution?

THESIS OUTLINE

The four research questions are addressed and discussed in the following seven chapters. The order of the chapters is overall in line with the order of the research questions and the conceptual frame work (Fig. 1.1), but the final answers, most notably those to QUESTION 2, 3 and 4 are presented in the synthesis of CHAPTER 8, where I integrate the findings from all chapters.

In CHAPTER 2 I assess to what extent our current knowledge on light acclimation of tropical trees applies to dry tropical ecosystems. I evaluate sun–shade plasticity of leaf traits that are important for the heat, water, and carbon balance of the plant, of 43 tropical dry forest tree species. I wanted to know if leaf trait plasticity is related to maximum adult stature, juvenile crown exposure, and ontogenetic changes in crown exposure of the species and how sun-shade plasticity varies among tropical forests that differ in annual precipitation.

In CHAPTER 3 I address the variation in soil water availability in a dry forest and moist forest by examining seasonal changes in soil water potentials along a topographical gradient and with soil depth. I also investigate the implications of seasonal drought on the water status of tree saplings by evaluating changes in predawn and midday leaf water potentials throughout the dry season.

In CHAPTER 4 I examine variation in morphological seedling traits of tropical dry and moist forest tree species. Traits were selected based on their importance for water or light acquisition, water and carbon conservation or continued plant functioning during drought. To identify species traits underlying drought-tolerance I evaluated how morphological seedling traits differed between dry and moist forest tree species, whether functional strategies of species could be identified, and whether there is a functional basis for a trade-off between drought and shade-tolerance.

In CHAPTER 5 I analyse vulnerability curves (the relation between percentage loss of hydraulic conductivity and xylem potential) for saplings of 13 tropical dry forest tree species differing in life history strategy and leaf phenology. I examined how cavitation resistance (i.e. P_{50}, the xylem pressure at 50% loss of hydraulic conductivity) is influenced by stem and leaf traits and how it determines the leaf water potential in the field.

In CHAPTER 6 I assess hydraulic conductivity (K_S and K_L) of saplings of 40 co-existing dry forest tree species and evaluate how it was related to plant traits, and the moisture and light requirements of the species.

In CHAPTER 7 I compare functional traits of 38 dry and moist forest tree species and quantify their ability to survive drought in a dry-down experiment under standardized conditions. I examine how seedling traits are related to species position along the rainfall gradient, what functional groups can be distinguished, and what seedling traits are good predictors for drought survival and species distribution.

Finally, in CHAPTER 8 I summarise the main findings of the different chapters and I present a synthesis in which I link back to the general research questions.

STUDY SITES

The field studies and experiments that form the backbone of this dissertation were carried in the lowlands of eastern Bolivia, in the department of Santa Cruz. I worked in two distinct forest types situated at the transition between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Killeen *et al.* 1998; Jardim *et al.* 2003). The sites are classified as tropical lowland deciduous dry forest (Inpa) and tropical lowland semi-deciduous moist forest (La Chonta) (Fig. 1.2) and will hereafter be referred to as dry and moist forest respectively. Both forests are located on the Precambrian Brazilian shield (Cochrane 1973) and are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF). Forests differ considerably in structure, diversity and species composition (Peña-Claros *et al.* submitted manuscript).

Moist forest

The moist forest site, La Chonta, is a forestry concession (15°47'S, 62°55'W) located some 30 km east of the town Ascensión de Guarayos and has a mean annual precipitation of 1580 mm (meteorological data from 2000-2007 at La Chonta sawmill). Monthly potential evapotranspiration exceeds rainfall only in July and the dry season is therefore only 1 month long. Mean annual temperature is 25.3 °C. Soils are relatively fertile inceptisols with a high cation exchange capacity and especially rich in P and Ca (Peña-Claros *et al.* submitted manuscript). The forest has a mean stem density of 367 trees ha^{-1}, a basal area of 19.3 m^{2} ha^{-1}, and a species richness of 59 ha^{-1} (trees $\geq$ 10 cm dbh, Peña-Claros *et al.* submitted manuscript). The average canopy height is about 27 m and about one-third of the canopy species shed their leaves in the dry season. Most common tree species are *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr. (Moraceae), *Ampelocera ruizii* Klotzsch (Ulmaceae) and *Hirtella triandra* Sw. (Chrysobalanaceae).

Dry forest

The dry forest site, Inpa, is situated in a privately owned concession exploited for timber by Inpa Parket ltda. (16°07'S, 61°43'W). The dry forest is located some 40 km east of the town of Concepción. It has a mean annual precipitation of 1160 mm (meteorological data from 1943-2005 from AASANA for Concepción) with a dry period of three months (June - September) when potential evapotranspiration exceeds rainfall. Mean annual temperature is 24.3 ºC. The study area has generally poor soils, classified as oxisols (Pariona 1996). The forest has a mean stem density of 420 trees ha^{-1}, a basal area of 18.3 m^{2} ha^{-1}, and a species richness of 34 ha^{-1} (trees $\geq$ 10 cm diameter at breast height; Peña-Claros *et al.* submitted). Average canopy height is about 20 m and virtually all canopy trees shed their leaves in the dry season. The most dominant species are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Flacourtiaceae), and *Caesalpinia pluviosa* DC (Fabaceae).

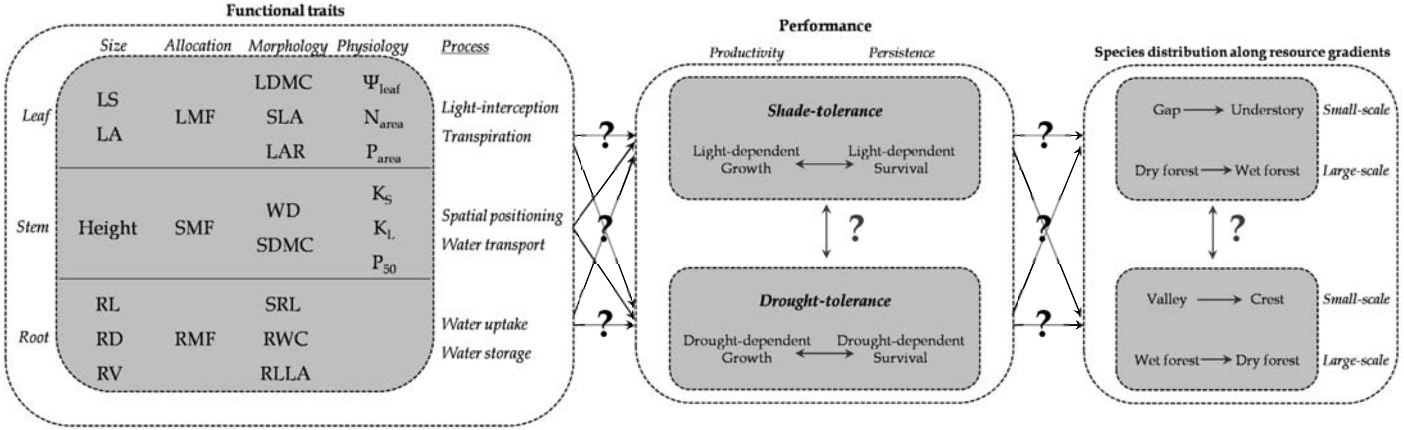

Figure 1.1

Conceptual framework linking functional traits to species performance (drought- and shade-tolerance) and species distribution. Functional traits are expressions of size, biomass allocation, morphology and physiology and subdivided into leaf, stem and root traits and their serve as estimators of plant processes, like light interception or water transport, which will determine species shade- and drought-tolerance, which can in turn determine where species are found in the landscape. The question marks indicate the main focal points of this dissertation; How do traits influence drought- and shade-tolerance?, Is there a trade-off between the two?, How does this influence species distribution along resource gradients? Trait abbreviations are; LS – leaf size, LA – leaf area, LMF – leaf mass fraction, LDMC – leaf dry matter content, SLA – specific leaf area, ψ_{leaf} – leaf water potential, N_{area} - Nitrogen concentration per unit leaf area, P_{area} – Phosphorus concentration per unit leaf area, SMF – stem mass fraction, WD – wood density, SDMC – stem dry matter content, K_S – sapwood specific hydraulic conductivity, K_L – leaf specific hydraulic conductivity, P_{50} – cavitation resistance, RL – root length, RD - rooting depth, RV – rooting volume, RMF – root mass fraction, SRL – specific root length, RWC – root water content, RLLA – root length per unit leaf area.

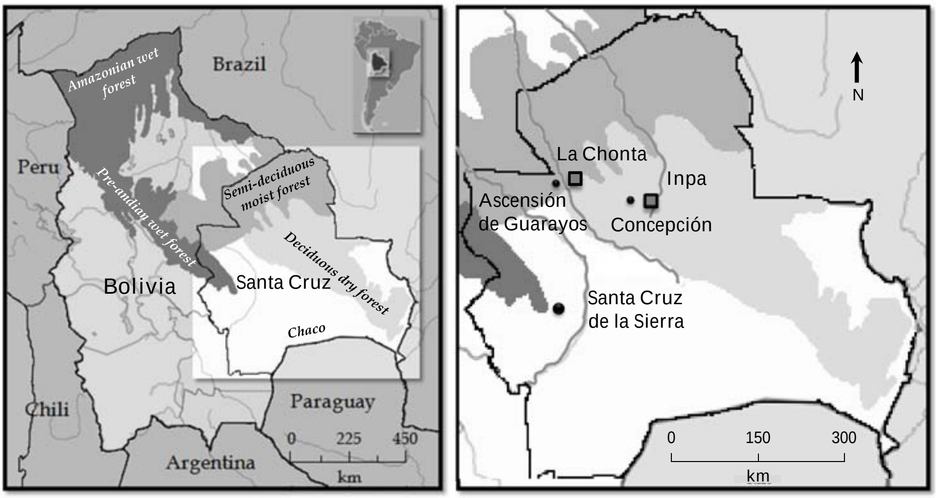

Figure 1.2.

Location of the study sites in the eastern lowlands of Bolivia. La Chonta is a tropical lowland semi-deciduous moist forest located some 30 km east of the town of Ascensión de Guarayos and Inpa is the tropical lowland deciduous dry forest, located some 40 km east of the town of Concepción.

Chapter 2

Light-dependent leaf trait variation in 43 tropical dry forest tree species

Lars Markesteijn, Lourens Poorter and Frans Bongers

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ABSTRACT

Our understanding of leaf acclimation in relation to irradiance of fully grown or juvenile trees is mainly based on research involving tropical wet forest species. We studied sun-shade plasticity of 24 leaf traits of 43 tree species in a Bolivian dry deciduous forest. Sampling was confined to small trees. For each species, leaves were taken from five of the most and five of the least illuminated crowns. Trees were selected based on the percentage of the hemisphere uncovered by other crowns. We examined leaf trait variation and the relation between trait plasticity and light demand, maximum adult stature, and ontogenetic changes in crown exposure of the species. Leaf trait variation was mainly related to differences among species and to minor extent to differences in light availability. Traits related to the palisade layer, thickness of the outer cell wall, and N_{area} and P_{area} had the greatest plasticity, suggesting their importance for leaf function in different light environments. Short-lived pioneers had the highest trait plasticity. Overall plasticity was modest and rarely associated with juvenile light requirements, adult stature, or ontogenetic changes in crown exposure. Dry forest tree species had a lower light-related plasticity than wet forest species, probably because wet forests cast deeper shade. In dry forests light availability may be less limiting, and low water availability may constrain leaf trait plasticity in response to irradiance.

KEYWORDS

Bolivia, crown exposure, leaf traits, light acclimation, plasticity, tropical dry deciduous forest

INTRODUCTION

Trees are long-lived and sessile organisms that subsist in a spatially and temporally highly heterogeneous environment. Trees should therefore possess the capacity to adjust their leaves to their environment. In tropical wet forests light is considered to be the most limiting resource for tree growth and survival (Whitmore 1996) and a major axis of differentiation for tropical tree species. In contrast, studies on leaf trait variability from (semi-)arid woody vegetations, such as the Mediterranean maquis (e.g. Gratani and Varone 2004) and the Californian chaparral (e.g. Ackerly 2004), have generally focused on leaf traits of shrub species in relation to water availability. Recently, several studies have focused on leaf trait acclimation in response to both light and water availability, thus more closely approximating the reality in the field (Sack et al. 2003, Sánchez-Gómez et al. 2006, Quero et al. 2006). Although authors found that shaded conditions enhance seedling tolerance to drought (Quero et al. 2006) and that the impact of drought on seedling survival and growth rates was stronger in high light than in low light conditions (Sánchez-Gómez et al. 2006), clear functional types of species able to tolerate a combination of shade and drought are not yet defined (Sack et al. 2003).

Our current knowledge of leaf responses to irradiance in the tropics is mainly based on research conducted in wet forests (e.g. Bongers and Popma 1988, Poorter et al. 2000) or on small seedlings. Sun leaves grow in a high resource environment and are often relatively thick and small with a low surface to volume ratio. Thicker leaves have a reduced light absorption per unit biomass (Agusti et al. 1994) and an increased photosynthesis per unit leaf area (Björkman 1981, Klich 2000). Photosynthetic capacity is enhanced through investment in thicker and/or extra layers of palisade parenchyma tissue and increased nitrogen concentration per unit leaf area (Björkman 1981, Poorter et al. 1995, Poorter 1999). Overheating might be a severe problem in high light when leaf temperatures exceed the photosynthetic optimum, especially if water availability is low (Smith 1978). Smaller and/or slender leaves have a reduced boundary layer resistance (Givnish 1984) and are thus capable of regulating their temperature through better convective cooling of the leaf area (Parkhurst and Loucks 1972). Leaf cuticles and epidermises may reduce water loss through evaporation (Gamage et al. 2003, Mendes et al. 2001) and protect the photosynthetic tissue from excessive irradiance through increased reflectance (Roth 1984). High radiation loads and high vapour pressure deficits result in greater transpiration rates of sun leaves, and thus a large water flow to the leaves is needed. This can be facilitated by large xylem conduits (Zimmermann 1983), relatively thick internodes in relation to the leaf area (cf. Westoby and Wright 2003), and a high leaf hydraulic conductance (Sack et al. 2005).

Light is a limiting resource for growth in the shaded understory. Trees growing in the shaded understory enhance their light interception through the formation of relatively large, thin leaves with a low leaf mass per unit leaf area (LMA) (Evans and Poorter 2001). They may forage for light and minimize self shading through the formation of cheap petioles with a high petiole length per unit petiole mass. Respiratory carbon losses are reduced through low protein and nitrogen concentrations (Sims and Pearcy 1989).

The magnitude of acclimation that a species can realize in response to differences in irradiance can be referred to as plasticity. Plasticity enhances plant performance and is thought to differ predictably among functional groups. Pioneer species that regenerate in open areas and forest gaps were hypothesized to have a higher plasticity than shade tolerant species, because they grow in a more variable environment. (Bazzaz 1979, Bazzaz and Wayne 1994). It is a certainty that formed gaps will close, allowing for selection on high acclimation potential. The high resource availability in early successional habitats allows pioneer species to support the carbon investment costs that come along with a higher acclimation potential. Still there is little consensus about this hypothesis. Some studies found plasticity to be similar for pioneer and shade tolerant species (Sims and Pearcy 1989, Kitajima 1994), while others actually found less plasticity in pioneers than in shade tolerant species (Popma et al. 1992). Grubb (1998) suggested that these apparently contradictory results might have been found because pioneers in the seedling stage are more plastic, whereas in the adult stage shade tolerant species are more plastic. Contradictory results may also partly be explained by the fact that in many studies only a few species and a few leaf traits have been evaluated and differing methods were used to calculate and define plasticity. In addition, researchers have often assigned species arbitrarily to functional groups, without an objective, quantitative measure of the light demand of the species.

Popma et al. (1992) argued that pioneers do not need to have a high plasticity because they always grow in high light and do not survive deep shade. Instead, plasticity should be highest for tall species that establish in the shaded understory and are subject to large ontogenetic changes light availability during their life cycle (cf. Thomas and Bazzaz 1999, Poorter et al. 2005). Close relations of leaf trait plasticity with maximum adult stature and ontogenetic crown exposure may thus be expected.

The magnitude of plasticity is likely smaller in tropical dry forest than in tropical wet forest tree species. Tropical dry forests are characterized by a prolonged dry season in which the vegetation is subject to low soil water availability and high vapour pressure deficit of the air (Bullock et al. 1995). Light penetration in dry forests is relatively high compared to wet forests (5-10% in the wet season in dry forests vs. 0.4-2.0% yr-round in wet forests, Coomes and Grubb 2000), due to a low and open canopy and low stem densities. These levels are even higher during the dry season, when many canopy and subcanopy species shed their leaves (Parker et al. 2005). Leaf trait acclimation in response to light availability is therefore likely to be less pronounced in tropical dry forests than in wet forests.

In this study we evaluate leaf characteristics and evaluate sun–shade plasticity of 43 tropical dry forest tree species. Twenty-four morphological, anatomical and chemical leaf traits that are important for the heat, water, and carbon balance of the plant are assessed. Leaf trait plasticity is related to quantitative measures of maximum adult stature, juvenile crown exposure, and ontogenetic changes in crown exposure of the species. We made the following three predictions: (1) Functional groups of species related to shade-tolerance differ in leaf trait plasticity in response to irradiance. Pioneer species grow in a more variable habitat with higher resource availability and are thus expected to have high leaf trait plasticity, whereas shade-tolerant species tend to spend their entire life cycle in the low resource environment of the forest understory, with a marginally positive carbon balance, and therefore should have less potential to acclimate and less plasticity. (2) There is a positive relationship between leaf trait plasticity and maximum adult stature, juvenile crown exposure, and ontogenetic changes in crown exposure of the species. Tall species establish in the shaded forest understory, but, during their life cycle, endure more changes in light availability than small species. This requires a greater ability to adjust to their changing growth environment. (3) Dry tropical forests tree species will have smaller leaf trait plasticity in response to irradiance than tree species from wetter forest types. As light is less of a limiting factor in dry forests, the necessity of a high light-related plasticity is smaller for dry forest tree species.

METHODS

Study area

This study was conducted in the INPA forest (16°07′ S, 61°43′ W) in the lowlands of eastern Bolivia. The forest can be classified as a tropical lowland dry deciduous forest, situated at the transition zone between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Killeen et al. 1998, Jardim et al. 2003).

The study area has a mean altitude of 458 m and is located on the Precambrian Brazilian shield. Soils are oxisols and are low in nutrients. Mean annual temperature at Concepcíon, ca. 40 km from the study site, is 24.3ºC, and the mean annual precipitation is 1160 mm with a dry season (<100 mm rainfall per mo) from April until October. From June through September, the potential evapotranspiration exceeds the mean monthly rainfall, which can result in a water deficit. The forest canopy has an average height of 22 m with emergent trees growing up to 30 m. The forest has a density of 437 stems ha^{-1}, a basal area of 19.7 m^{2} ha^{-1}, and a species richness of 34 ha^{-1} (trees $\geq$ 10 cm dbh; Instituto Boliviano de Investigación Forestal IBIF, Santa Cruz de la Sierra, Bolivia, unpublished data). The forests in the region have previously been classified as semi-deciduous forests (Killeen et al. 1998), because most of the subcanopy trees, shrubs and lianas are evergreen or semi-evergreen (Killeen et al. 1998). Because the canopy of the forest at INPA is fully deciduous in the dry season, we choose to classify this forest as a dry deciduous forest instead of a semi-deciduous forest.

The most dominant species at INPA (listed in decreasing order of basal area (m^2 ha^{-1}) are: Acosmium cardenasii H.S. Irwin & Arroyo (Fabaceae), Casearia gossypiosperma Briquet (Flacourtiaceae), Caesalpinia pluviosa DC (Fabaceae), Neea cf. steinbachii (Nyctaginaceae), Machaerium acutifolium Vogel (Fabaceae), Anadenanthera macrocarpa Benth (Fabaceae), Piptadenia viridifolia (Kunth.) Benth (Fabaceae) and Centrolobium microchaete (Benth.) H.C. Lima (Fabaceae) (IBIF, unpublished data). Nomenclature follows that of the nomenclature database of the Missouri Botanical Garden (W^3TROPICOS; www.mobot.org).

Study species

We studied leaf traits of 43 tree species belonging to 40 genera, 24 families, and 19 orders. Among the selected species are some of the most abundant species in this type of forest, as well as several commercially valuable timber species (Table 2.1). With six species, Fabaceae is the biggest family in this study, which is in line with its dominance in this dry deciduous forest. All species together represent more than 77% of the stems larger than 10 cm dbh in the permanent sample plots (IBIF unpublished data).

Species varied in leaf form and habit, maximum adult stature, and shade-tolerance. Maximum adult stature (H_{max}) was calculated for each species as its asymptotic height (cf. Thomas 1996) using species-specific height-diameter relationships (Verweij 2004) and the diameter of the third thickest tree in the permanent sample plots (thus avoiding outliers). We classified the species into four guilds of shade-tolerance (cf. Finegan 1992) based on their light requirements and longevity (Mostacedo et al. 2001, Jardim et al. 2003, Justiniano et al. 2004) and additional field observations on the habitat preference of the species (L. Poorter personal observation). Short-lived pioneers (SLP) are species that need high light to establish and grow to their adult stature and have a lifespan up to 30 yr. These SLP are the "typical" pioneers sensu stricto, that can form dense stands in disturbed areas or large treefall gaps (cf. Kammesheidt 2000). Long-lived pioneers (LLP) need intermediate light to establish and grow to the high light environment of the forest canopy. They live longer than 30 yr. LLP are pioneers sensu lato that can establish under a wider range of light conditions. Partial shade tolerant species (PST) can establish in the shaded understory, but need more light in later stages of their lifecycle to reach their maximum stature in the high light environment of the canopy. Shade tolerant species (ST) are species that can complete their entire life-cycle in the shade. We included 20 ST species, 10 PST species, nine LLP species and four SLP species.

Data from a separate study (L. Poorter unpublished data) provided an objective and quantitative measure of light demand, based on the analysis of height-light trajectories of each species. For a median of 133 (range 16-9064) individuals per species ranging from seedlings to adult trees, the height and crown exposure (CE) were estimated. The CE varies

Table 2.1

Species list with the scientific names of the 43 studied species. Functional groups related to shade-tolerance (Guild; ST = shade tolerant, PST = partial shade tolerant, LLP = long-lived pioneer, and SLP = short-lived pioneer species), mean canopy openness above the sampled individuals per species in the shade (CO$_{shade}$) and sun (CO$_{sun}$), maximum adult stature (H$_{max}$), average crown exposure at 2 m height (CE$_{juv}$), and the ontogenetic change in crown exposure (CE$_{change}$) are given for each species (L. Poorter unpublished data). Citations follow the nomenclature database of Missouri Botanical Garden (W^{3}Tropicos); www.mobot.org). For Pouteria gardneriana, few adult trees were found, so no reliable estimate of H$_{max}$ and CE$_{change}$ can be given. Urera caracasana is a SLP with a surprisingly low CE$_{juv}$ (1.58). It seems to establish from seed in disturbed areas. Juveniles die back in the dry season and resprout again in the wet season. Most juveniles in this study were found in the shade and had resprouted from root systems of old individuals that once established in gaps and were overgrown.

Species	Family	Guild	CO$_{shade}$ (%)	CO$_{sun}$ (%)	H$_{max}$ (m)	CE$_{juv}$	CE$_{change}$	Plasticity
Acosmium cardenasii H.S. Irwin & Arroyo	Fabaceae	ST	7	54	25	1.44	2.86	14.86
Actinostemon concepcionis (Chodat & Hassl.) Hochr.	Euphorbiaceae	ST	5	47	5	1.4	0.62	16.72
Ampelocera ruizii Klotzsch	Ulmaceae	PST	11	38	20	1.59	1.36	14.75
Aspidosperma cylindrocarpon Müll. Arg.	Apocynaceae	PST	12	57	25	1.31	2.74	9.27
Aspidosperma tomentosum Mart.	Apocynaceae	PST	11	54	23	1.31	2.86	11.88
Astronium urundeuva (Allemao) Engl.	Anacardiaceae	LLP	9	72	28	2.42	2.3	8.63
Bougainvillea modesta Heimerl	Nyctanginaceae	LLP	14	45	23	2.12	-0.01	17.05
Caesalpinia pluviosa DC.	Fabaceae	PST	11	49	28	1.81	2.82	16.57
Capparis prisca J.F. Macbr.	Capparaceae	ST	15	64	16	1.59	1.01	12.79
Cariniana ianeirensis R. Knuth	Lecythidaceae	PST	13	46	28	1.9	2.75	10.96
Casearia gossypiosperma Briq.	Flacourtiaceae	PST	13	43	18	1.71	2.1	10.32
Ceiba speciosa (A. St.-Hil.) Ravenna	Bombacaeae	LLP	14	55	21	1.64	2.06	20.51
Centrolobium microchaete (Mart. Ex Benth.) Lima ex. G. P. Lewis	Fabaceae	LLP	7	61	28	1.93	2.46	29.53
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	Sapotaceae	ST	16	42	14	1.42	0.82	16.99
Combretum leprosum Mart.	Combretaceae	ST	16	57	22	1.92	2.01	20.04
Copaifera chodatiana Hassl.	Fabaceae	ST	11	73	25	1.87	2.93	10.33
Eriotheca roseorum (Cuatrec.) A. Robyns	Bombacaeae	LLP	11	59	25	1.64	2.64	12.11
Erythroxylum daphnites Mart..	Erythroxylaceae	ST	6	50	2	2.19	1	10.33
Esenbeckia almawillia Kaastra	Rutaceae	ST	3	59	2	1.64	0.02	12.95
Galipea ciliata Taub.	Rutaceae	ST	6	64	11	1.49	0.48	20.51
Gallesia integrifolia (Spreng.) Harms	Phytolaccaceae	PST	7	49	22	1.81	1.78	17.7
Jacaratia sp.	Caricaceae	ST	7	30	2	1.51	0	16.45
Manihot guaranitica Chodat. & Hassl.	Euphorbiaceae	SLP	13	84	6	2.67	0.34	13.93
Myrciaria cauliflora (Mart.) O. Berg	Myrtaceae	ST	5	58	6	1.7	0.06	20.23
Myrciaria sp.	Myrtaceae	PST	11	59	10	1.64	0.61	26.9
Neea cf. steimbachii	Nyctanginaceae	ST	8	42	12	1.63	0.56	16.65
Ouratea sp.	Ochnaceae	ST	8	60	11	1.78	0.56	9.41
Phyllanthus sp. nov.	Euphorbiaceae	ST	6	26	7	1.6	0.38	22.02
Phyllostylon rhamnoides (J. Poiss.) Taub.	Ulmaceae	PST	9	55	26	1.49	2.78	12.99
Platymiscium ulei Harms	Fabaceae	LLP	9	70	27	2.52	1.85	13.2
Pogonopus tubulosus (A. Rich.) K. Schum.	Rubiaceae	ST	6	53	9	1.67	0.51	15.39
Pouteria gardneriana (A. DC.) Radlk.	Sapotaceae	ST	8	65		1.44		15.16
Simira rubescens (Benth.) Bremek. ex Steyerm.	Rubiaceae	ST	7	59	16	1.62	1.2	13.45
Solanum riparium Pers	Solanaceae	SLP	33	74	15	3	0.49	23.48
Spondias mombin L.	Anacardiaceae	LLP	9	63	25	2.4	1.75	11.01
Sweetia fruticosa Spreng.	Fabaceae	PST	11	55	24	1.7	2.6	17.52
Tabebuia impetiginosa (Mart. Ex DC.) Standl.	Bignoniaceae	LLP	5	57	30	2.42	2.2	15.46
Tabebuia serratifolia (Vahl) G. Nicholson	Bignoniaceae	LLP	8	55	28	1.27	3.44	26.46
Talisia esculenta (A. St. Hil.) Radlk.	Sapindaceae	ST	9	39	15	1.81	1.19	23.9
Trichilia elegans A. Juss.	Meliaceae	ST	6	54	24	1.24	2.27	15.78
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	SLP	10	82	10	2.29	0.47	22.53
Urera caracasana (Jacu.) Gaudich. Ex Giseb.	Urticaceae	SLP	15	79	16	1.58	0.95	16.51
Zanthoxylum monogynum A. St. Hil.	Rutaceae	ST	6	75	10	1.46	-0.16	13.69

from 1 if the tree crown does not receive any direct light, to 2 if it receives lateral light, 3 if it receives overhead light on part of the crown, 4 when it receives overhead light on the whole crown, to 5 if it has an emergent crown that receives light from all directions (Dawkins and Field 1978). CE can be measured repeatedly, and there is a close relation between CE and both canopy openness (Davies et al. 1998) and incident radiation (Clark et al. 1993). For each species, we related CE to tree height, using a multinomial regression analysis (L. Poorter et al. unpublished manuscript, cf. Poorter et al. 2005) and calculated the average crown exposure at 2 m height (CE_{juv}) and maximum adult stature (CE_{adult}). The difference between CE_{juv} and CE_{adult} was used to estimate the ontogenetic change in CE for each species (CE_{change}) (Table 2.1). It should be emphasized that these values indicate the average CE values at the population level. At a given height individuals of the same species may be found under a wide range of crown exposures, and we used these extreme individuals as sun and shade trees for the sampling of leaves used in the present study. We used the CE and guilds as two complementary approaches to evaluate hypotheses about plasticity. The CE is a quantitative measure of light demand; whereas the guilds capture both juvenile crown exposure and ontogenetic changes in crown exposure (PST and LLP have larger CE_{change} than the two other guilds).

Leaf collection

Sun and shade leaves of each species were collected in the wet season of 2003-2004, by sampling five trees per species in full sunlight and five trees growing in shaded conditions. Sun and shade trees were selected based on the canopy openness (CO) above their crowns. CO was estimated for every sample tree as the percentage of the hemisphere above the tree crown that is not covered by crowns of other trees. Although the maximum and minimum CO at which individuals could still be found is rather species-specific, we applied the rule of thumb that the CO of sun individuals was at least 50% and that of shade individuals at most 15%. For species that could not be found within these ranges, the most highly and least illuminated individuals found were sampled. Average CO of the sampled sun individuals was 56.5 ± 0.3 % (mean ± SE) and of the shade individuals 9.8 ± 0.1 (mean ± SE) (Table 2.1). Leaves were sampled from trees between 10–20 cm dbh and 10–20 m height, to reduce the confounding effect of tree size on leaf traits (Koch et al. 2004). Jacaratia sp., Erythroxylum daphnites, Esenbeckia almawillia, Actinostemon concepcionis, Myrciaria cauliflora, Manihot guaranitica, Phyllanthus sp. nov., and Pogonopus tubulosus, reached only a maximal height of 2-9 m (Table 2.1). For these species, the leaves were collected from the tallest individuals. For every sample tree, we estimated the diameter at breast height (dbh), total height, and the percentage canopy openness. To minimize trait variation related to the position of sampled leaves within the crown of the individual trees, we selected trees of the same height (especially within species) and sampled five leaves per tree from the outer leaf shell midway between the top and bottom of the crown. All sun leaves were collected form the most exposed side and all shade leaves from the least exposed side of the crown. Leaves were cut with a pair of extendable pruning shears and transported to the field station in plastic bags. To minimize leaf trait variation caused by the age of the sampled leaves, we selected leaves that were young and fully expanded. We also selected leaves with minimal signs of herbivore or pathogen damage.

In the field station a cross-section of one leaf per tree was stored in 70% ethanol (EtOH) for anatomical analysis. For compound and lobed leaves, a cross-section was made of an average-sized foliole or lobe.

Leaf morphology

For each tree, four leaves were measured for the length (LL) and width (LW) of the leaf blade. Folioles were considered to be functional equivalents of simple leaves and were treated accordingly in this study. Average-sized folioles were used in the case of compound leaves. The length of the petiole and the length and diameter of the internode section, below the corresponding node, were also measured. Leaf thickness (LT; µm) was measured with a micrometer. Leaves were rehydrated overnight in wet tissue in a refrigerator, dried with a tissue, and weighed to determine the saturated fresh mass. Leaves and folioles were scanned with a desktop-scanner, and their surface area (LA; cm^2) was determined using pixel-counting software (Van Berloo 1998). Leaf toughness (LTO) was determined with a penetrometer (punch-head; ø 3 mm; 7 mm^2). With this device, the leaves were punctured between the veins with the head of a nail. The nail was connected to a reservoir, which was gradually filled with water to increase the mass on the nail until the lamina finally ruptured. The mass at the moment of penetration was converted to a measure for leaf toughness ($N{\cdot}cm^{-2}$), a proxy for leaf toughness. Leaf toughness was not determined for *Caesalpinia pluviosa* because its folioles were too small. Thereafter, the leaves, petioles and internodes were oven dried for 48 h at 65ºC and measured again for their dry mass.

From these measurements, we calculated the following morphological traits: leaf density (LD; leaf dry mass / (leaf area × leaf thickness); g cm^{-3}), leaf slenderness (LS; leaf length / leaf width; $cm{\cdot}cm^{-1}$), leaf mass per area (LMA; leaf dry mass / leaf area; $g{\cdot}m^{-2}$), leaf dry matter content (LDMC; leaf dry mass / fully saturated leaf fresh mass; g g^{-1}), specific petiole length (SPL; petiole length / dry petiole mass; cm g^{-1}), and the internode to leaf area ratio (ILAR; internode cross-sectional area / leaf area; cm^2 cm^{-2}) (Table 2.2). LTO is an indicator of resistance to herbivory, the LS of the capacity to reduce overheating by a reduction of the boundary layer. LDMC indicates the amount of dry mass invested per unit leaf fresh mass and LMA, the amount of biomass a plant invests to produce a unit leaf surface for light capture. Both are proxies for leaf construction costs. SPL indicates the light foraging capacity given a fixed amount of biomass for petiole construction, and the ILAR is an estimate of the water supply capacity to the leaf.

Table 2.2

The 24 leaf traits included in this study and the abbreviations used.

Trait	Abbreviation	Unit
MORPHOLOGY		
Leaf length	LL	cm
Leaf width	LW	cm
Leaf area	LA	cm^2
Leaf thickness	LT	µm
Leaf toughness	LTO	$N\ cm^{-2}$
Leaf density	LDE	$g\ cm^{-3}$
Leaf shape index	LS	$cm\ cm^{-1}$
Leaf mass per unit leaf area	LMA	$g\ m^{-2}$
Leaf dry matter content	LDMC	$g\ g^{-1}$
Specific petiole length	SPL	$cm\ g^{-1}$
Internode to leaf area ratio	ILAR	$mm^2\ cm^{-2}$
ANATOMY		
Thickness of the outer cell wall	TOC	µm
Upper epidermis thickness	UET	µm
Palisade parenchyma thickness	PPT	µm
Spongy parenchyma thickness	SPT	µm
Lower epidermis thickness	LET	µm
Palisade to spongy parenchyma ratio	PSPR	$\mu m\ \mu m^{-1}$
Xylem conduit diameter	XCD	µm
Xylem conduit density	XCDE	mm^{-2}
Number of palisade parenchyma cell layers	PPL	
CHEMISTRY		
Nitrogen concentration per unit leaf mass	N_{mass}	$mg\ g^{-1}$
Phosphorus concentration per unit leaf mass	P_{mass}	$mg\ g^{-1}$
Nitrogen concentration per unit leaf area	N_{area}	$mmol\ m^{-2}$
Phosphorus concentration per unit leaf area	P_{area}	$mmol\ m^{-2}$

Leaf anatomy

Stored leaf samples were dehydrated and embedded in paraffin. The embedded samples were then cross-sectioned with a retraction-microtome (Microm HM350; Zeiss, Walldorf, Germany) and mounted on a microscope slide with glycerin-gelatin. After de-waxing the paraffin from the tissue with tert-butyl alcohol and EtOH series, the tissue sections were stained with 0.01% toluidine blue in demineralised water. Images of the cross-sectional lamina and mid-rib were digitized using a microscope camera and analyzed with Image J (http://rsb.info.nih.gov/ij/).

From the digital images, we measured the thickness of the outer cell wall (TOC; µm), upper epidermis (UET; µm), palisade parenchyma (PPT; µm), spongy parenchyma (SPT; µm), and lower epidermis (LET; µm) and counted the number of palisade parenchyma cell layers (PPL). We measured the diameter of the five largest xylem conduits (XCD; µm) in the midrib of the leaf as the average of two perpendicular diameters and determined the xylem conduit density (XCDE; mm^{-2}) by counting the number of conduits in a given cross-sectional area of the xylem tissue. Additional observations were made whether additional tissue layers, such as a hypodermis, were present. From these data, we calculated the palisade to spongy parenchyma ratio (PSPR; palisade parenchyma thickness / spongy parenchyma thickness; $\mu m \cdot \mu m^{-1}$) (Table 2.2).

Finally, we determined for each species the mass-based nitrogen concentration (N_{mass}; $mg \cdot g^{-1}$), with the Kjeldahl microassay protocol (Archibald 1958), and the phosphorus concentration (P_{mass}; $mg \cdot g^{-1}$) for pooled leaf samples per light environment. From these data, we calculated the area-based nitrogen (N_{area}; $mmol \cdot m^{-2}$) and phosphorus concentration (P_{area}; $mmol \cdot m^{-2}$).

Statistics

For each leaf trait, an arithmetic average was calculated per tree from four sampled leaves. PPL was untransformed, LDMC was arcsine-transformed and the other leaf characters were $\log_{10}$-transformed prior to analysis to improve normality and homoscedasticity.

Leaf traits of sun and shade leaves were compared using a full factorial two-way-ANOVA with species and light level as fixed factors. The amount of variation explained ($\eta^2 \times 100\%$) by the species, light, and the interaction effect was calculated as the sum of squares of the effect divided by the total sum of squares of the model. η^2 is an equivalent of R^2. If species have a smaller among-species variance of a leaf trait in one light environment compared to another, then this would be an indication that species show a convergent evolution of the trait in that light environment (cf. Bongers and Popma 1988). We therefore analyzed the differences in variance between sun and shade leaves with a two-tailed F test, using the mean trait values per species in each light environment. Leaf trait plasticity was calculated for each species based on the mean leaf trait values in the sun and in the shade (cf. Valladares et al. 2000b). This plasticity index was calculated as the absolute difference between the maximum trait value in one of the light environments and the minimum trait value in the other light environment, divided by the maximum value, and multiplied by 100% (cf. Valladares et al. 2000b). Total plasticity per species was expressed as the average plasticity of all 24 leaf traits. Using Pearson correlation analyses, we investigated the relations between sun and shade values of the leaf traits and the relations between leaf trait plasticity and CE_{juv}, CE_{change}, and H_{max} using the species average. Statistical analyses were performed with SPSS 12.0.1 (SPSS Inc. Chicago, USA).

RESULTS

Species and light environment

Species and light environment had a large effect of leaf morphology, anatomy, and chemistry (Table 2.3). All leaf traits differed strongly among species ($P < 0.001$), which explained most of the leaf trait variation (mean 77%, range 34–95). Light had a significant effect on 16 of 24 leaf traits and explained considerably less of the variation in leaf traits (mean 3.4%, range 0.2–10). There was a significant species and light interaction effect for 14 of 24 leaf traits. For these traits, species responses to light explained an additional 3.9% of the variation (range 1.1-7.6). Light did not have a significant direct or interaction effect on leaf slenderness and xylem conduit diameter. Light did not have a significant effect on the chemical traits N_{mass} and P_{mass} either and no interaction effect could be calculated here because N and P were determined for each species based on pooled leaves. An absence of a significant species-light interaction effect indicates that all species have a similar response to light. Species thus had a similar response to the light for leaf slenderness, LDMC, internode to leaf area ratio, upper and lower epidermis thickness, and xylem conduit density.

Table 2.3

Two-way-ANOVA with the effect of species (n=35-43) and light level (n=2; SH = shade, SU = sun) on leaf traits (total n=360-380). F-values and the level of significance (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$) and the η^2 of the effects and the total model are given. η^2 is an equivalent of R^2 and was calculated as the sum of squares of the effect in proportion to the total sum of squares (*100%). The back-transformed mean is given for pooled individuals of sun and shade leaves. The plasticity in leaf traits was calculated as the absolute difference between the maximum average trait value in one of the light environments and the minimum trait value in the other light environment, divided by the maximum value (*100%). PPL was untransformed; LDMC was arcsine transformed and all other leaf traits were $\log_{10}$-transformed prior to analysis. The Pearson correlation coefficients indicate the correlation between trait values of the species in sun and shade (n=35-43). The two-tailed F-test tests for differences in among species variance between shade and sun leaves. See table 2.2 for the trait abbreviations.

		Species			Light			Interaction			η^2	SH	SU	Plasticity	Pearson	F-test	
	n	F	p	η^2	F	p	η^2	F	p	η^2	total	mean	mean	(%)	r	variance	p
MORPHOLOGY																	
LL (cm)	37	100	***	89.9	20	***	0.5	2	***	1.9	93	9.9	9.17	7.4	0.96		
LW (cm)	37	149	***	93.4	13	***	0.2	2	**	1.2	95.1	4.85	4.52	6.9	0.97		
LA (cm^2)	37	125	***	91.8	15	***	0.3	2	***	1.7	94.1	30.2	26	14	0.96	shade>sun	*
LT (µm)	37	25	***	69	42	***	3.2	2	**	5.1	77.6	165	184	10.5	0.84		
LTO (N cm^{-2})	36	38	***	79.6	3	ns	0.2	2	*	3.3	83.3	27	28.6	5.4	0.92		
LDE (g cm^{-3})	37	26	***	95.1	2	ns	0	2	***	1.1	96.5	0.07	0.08	6	0.96		
LS (cm cm^{-1})	37	63	***	87.3	1	ns	0.1	1	ns	1.2	89.2	2.05	2.04	0.5	0.96		
LMA (g m^{-2})	37	35	***	75	60	***	3.6	2	**	3.8	82.1	49	57.6	15	0.88		
LDMC (g g^{-1})	37	19	***	65.4	13	***	1.3	1	ns	4.9	71.6	0.28	0.3	6.7	0.88		
SPL (cm g^{-1})	37	40	***	80.2	3	ns	0.2	2	**	3.8	85.4	119	109	8.8	0.89		
ILAR (mm^2 cm^{-2})	37	5	***	33.6	4	*	0.9	1	ns	10.3	44.7	0.09	0.11	15.7	0.52	shade>sun	***
ANATOMY																	
TOC (µm)	35	32	***	71.4	106	***	6.9	2	*	3.8	83.6	0.93	1.17	20.2	0.84	shade<sun	*
UET (µm)	36	21	***	69.6	9	**	0.9	1	ns	3.5	75	8.88	9.56	7.2	0.89		
PPT (µm)	36	22	***	61.8	122	***	9.9	2	***	5.9	78.9	21	27.9	24.6	0.85		
SPT (µm)	36	31	***	75.5	1	ns	0.1	2	***	5.1	81.6	35.6	36.8	3.2	0.85		
LET (µm)	36	20	***	68.7	6	*	0.6	1	ns	4.9	74.9	6.16	6.46	4.6	0.87		
PSPR (µm $µm^{-1}$)	36	25	***	66.7	72	***	5.5	3	***	7.6	80	0.59	0.76	22.2	0.79	shade<sun	**
XCD (µm)	35	57	***	86.7	1	ns	0.1	1	ns	2	89.2	9.98	9.69	2.9	0.95		
XCDE (mm^{-2})	35	47	***	83.2	1	ns	0.1	2	***	3.8	87.6	5959	6323	5.8	0.92		
PPL	36	20	***	63.2	59	***	5.4	2	***	7.1	76.6	1.32	1.63	18.8	0.80		
CHEMISTRY																	
N_{mass} (mg g^{-1})	43	14	***	93.4	1	ns	0.1					3.1	3.15	1.5	0.87		
P_{mass} (mg g^{-1})	43	10	***	90.9	0	ns	0					0.15	0.15	0.3	0.82		
N_{area} (mmol m^{-2})	43	9	***	82.9	33	***	7.6					108	129	16.3	0.79		
P_{area} (mmol m^{-2})	43	7	***	83.1	15	***	4.4					2.38	2.81	15.3	0.74		

Differences between sun and shade leaves

Light had a significant effect on 16 of the 24 leaf traits and explained an average 3.4% of the leaf trait variation (Table 2.3). Light explained the largest proportions of variation for palisade parenchyma thickness (9.9%), N_{area} (7.6%), thickness of the outer cell wall (6.9%), palisade to spongy parenchyma ratio (5.5%), and the number of palisade parenchyma cell layers (5.4%).

Sun leaves were shorter, narrower, smaller, and thicker than shade leaves. Sun leaves had a higher LMA, LDMC, and a higher N and P concentration per unit leaf area (N_{area}, P_{area}), but sun and shade leaves did not differ in slenderness, leaf toughness and density, or specific petiole length.

Anatomically, the greater thickness of sun leaves could be attributed to their thicker outer cell wall, upper epidermis, palisade parenchyma, and lower epidermis. Sun leaves had a higher palisade to spongy parenchyma ratio. Part of this increase can be ascribed to the increased number of palisade parenchyma cell layers in sun leaves compared to shade leaves. Sun and shade leaves did not differ in the mean thickness of the spongy parenchyma nor the diameter and density of xylem conduits of the midrib.

For all leaf traits sun and shade values were highly correlated (average $r = 0.86$, range 0.52-0.97, $p < 0.001$ in all cases) (Table 2.3). Few traits showed differences in species variance between sun and shade leaves. The species variance in leaf area and internode to leaf area ratio was lower in sun leaves than in shade leaves, suggesting convergent evolution in these leaf traits in the sun. The variance in thickness of the outer cell wall and palisade to spongy parenchyma ratio was lower in shade leaves than in sun leaves.

Leaf trait plasticity in response to irradiance

For the morphological leaf traits, internode to leaf area ratio (15.7%), LMA (15.0%), leaf area (14.0%), and leaf thickness (10.5%) were among those with the greatest plasticity. LDMC (6.7%), leaf length (6.9%), and width (7.4%) were among the traits with the lowest morphological plasticity, while still being significantly different between sun and shade leaves. P_{mass} (0.3%) had the lowest plasticity (Table 2.3). For the anatomical traits, three of the four that had the highest plasticity were related to the palisade parenchyma tissue, namely palisade parenchyma thickness (24.6%), palisade to spongy parenchyma ratio (22.2%), and the number of palisade parenchyma cell layers (18.8%). Also the thickness of the outer cell wall (20.2%) had a high plasticity. The thickness of the lower and upper epidermis (4.6% and 7.2%) had the lowest plasticity, while still significantly different between sun and shade leaves. Xylem conduit diameter (2.9%) had the lowest plasticity among all anatomical traits (Table 2.3). Morphological, anatomical, and chemical traits did not differ significantly in their mean plasticity (ANOVA: $F_{3, 20} = 0.7$; $P > 0.05$).

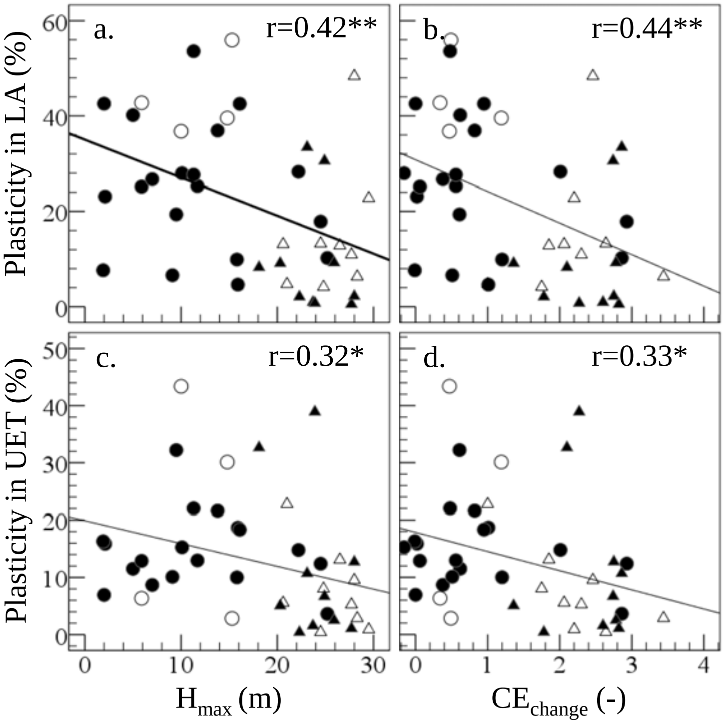

Figure 2.1.

Correlations between leaf trait plasticity, adult stature (H_{max}) and ontogenetic changes in crown exposure (CE_{change}) of 43 tropical dry forest tree species. Plasticity in leaf area (LA) with H_{max} (A) and CE_{change} (B) and plasticity in upper epidermis thickness (UET) with H_{max} (C) and CE_{change} (D) are shown. Leaf trait plasticity is calculated as the absolute difference between the maximum average value in one light environment and the minimum average trait value in the other light environment divided by the maximum value (*100). Functional groups related to shade-tolerance are indicated with different symbols: shade tolerant species (filled dots), partial shade tolerant species (filled triangles), long-lived pioneers (open triangles) and short-lived pioneers (open dots). Regression lines and Pearson correlations are shown. * $p < 0.05$, ** p <

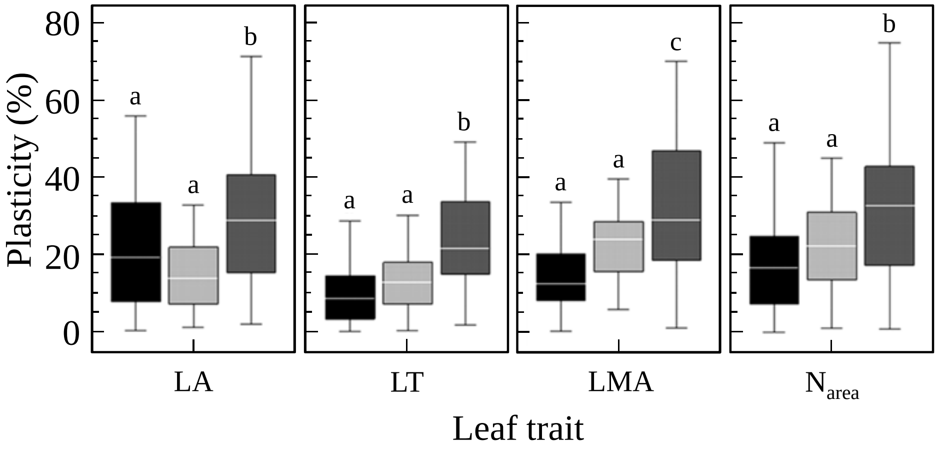

Figure 2.2.

Leaf trait plasticity for 3 forest types differing in mean annual precipitation. INPA (black) is the dry forest described in this study, the moist forest values (La Chonta) (light gray) were derived from Rozendaal et al. (2006) and wet forest values (Los Tuxtlas) (dark gray) from Bongers and Popma (1988). The median (white line), interquatile range (upper and lower limits of the boxes; 75 and 25 percentile) and the total variation in plasticity (whiskers) are given for each trait. Boxes indicated with a different letter differ significantly at a P-level of 0.05 (Student's-Newman-Keuls-test). The plasticity in leaf traits per species was calculated as 100 * the absolute difference between the maximum and the minimum trait value divided by the maximum value. See table 2.2 for the trait abbreviations.

above the sampled sun (CO = 56.5 ± 0.3%) and shade trees (CO = 9.8 ± 0.1%). Species respond differently to an increase in light, as indicated by the high number of significant species–light interaction terms (Table 2.3). Different tree species thus have different ways of coping with resource capture and conservation.

Although the light effect explained minor proportions of the leaf trait variation, sun and shade leaves did differ in most traits. Results are overall in line with past studies reviewing the matter of leaf acclimation to irradiance (see, e.g., Bongers and Popma 1988, Sims and Pearcy 1989, Cao 2000, Evans and Poorter 2001, Rozendaal et al. 2006). While species differed substantially in their response to irradiance, there is a high correlation between species trait values in the sun and the shade (Table 3). This means that the species ranking for trait values is largely maintained in both light environments and that there is no crossover in trait performance between low and high irradiance. Shade tolerant and pioneer species may therefore specialize for different environments because of differences in their inherent traits (cf. Kitajima and Poorter 2008), rather than through phenotypic differences in trait values at low and high irradiance (cf. Sack and Grubb 2003).

The among-species variance of four of the 24 traits differed significantly between sun and shade leaves. Bongers and Popma (1989) argued that, if the among-species variance of a trait in a given light environment is smaller, the state of this trait has a greater importance for the performance of the leaf in that environment. A smaller among species variance therefore indicates convergent evolution in that light environment. We found a smaller variance in leaf area in the sun. Sun leaves are smaller to allow more effective cooling of the leaf area as they have a thinner boundary layer (Parkhurst and Louks 1972, Givnish 1984), thus avoiding supra-optimal leaf temperatures for photosynthesis. We also found a smaller variance in the internode to leaf area ratio. Sun leaves have a higher internode to leaf area ratio to compensate for the higher transpiration with an increased water supply (cf. Westoby and Wright 2003). In this way, plants increase the vessel number, rather than the vessel density or diameter. The variances in thickness of the outer cell wall and in the palisade to spongy parenchyma ratio were smaller in the shade (Table 2.3). Shade leaves have a thinner upper epidermis with a thinner outer cell wall, apparently because they need less protection than sun leaves. The outer cell wall and upper epidermis protect the leaf as they minimize the damaging effect of high irradiance through reflection of the excessive light (Roth 1984, Bondada et al. 1996) and reduce cuticular evaporation (Hall and Jones 1961). Shade leaves have a smaller palisade to spongy parenchyma ratio. The relatively thick spongy parenchyma layer is especially useful to enhance backscattering within the leaf of diffuse understory light. Bongers and Popma (1988) also found smaller variances in palisade to spongy parenchyma ratios in shade leaves in Los Tuxlas. Sun plants may regulate leaf temperatures through smaller leaves or an increased transpiration. Such a water-spending strategy is counterintuitive, however, given the limited water availability in the dry season. Sun trees may avoid dry-season water stress by exploring deeper soil layers, a larger soil volume for water (Poorter and Hayashida 2000), or by having a deciduous leaf habit. Of the species included in this study, we observed that at least 22 species showed a deciduous leaf habit in the dry season. Despite the fact that light acclimation and dynamic responses to light have been reported vary substantially with leaf longevity (Kursar and Coley 1993, 1999), leaf trait plasticity did not differ between evergreen (N = 14) and deciduous species (N = 22) in our study (t test: $1.45 \leq t \leq 1.32$; $P > 0.05$; df = 34).

Leaf trait plasticity varies between 0.3 and 24.6%. Leaf traits that have the greatest plastic response could be more important for leaf functioning in different light environments (Bongers and Popma 1988). If this were the case in our forest, palisade parenchyma thickness, palisade to spongy parenchyma ratio, thickness of the outer cell wall, the number of palisade parenchyma cell layers, N_{area} and P_{area} are most critical for light acclimation in our species. Three of these traits are anatomical and directly related to the palisade parenchyma tissue. The palisade parenchyma, N_{area} and P_{area} all play a distinct role in enhancing the photosynthetic capacity of the leaf (Evans 1999). The internode to leaf area ratio, the most plastic morphological trait in this study, is related to water supply and the thickness of the outer cell wall is related to water conservation. A high light-related plasticity was also found in N_{area} and palisade parenchyma thickness of 61 Mexican wet forest species (Bongers and Popma 1988). Rozendaal et al. (2006) analyzed the plasticity of 39 Bolivian moist forest species and found a high plasticity in internode to leaf area ratio, SLA, N_{area}, and P_{area}.

Plasticity among functional groups

Plasticity of four leaf traits was greatest for short-lived pioneers, in line with our first hypothesis. Yet, we did not expect that functional groups would differ in the plasticity of only so few leaf traits (cf. Sack et al. 2003). Many other studies showed considerable differences among functional groups (Popma et al. 1992, Kitajima 1994, Strauss-Debenedetti and Bazzaz 1996, Valladares et al. 2002). We may argue that, for relatively open forests such as tropical dry forests, plant traits and plasticity might be more closely related to drought-tolerance than to shade-tolerance.

In our study only the plasticity of leaf size parameters (LL, LW, and LA) and upper epidermis thickness differed among functional groups. For these traits, short-lived pioneer species had the greatest plasticity. This is in line with the hypothesis as formulated by Strauss-Debenedetti and Bazzaz (1996), which assumes that pioneer species have greater plasticity because they grow in more heterogeneous habitats, but in contrast with results from other studies (Sims and Pearcy 1989, Popma et al. 1992, Kitajima 1994, Rozendaal et al. 2006).

Plasticity in relation to adult size and crown exposure

Most leaf trait plasticity parameters were not correlated to maximum adult stature or ontogenetic crown exposure of the species. The lack of a relation with H_{max} is surprising because tall trees generally have to cope with all the changes in light environment that occur from the understorey to the forest canopy (cf. Poorter et al. 2005). Therefore we expected H_{max} and CE_{change} to be positively related to plasticity. That this is not the case may be because ontogenetic changes in crown exposure are related to ontogenetic plasticity, rather than the sun-shade plasticity derived from sun and shade trees of similar age. It might also be related to the fact that differences in light availability, especially during the dry period, are less pronounced in the deciduous dry forest, which therefore may not act as the only selective force. Low water availability in the dry season might constrain sun-shade plasticity and partly explain our counterintuitive results.

Leaf trait plasticity in dry and wet forests

Although sun and shade leaves differed in most leaf traits, the percentages of explained variation were generally low (Table 3). Only 3% of the total variation in leaf traits could be explained by differences between sun and shade leaves, while the same factor explained 8% of the leaf trait variation of 39 Bolivian moist forest tree species (Rozendaal et al. 2006). The smaller light effect in our study may well be the result of the more open and deciduous character of the dry forest compared to the moist forest.

When we compared the plasticity in leaf characteristics between three forests differentiated by water availability (Table 2.5), it was clear that the wet forest had greatest plasticity, while the differences between the other two forests were minor (Fig. 2.2). This is most probably related to variability in light availability which is much higher in Los Tuxtlas. The vegetation there is much denser with a much deeper shade year-round in the non-gap areas, while the vegetation in the other two forests is rather open. For such forests, leaf trait acclimation to differences in light availability may thus be not well-defined, because light is not as limiting as in hyperwet forests. An alternative explanation is that in the wet forest the shade leaves have been sampled in deeper shade. Given that the largest changes in leaf traits occur at the lowest light levels (Poorter 1999), this might have led to a different observed plasticity among forest types. We acknowledge that water and light availability are often interacting factors, especially in drier ecosystems. Lower water availability has been reported to reduce plant response to irradiance (Sánchez-Gómez et al. 2006, Quero et al. 2006). We do not believe that in this deciduous dry forest water is a limiting factor during the wet season, when these leaves are formed. Still tree species may follow a "conservative resource-use strategy" involving relatively low leaf-level responses to irradiance (cf. Valladares et al. 2000a).

Summarizing, we found that in the deciduous dry forest leaf trait variation is mainly explained by differences among species and only to a minor extent by differences in light availability. Sun-shade plasticity is therefore not large, and as a result, this plasticity is only very sporadically related to (ontogenetic changes in) the light requirements of the species. In relatively open dry forests, light-related plasticity seems to be less essential for species growth and survival than in wet forests, and the low water availability in dry forests may constrain the magnitude of leaf trait plasticity in response to irradiance.

Table 2.5

One-way-ANOVA and t-test with species plasticity in leaf traits for 2-3 forest types differing in mean annual precipitation. INPA (n=43) in is the dry forest described in this study, the moist forest values (La Chonta) (n=39) were derived from Rozendaal et al. (2006) and wet forest values (Los Tuxtlas) (n=62) from Bongers and Popma (1988). The mean plasticity (in %) is given for each forest type: values indicated with a different letter differ significantly at the 0.05 level (Student's-Newman-Keuls-test). The plasticity in leaf traits per species was calculated as the absolute difference between the maximum and the minimum trait value divided by the maximum value. See table 2.2 for the trait abbreviations.

	Statistics		INPA (dry forest)		La Chonta (moist forest)		Los Tuxtlas (wet forest)	
Precipitation			1100 mm		1517 mm		4639 mm	
Dry period			6-7 months		4-5 months		1-2 months	
Temperature			24.3 ºC		25.3 ºC		24.6 ºC	
ANOVA	F	p						
LL	11	***	11.5	a	7.82	a	17.4	b
LW	12	***	11.6	a	9.54	a	18.7	b
LA	10	***	21.6	a	15.7	a	30.2	b
LT	22	***	10.9	a	13	a	23.6	b
LDE	21	***	16.6	a	15.4	a	35.7	b
LS	13	***	5.68	a	5.43	a	11.8	b
LMA	23	***	15.7	a	22.7	b	33.4	c
LDMC	7.4	***	11.4	a	10.4	a	17.2	b
N_{mass}	10.1	***	8.3	a	8.9	a	16.2	b
P_{mass}	2.5	ns	15.8		13.6		19.5	
N_{area}	9.8	***	17.8	a	23.1	a	31.3	b
P_{area}	7.8	***	20.6	a	22.4	a	32	b
T-TEST	t	p						
LTO	1.2	ns	12.2		10.1		-	
SPL	1	ns	21.5		18.4		-	
ILAR	1.4	ns	36.7		29.9		-	
UET	-3.9	***	12.9	a	-		25.2	b
PPT	-2.6	*	24	a	-		32.1	b
SPT	-5.6	***	15.1	a	-		32.3	b
LET	-5.6	***	11.4	a	-		24	b
PSPR	-1.9	*	24.8	a	-		32.3	b
PPL	-1.4	ns	16.9		-		22.7	

Anadenanthera colubrina
(Fabaceae)

Chapter 3

Seasonal variation in soil and plant water potentials in Bolivian tropical moist and dry forests

Lars Markesteijn, José Iraipi, Frans Bongers and Lourens Poorter

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ABSTRACT

Heterogeneity in soil water availability codetermines species distribution in tropical forests. We determined the seasonal variation in soil matric potentials (ψ_{soil}) along a topographic gradient and with soil depth in a tropical dry and moist forest and analysed its effect on predawn leaf water potentials (ψ_{pd}) and drought response (standardised midday leaf water potential; ψ_{md}) of tropical tree saplings that differ in shade-tolerance and leaf phenology. In both forests ψ_{soil} changed during the dry season, but the drop was more extreme in the dry forest Crests were on average drier than slopes and valley bottoms and their soils remained dry for a longer period of time. In the dry forest the top soils was drier than deep soil in the dry season, but the inverse was found in the wet season. Species showed different seasonal patterns in ψ_{pd} in both forests. Short-lived pioneer species were found on wetter soils than drought-deciduous and shade-tolerant species. In the dry forest the shade-tolerant species occurred at the driest sites. Moist forest species did not differ in drought response, but the dry forest pioneer showed a larger drought response than the other two dry forest species. Heterogeneity in soil water availability in the two forests and among species differences in moisture requirements and drought response suggest a great potential for niche differentiation. Species may coexist at different topographical locations, by extracting water from different soil layers and / or by doing so at different moments in time.

KEYWORDS

Soil water availability, drought, leaf water potential, soil depth, niche partitioning, tropical dry forest, tropical moist forest, Bolivia

INTRODUCTION

Tropical lowland forests are found under different rainfall regimes. The majority of tropical forests have a pronounced dry season, and even in perhumid forests extended periods of drought can occur (e.g. Walsh and Newbery 1999, Burslem et al. 1996, Potts 2003). Tropical tree diversity and species distribution are to a great extent explained by the amount of annual precipitation, length of the dry period and the cumulative water deficit (e.g. Gentry 1988, Swaine and Becker 1999, Bongers et al. 1999, Poorter et al. 2004, Killeen et al. 2007) and within forests, topographical variation in water availability is an important factor influencing species distribution (Clark 1999, Webb and Peart 2000, Valencia et al. 2004, Comita and Engelbrecht 2009).

Topography controls the distribution of water and through surface run-off or lateral flow sediments and solutes are redistributed over the landscape. This affects soil depth, the ground water depth and soil properties (Sollins 1998, Lavelle and Spain 2002). At crests, ridges and steep upper slopes, high sediment removal rates result in shallow soils with a high sand content. Lower slopes and flat valleys, where weathering rates may exceed sediment removal, have deeper soils with higher clay and silt contents (Lescure and Boulet 1985, Johnsson and Stallard 1989, Pachepsky et al. 2001, Itoh et al. 2003). Resulting differences in soil texture influence water availability to the plants as fine soils have a higher water retaining capacity than coarse soils (Jenny 1980) and thus soil water availability generally increases down-slope (Becker et al. 1988, Daws et al. 2002). Topography has therefore potentially a strong effect on patterns of seedling emergence and mortality (Daws et al. 2005). Species occurrence along topographical gradients will additionally be influenced by several other covariables. Studies have shown that soil nutrients are relatively scarce on crest and elevated areas, compared to lower slopes or valleys (Tanner 1977, Gartlan et al. 1986, Baillie et al. 1987, Tanner 1992, Johnson 1992), while along large catenae strong winds can have a selective impact on the vegetation (Lawton 1982, Bellingham 1991) and an increased incidence of landslides may affect species occurrence (Guariguata 1990).

Especially young trees will experience drought stress as they have limited access to soil water with their relatively short or shallow root systems (Markesteijn et al. 2009). The success of species to occupy different niches with respect to water availability will thus largely depend on their ability to tolerate water stress and compete for water during drought (Engelbrecht and Kursar 2003).

Drought-tolerance is codetermined by a suite of functional traits, which include for instance high cavitation resistance (Zimmerman 1983, Tyree et al. 1994), strong stomatal control (Slot and Poorter 2007) or the maintenance of tissue turgor pressure at low leaf water potentials (Nunes et al. 1989, Engelbrech and Kursar 2003). It has recently been found that especially their capacity to tolerate low leaf water potentials determines drought survival and distribution of tropical tree species (Engelbrecht *et al.* 2007, Kursar *et al.* 2009).

The leaf water potential is a measure of the plant water status and mirrors the balance between the plants´ water loss and its water supply. Water loss is determined by the atmospheric evaporative demand and water supply is determined by soil water availability and plant hydraulic architecture (reviewed in Bhaskar and Ackerly 2006). Leaf water potentials show distinct diurnal and seasonal patterns of rise and decline that track patterns of evaporative demand and water supply. At a given point in time, the midday leaf water potential, which is measured when the sun has reached its zenith and diurnal vapour pressure deficits are highest, expresses the maximum leaf level water deficit the plant has to endure during the day (Pockman and Sperry 2000). At night, when transpiration is at a minimum, leaves are replenished until equilibrium between the soil and leaf water potential is reached. Hence the predawn leaf water potential, measured just before sunrise is an integral expression of the water potential of the soil just next to the roots and is a good predictor of the plant water availability.

While water availability is an important environmental factor for species occurrence in and among tropical forests, studies that actually quantify variation in soil water availability in tropical forests are rare. In this study we addressed this variation in a tropical dry deciduous forest and a tropical moist semi-deciduous forest by examining seasonal changes in soil matric potentials along a topographical gradient and with soil depth. We also investigated the implications of drought on the water status of saplings of tree species by monitoring the relative changes in predawn and midday leaf water potentials throughout the dry season. The following questions were addressed; 1) How do dry and moist forests differ in seasonal and topographical soil water potential?, 2) how does soil water potential vary with soil depth?, and 3) how does the seasonality of soil water potential affect the leaf water status of tree saplings?

METHODS

Study sites

Fieldwork was carried out in a lowland moist and a dry tropical forest in the department of Santa Cruz, Bolivia. Both forests are located on the Precambrian Brazilian shield (Chrochane 1973) in the transition between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Killeen *et al.* 1998, Jardim *et al.* 2003). Both forests are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF) and differ considerably different in terms of structure, diversity and species composition (Peña-Claros *et al.* submitted).

The moist site (La Chonta; 15°47'S, 62°55'W; 30 km east of Ascension de Guarayos) is classified as a tropical lowland semi-evergreen moist forest and has a mean annual precipitation of 1580 mm (meteorological data from 2000-2007 at La Chonta). Monthly potential evapotranspiration exceeds rainfall only in July and the dry season is therefore only 1 month long (Fig 3.1). The mean annual temperature is 25.3 °C. Soils are fertile inceptisols with a high cation exchange capacity and especially rich in P and Ca (Peña-Claros et al. submitted). The forest has a mean stem density of 367 trees ha^{-1}, a basal area of 19.3 m^{2} ha^{-1}, and a species richness of 59 ha^{-1} (trees $\geq$ 10 cm dbh, Peña-Claros et al. submitted). The average canopy height is about 27 m and ca. 30% of the canopy species shed their leaves in the dry season. Most common species are Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr. (Moraceae), Ampelocera ruizii Klotzsch (Ulmaceae) and Hirtella triandra Sw. (Chrysobalanaceae).

The dry site (Inpa; 16°07'S, 61°43'W), classified as a tropical lowland dry deciduous forest, has a mean annual precipitation of 1160 mm (meteorological data from 1943-2005 from AASANA for Concepción at 40 km) with a period of three months (June - September) when the potential evapotranspiration exceeds rainfall. Mean annual temperature is 24.3 ºC. The study area has generally poor soils, classified as oxisols (Pariona 1996). The forest has a mean stem density of 420 trees ha^{-1}, a basal area of 18.3 m^{2} ha^{-1}, and a species richness of 34 ha^{-1} (trees ≥ 10 cm diameter at breast height; Peña-Claros et al. submitted). Average canopy height is 20 m and virtually all canopy trees shed their leaves in the dry season. The most dominant species are Acosmium cardenasii H.S. Irwin & Arroyo (Fabaceae), Casearia gossypiosperma Briquet (Flacourtiaceae), and Caesalpinia pluviosa DC (Fabaceae).

Soil water availability

In both forests soil water availability was assessed along a topographical gradient. Applying a stratified random design, ten valley bottom-, slope- and crest-locations were randomly selected in the landscape. Different sampling points were located at least 50 m from each other. Sampling started in April 2007, at the end of the wet season, and continued throughout the dry season until the beginning of the next wet season in November 2007.

Leaf litter and coarse debris were carefully removed from the soil surface before sampling. Soil samples were taken with a soil auger, pooling the first 20 cm of top soil. At four of the ten locations per topographical position, soil samples were taken at six different depths, if possible, ranging from 20 to 120 cm. Again every 20 cm of soil were pooled. Sampling at deeper soil layers was often only possible at the valley positions, as the majority of the slope and crest positions had very shallow soils, often not more than 40 cm deep. Samples were sealed into plastic bags and transported to the field station.

Soil water availability was expressed as the soil matric potential (ψ_{soil}, in MPa). The matric potential of the soil becomes more negative with increasing drought and incorporates both the soil moisture content as the adhesive and cohesive forces in the soil matrix that capture the water between the soil particles (Jenny 1980). Soil matric potentials were determined with the filter paper method (Deka et al. 1995, Fawcett and Collis-George 1967). Collected soil samples were ground, after which half of the sample was placed in a small plastic container, covered by three Whatman nr. 42 filter papers (Whatman International Ltd., Kent, England) and topped with the second half of the sample. Containers were completely filled, firmly pressed, to avoid air pockets, hermetically sealed with duck tape, tagged and stored for at least seven days. After this incubation period the three filter papers were carefully removed from the soil sample. The middle paper was superficially cleaned of remaining soil particles and immediately weighted with a microbalance (with a 0.001 g precision) to determine its mass. With the dry mass of the filter papers known, the soil matric potential was estimated from the filter paper moisture content (FMC) following the protocol described by Deka et al. (1995), in which;

$$\mathrm{Log}_{10}(-\psi_p) = 5.144 - 6.699 * \mathrm{FMC} \qquad \text{, if } \psi_p < -51.6 \text{ kPa}$$

$$\mathrm{Log}_{10}(-\psi_p) = 2.383 - 1.309 * \mathrm{FMC} \qquad \text{, if } \psi_p > -51.6 \text{ kPa}$$

Plant water status

To study the effects of continued drought on the water status of juvenile trees we measured the predawn (ψ_{pd}) and midday leaf water potentials (ψ_{md}) of three different species at monthly intervals in both a dry and a moist tropical forest. Tree species were selected at the extremes of the shade- and drought-tolerance continuum: we included both typical shade-tolerant species and typical short-lived pioneers with an evergreen leaf habit at the sapling stage, and a drought-deciduous species in each forest. One species was in common between forests. Leaf water potentials were measured using the pressure bomb technique (Tyree and Hammel 1972). Leaf water potential measurements were taken in the same period as those of the soil water potential. Per species ten saplings (1 – 1.5 m tall) with fully illuminated crowns were selected along logging roads. Leaf water potentials were measured predawn (ca. 5.30h) and at midday (ca. 14.00h) on mature, exposed and fully expanded leaves, showing no signs of pathogen or herbivore damage. Next to each sapling soil samples (0 – 20 cm) were collected with an auger at midday to assess the soil matric potentials. Soil sampling and estimation of soil matric potentials were done as described earlier (cf. Deka et al. 1995).

Data analyses

To improve normality and homoscedasticity of the data, the soil and leaf water potentials were $\log_{10}$-transformed ($y = -\mathrm{Log}_{10}(-\psi + 1)$). To evaluate how seasonal and topographical variation in soil matric potential varied between both forests, we conducted a repeated measures ANOVA. Soil matric potential was included as the dependent variable, and forest (moist, dry) and topographical position (valley, slope, crest) as independent factors. The values for each month were included as the repeated measure over time (n= 7; April-October). The amount of variation explained by the forest, species and time was calculated as the sum of squares of the effect divided by the total sum of squares of the model (η^2 * 100%). η^2 is equivalent to R^2. The generally shallow soils at slope and crest positions resulted in missing values from deep soil layers. To avoid an unbalanced design and loss of degrees of freedom only the values for the first 20 cm of top soil were included in this analysis,

To evaluate how soil water potentials varied with soil depth and how these patterns shift with ongoing drought, a repeated measures ANOVA was conducted. The model included the observed soil matric potential as the dependent variable, and forest (moist, dry) as the independent factor. This particular model included two repeated measures. As before, ´month´ was included as the measure over time, and additionally ´depth´ was included as a repeated measure along the soil profile. The analyses was run on the soil matric potential values collected at valley positions only, as the shallow soils at slope and especially crest positions generally prevented sampling deeper than 40 to 60 cm.

To evaluate how different tree species respond to a given plant water availability a repeated measures ANCOVA was carried out. Midday leaf water potential was included as

Table 3.1

Relationship between species-specific midday leaf water potentials, soil matric potentials and predawn leaf water potential. The table shows the linear relations between the midday leaf water potentials, soil matric potentials and predawn leaf water potentials of the five moist and dry forest tree species (log-log scale); n = 28. (4 trees x 7 months), except for Sweetia fruticosa (n = 24), as it shed its leaves in August. r^2 and the significance level are given (α=0.05); ^{ns} $P > 0.05$, *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). The last column gives the midday leaf water potential (ψ_{md}) of the species at a standardised predawn leaf water potential (ψ_{pd}) of -0.98 MPa. Numbers with different letters vary significantly.

Species	ψ_{soil}		ψ_{pd}		ψ_{md} (MPa)	
	r^2	P	r^2	P		
MOIST FOREST						
Ampelocera ruizii	0.21	*	0.41	***	-1.83	c
Sweetia fruticosa	0.45	***	0.65	***	-1.97	c
Trema micrantha	0.16	*	0.28	**	-1.67	c
DRY FOREST						
Acosmium cardenasii	0.13	ns	0.78	***	-2.92	b
Sweetia fruticosa	0.01	ns	0.56	***	-3.12	ab
Solanum riparium	0.16	*	0.69	***	-3.33	a

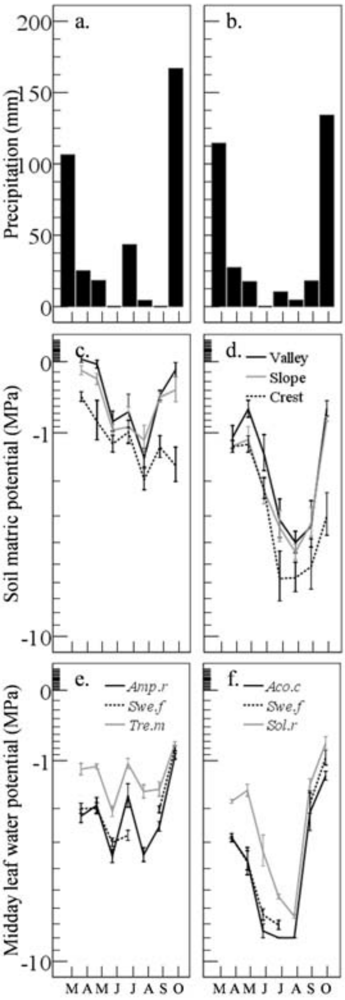

Figure 3.1

Seasonal variation in precipitation, soil matric potentials and midday leaf water potentials. The graph shows the precipitation in the moist (A.) and dry forest (B.). The bars represent the sum of the precipitation of March 2007 and the months covered by this study (April – October 2007) (Data from the nearby towns of Ascención de Guarayos (A.) and Concepción (B.). Figures C. and D. represent the seasonal and topographical variation in soil matric potentials (logarithmic scale) in the moist and dry forest respectively, with different topographical positions represented by the different lines. Valleys are represented by the continuous black lines, slopes by the continuous grey lines and crests by the dotted black lines. Figures E. and F. give seasonal variation in the mean midday leaf water potential (logarithmic scale) of three moist forest and three dry forest species. Whiskers give the standard error for every month.

RESULTS

Between forest variation in seasonal and topographical soil water availability

The ψ_{soil} showed a clear seasonal pattern of variation, which varied with forest type and topography (Table 3.2, Fig. 3.1). Time explained 45% of the total variation, the interaction forest x time explained 10%, and topography x time 4% of the variation. The three-way interaction was not significant (Table 3.2).

The first ψ_{soil} measurements were taken in April, at the onset of the dry season, when monthly precipitation had first dropped below 100mm (Fig. 3.1). In April ψ_{soil} were still relatively high in both moist (-0.2 MPa) and dry forest (-1.1 MPa), probably due to residual soil moisture from March, when precipitation was still relatively high (>100mm). From April onwards ψ_{soil} declined until reaching their lowest values in August (on average -1.4 vs. -4.4 MPa), at the height of the dry season. In the dry forest, ψ_{soil} were persistently low in July, August and September. In contrast, in the moist forest ψ_{soil} were relatively high in July, probably in response to erratic rainfall in that month (Fig. 3.1). In the moist forest increased ψ_{soil} in September suggest an earlier end of the dry season.

Across the season ψ_{soil} was, on average, lower in the dry forest (-2.1 MPa) than in the moist forest (-0.7 MPa) and varied among valleys (-0.9 MPa), slopes (-1.1 MPa) and crests (-1.8 MPa). In both moist and dry forest crest positions were significantly drier (-1.0 and -2.7 MPa) than valleys (-0.4 and -1.6MPa) and slopes (-0.5 and -2.0). Although the variation explained by topography was relatively low compared to the variation explained by forest type, the effect of topography is more pronounced in the dry forest than in the moist forest, accounting for 4.4% versus 1.5% of the within-forest variation (Table 3.2, Fig. 3.2).

Table 3.2

Seasonal and topographical variation in soil water availability of two tropical forests. The table shows the results of an ANOVA with time as a repeated measure, forest and topographical position as independent factors and soil matric potential as the dependent variable. F and P-values of within- and between-subject effects are given, as is η^2, a measure of the total amount of variation explained by the effects.

Effects		Statistics		
		F	P	η^2 (%)
Within-Subjects				
	Time	61	***	45
	Time * Forest	14	***	10
	Time * Topography	3	**	4.4
	Time * Forest * Topography	1	ns	1.1
Between-Subjects				
	Forest	274	***	12
	Topography	32	***	2.8
	Forest * Topography	1	ns	0.0

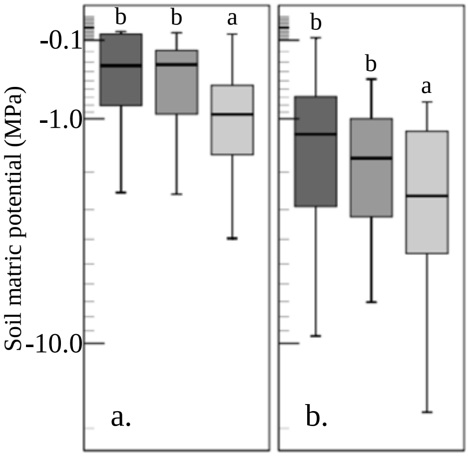

Figure 3.2

Differences in soil matric potentials within forests along a topographical gradient. The graph describes soil matric potentials (logarithmic scale) in the moist (a) and dry forest (b) at different topographical positions; valleys (dark gray), slopes (medium gray) and crests (light grey). The median (black horizontal bar), interquartile range (upper and lower limits of the boxes; 75 and 25 percentile), and the total variation in soil matric potentials are given. Within forests, topographical positions with different letters vary significantly (α=0.05) (Tukey-test); *** P < 0.001.

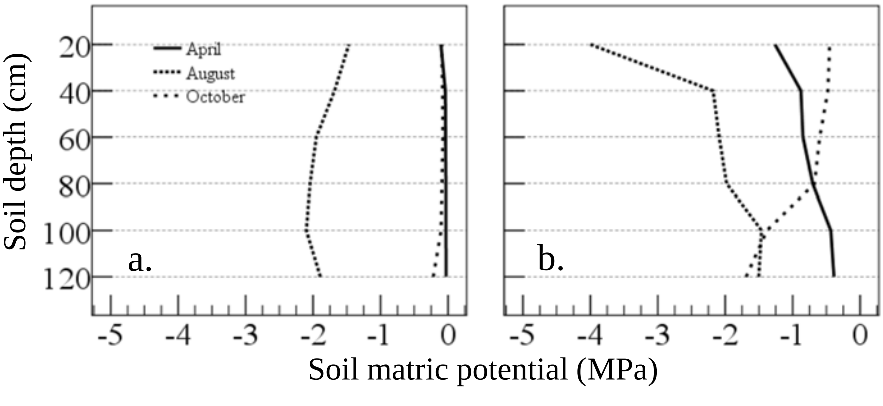

Figure 3.3

Changes in soil matric potentials with soil depth. The graphs shows how soil matric potentials change with soil depth in the moist (a) and dry forest (b) and how these patterns shift throughout the dry season. Lines give the patterns for different months (April, August and October).

soil matric potentials between the upper and deeper soil layers slightly increased over time, however, indicating that top soils dried out faster. In October, after the onset of the wet season, the vertical pattern suddenly shifted. Deeper soil layers ended up being much drier than upper soil layers, as it took a considerable amount of time for rain water to percolate down the soil profile.

Table 3.3

Seasonal changes in soil water availability with soil depth in two tropical forests. The table shows the results of an ANOVA with time and soil depth as repeated measures, forest as independent factor and soil matric potential as the dependent variable. F and P-values of within- and between-subject effects are given, as is η^2, a measure of the total amount of variation explained by the effects.

Effects		Statistics		
		F	P	η^2 (%)
Within-Subjects				
	Time	16	***	57
	Time * Forest	1.8	ns	6.3
	Depth	1.2	ns	0.3
	Depth * Forest	2.5	ns	0.6
	Depth * Time	6.7	***	5.3
	Depth * Time * Forest	4.5	***	3.6
Between-Subjects				
	Forest	41	***	12

The effect of drought on leaf water status of juvenile trees

The repeated measures ANOVA clearly demonstrates a change in ψ_{pd} potentials through the dry season in both forests and also a significant interaction with species (Table 3.4). This interaction was significant in the moist forest, but not in the dry forest ($P>0.05$). Seasonal patterns in ψ_{pd} track the seasonal changes in ψ_{soil}.

Ψ_{pd} differed among species in both the moist ($P<0.01$) and the dry forest ($P<0.001$). In the moist forest the short-lived pioneer species Trema micrantha, was on average found at wetter sites (lower ψ_{pd}) than the shade-tolerant species Ampelocera ruizii and the drought deciduous species Sweetia fruticosa (Fig. 3.4a). Differences among species became more pronounced with time (Fig. 3.4a). In the dry forest this micro-habitat differentiation among species was more pronounced (Fig. 3.4b) with the short-lived pioneer Solanum riparium on the wettest the shade-tolerant species Acosmium cardenasii on the driest sites, and the deciduous species Sweetia fruticosa on the intermediate dry sites.

By comparing the ψ_{md} among species at a common ψ_{pd}, the drought response of saplings could be assessed. The ANCOVA showed that there was a strong and significant effect of ψ_{pd} on ψ_{md}, explaining 19% of the total variation. The interaction effect of ψ_{pd} with species explained an additional 3% of the variation (Table 3.5). This indicated that the slopes of the relationship between predawn and midday leaf water potentials were different among species. At the standardised ψ_{pd} of -0.98 MPa, species differed substantially in ψ_{md} (Fig. 3.5). Interestingly, Solanum riparium, the dry forest pioneer, found in relatively wet micro-habitats in the dry forest, showed the greatest drought response (-3.33 MPa). Among moist forest species no differences in standardised ψ_{md} were found, but moist forest species did have higher ψ_{md} than the dry forest species (Fig. 3.5).

Table 3.4

Seasonal changes in predawn leaf water potentials among moist and dry forest tree species. The table shows the results of an ANOVA with time as a repeated measures, species as independent factor and predawn leaf water potential as the dependent variables. F and P-values of within- and between-subject effects are given, as is η^2, a measure of the total amount of variation explained by the effects.

Effects		Statistics		
		F	P	η^2 (%)
Within-Subjects				
	Time	47	***	50
	Time * Species	6	***	31
Between-Subjects				
	Species	17	***	3.5

Table 3.5

One-way ANCOVA showing the effect of species (n=6) on midday leaf water potentials. Predawn leaf water potential was included a covariate. Sum of squares, degrees of freedom, en the mean squares, F-values, significance levels (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$) and the amount of explained variation (η^2) of the effects are given.

Effect	SS	df	MS	F	P	η^2 (%)
Corrected Model	4.98	11	0.45	36.8	***	51
Intercept	0.80	1	0.80	64.9	***	8.1
Species	0.07	5	0.01	1.18	ns	0.7
ψ_{pd}	1.85	1	1.85	150	***	19
Species * ψ_{pd}	0.31	5	0.06	4.98	***	3.1

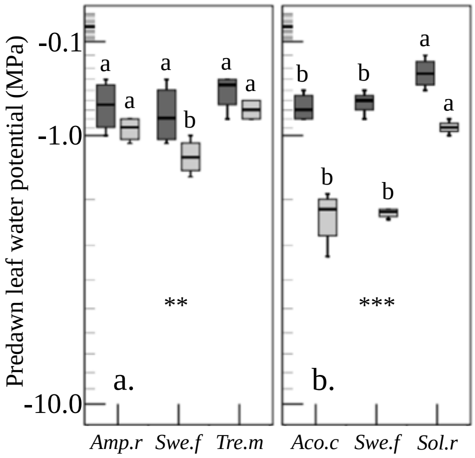

Figure 3.4

Differences in plant water availability among species within a tropical moist and dry forest. The graph describes leaf water potentials (logarithmic scale) in the moist (a) and dry forest (b) of five different species at the onset of the dry season (April; dark grey boxes) and halfway the dry season (July; light grey boxes) The median (black horizontal bar), interquartile range (upper and lower limits of the boxes; 75 and 25 percentile), and the total variation in soil matric potentials are given. Within forests and within month species with different letters vary significantly (Tukey-test); **

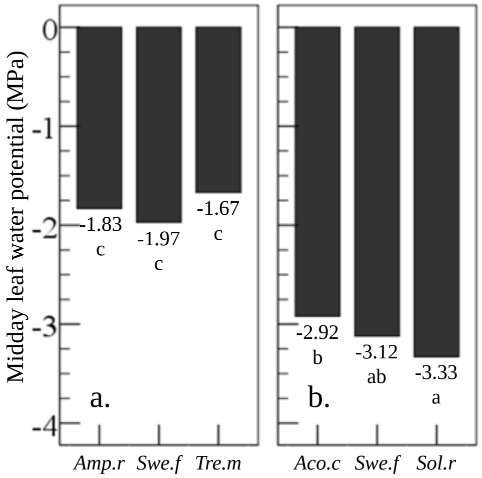

Figure 3.5

Among species differences in midday leaf water potentials (at a standardized predawn leaf water potential of -0.98 MPa). The graph describes leaf water potentials (logarithmic scale) of three moist (a) and dry forest tree species (b). Among species, different letters indicate significant differences ($P < 0.001$) as resulted from an F-test ($\alpha=0.05$), based on independent linear pair wise comparisons of standardized species means (with a Bonferoni adjustment for multiple comparisons).

Other abiotic factors may explain some of the ψ_{soil} differences between forests. In the dry forest almost all dominant canopy trees shed their leaves during the dry season, and thus the evaporative demand and atmospheric water deficit will be higher in the dry forest, whereas in the moist forest the relatively closed canopy can acts as a buffer to excessive evaporation and can substantially alter the sub-canopy microclimate. Still evergreen canopy trees in the moist forest maintain transpiration in the dry season, which explains why within moist forests the soil of gaps are wetter than those under the closed forest canopy (Veenendaal et al. 1996).

Within forest topography had a clear effect on soil water availability. Throughout the season valleys and slopes were relatively wet compared to crests. This corroborates with the findings of several other studies (Lescure and Boulet 1985, Butler et al. 1986, Becker et al. 1988, Ishizuka et al. 1998, Yanagisawa and Fujita 1999, Daws et al. 2002, Gibbons and Newbery 2003), underlining the importance of topography in redistributing soil water over the landscape.

How does the seasonality of soil water availability affect the leaf water status of juvenile trees?

Before evaluating the effect that seasonal drought had on the water status of juvenile trees we first assessed how to best express or define water availability to the plant. Plant water availability was measured in two ways; (1) as the soil matric potential (0 – 20 cm) next to the sapling using the filter paper method (cf. Deka et al. 1995), and (2) as the predawn leaf water potential, which reflects the mean soil water potential next to the roots. The midday leaf water potential was measured as an expression of the maximum drought response of the tree at a given soil water potential. Linear regression analyses examined the dependence of the midday leaf water potential on the soil matric potential and the predawn leaf water potential, respectively, and showed that for all species predawn leaf water potentials better explained midday leaf water potentials than soil matric potentials did, especially so for dry forest species (Table 3.1.). These results indicated that predawn leaf water potentials closer described the actual plant water availability than the soil matric potential of the top soil next to the plant.

Temporal variation in ψ_{pd} closely tracked ψ_{soil}, and the precipitation (Fig. 3.1). The ψ_{pd} is a good estimator of the actual water availability to a plant as it expresses the water potential of the soil immediately next to the root at any given moment in time. Ψ_{md} at the other hand expresses the minimum water potential a plant has to tolerate due to the leaf level water deficit at a given moment in time (Pockman and Sperry 2000). Although we sampled saplings growing under similar light conditions we found some differences in ψ_{pd} among species. Ψ_{pd} was similar among moist forest species, but the dry forest pioneer Solanum riparium had a higher ψ_{pd} than the other species, both in the wet and the dry season. This indicates that S. riparium grew on relatively wet soils in comparison to the other species (Fig. 3.4).

Pioneer species are light-demanders that generally realise high growth rates as they aim to quickly reach a dominant position in the forest canopy after disturbance or gap creation (Whitmore 1989). Pioneer species follow an acquisitive resource strategy and realise high photosynthetic rates with a high stomatal conductivity in order to maximise carbon gain and growth (Ellis 2000, Poorter and Bongers 2006). However this comes at the cost of an increased transpirational water loss at the leaf. Especially in dry forests, where evaporative demand is greater than in moist forests and the dry season forms a bottleneck for survival of juvenile trees (Engelbrecht et al. 2006), pioneer species will be filtered out of the landscape and persist in relatively wet habitats. A recent study addressed such hydraulic habitat partitioning among 40 different dry forest tree species and found that pioneer species had greater moisture requirements, and were thus less drought-tolerant, than shade-tolerant species (Markesteijn et al. submitted).

By comparing the ψ_{md} at a standardised ψ_{pd} of -0.98 MPa, we were able to evaluate species responses to drought under equal moisture conditions. While S. riparium grows in relatively wet soils compared to the other two dry forest species, it also had the lowest standardised ψ_{md} and thus the greatest drought response (Fig. 3.5). The fact that S. riparium showed the greatest drought response even though it occupied relatively wet habitats underlines the drought-intolerant nature of the species. Even with better access to soil water than the other dry forest species, the leaf level water deficits, catalysed by high transpiration and low stomatal control result a disproportional decrease in ψ_{md}. The relatively large potential gradient that is formed between soil and leaf will probably facilitate an increased hydraulic conductivity and promote continued physiological activity in the dry season. We did not actually combine leaf water status measurements with photosynthesis measurements, and thus it is hard to say whether at the height of the dry season S. riparium was still fully active. We observed that saplings of this species showed signs of wilting and a loss of turgor at midday in August, when drought was strongest, which suggests that the species was functioning suboptimal.

The drought-deciduous species S. fruticosa had relatively low ψ_{pd}, in the dry forest and in the moist forest dry season only. This species can thus grow on relatively dry soils compared to evergreen pioneers as T. micrantha and S. riparium. The deciduous leaf habit of S. fruticosa allows this by avoiding extreme water stress in the dry season. Interestingly, S. fruticosa was leafless in both forests at the same time rather than at the same soil water potential. Reich and Borchert (1984) proposed that in tropical dry forests leaf shedding should be induced by water stress early in the dry season. Our results show that this is not the case for S. fruticosa for which the timing of leaf shedding is apparently genetically determined or induced by other environmental factors than soil water, e.g. air humidity and temperature (cf. Wright 1991), leaving little room for phenotypic plasticity.

That S. fruticosa was able to grow on relatively dry soil in the moist forest (Fig. 3.4) may indicate that it occupies a clear ecological niche in this system. As niche differentiation between the evergreen species A. ruizii and T. micrantha seems to be governed by light partitioning under wet conditions, deciduous species can coexist with these species by being the better competitor in drier micro-habitats, where their survival probability is greater. Deciduousness is a major factor enhancing drought survival of tropical tree seedlings from both forests (Poorter and Markesteijn 2008).

Studies tend to find clear patterns of species-habitat associations along topographical gradients in tropical forests (Clark 1999, Webb and Peart 2000, Valencia et al. 2004) and e.g. Mediterranean chaparral scrublands (Meentemeyer et al. 2001, Ackerly et al. 2002). Still in many studies the topographical gradient is only assumed to represent a gradient in soil water availability, without actually quantifying to what extent. Species-habitat associations in the two forests we addressed here will still have to be investigated, but based on our present results we can at least point out that there is a great potential for habitat differentiation, especially in the dry forest and that different species may be physiologically or morphologically adapted to compete for water at different positions along the topographical gradient.

Within the forests the distribution of drought-intolerant evergreen pioneers is most likely restricted to relatively wet habitats, whereas evergreen shade-tolerant and drought-deciduous species are better equipped to tolerate low leaf water potentials in habitats of low soil water availability or evade excessive drought by shedding their leaves at the height of the dry season. In theory this would imply that along the topographical gradient in water availability we described in this paper, wet valley bottoms are most suitable for the establishment and survival of pioneer species. It should be more likely to find evergreen shade-tolerant and drought-deciduous species at the drier slopes and crests. As the higher soil water availability leads to denser vegetations in the valleys and as pioneers are light-demanding in nature, most will not be able to establish and compete in wet valleys, unless some kind of disturbance has created favourable light conditions. Instead pioneers, as S. riparium will have to increase their access to soil water in high light environments. They are thus either spatially restricted to relatively low, wet areas or they are able to increasing their access to soil water at the spot. Preliminary observations in the field suggested that S. riparium forms a rather extensive root system with a lot of lateral branching and it seems to exploit a greater volume of soil than the other species. We found this to be typical for seedlings of pioneer species in general (Markesteijn and Poorter 2009). In contrast seedlings of shade- and drought tolerant of many species were found to forage for water in deeper soil layers, but at first sight the two other species did not clearly show any deep rooting (Poorter pers. obs.). The temporal variation in soil water with soil depth suggests that deep rooting species would have an advantage in acquiring water from deeper soil layers in the dry season, as this is where water availability is greatest (Fig. 3.3), while shallow rooting species may be the first one to exploit relatively wet upper soil layers at the start of the wet season. Shallow rooting may also facilitate in exploiting incident rainfall as seemed to be the case in the moist forest in July, when midday leaf water potentials increased back to normal wet season values (Fig. 3.1e).

CONCLUSIONS

Water availability is one of the most important factors influencing species distribution in the tropics. Still studies that actually quantify water availability in tropical forests and its sources of variation are rare. In this study we demonstrated that tropical forests and especially dry systems show a great deal of temporal and spatial variation in soil water availability. Temporal variation mainly depends on the annual cycle of precipitation, although many other factors may be of influence. Spatial heterogeneity can be seen as two-dimensional. First of all there is a horizontal component in which soil water availability differs between forests and within forest along a topographical gradient. Secondly spatial variation is manipulated by the vertical redistribution of the water with soil depth. When combining the three dimensions topography, soil depth and time, a very complex mosaic of water availability emerges that shows a great potential for niche partitioning at various levels. In both moist and dry forests saplings of different tree species were shown to vary in moisture requirement and showed to respond differently to drought with a progressing dry season. If their morphological and physiological adaptations permit species to successfully compete for water at different topographical locations, or to tap their water from different soil layers and/or do so at different moments in time, a great variety of species may be allowed to coexist. Heterogeneity of soil water availability should thus be considered as one of the key processes explaining the high biodiversity of tropical forest in general and seasonally dry forests in specific.

Cariniana estrellensis
(Lecythidaceae)

Chapter 4

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

Lars Markesteijn and Lourens Poorter

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ABSTRACT

Water availability is the main determinant of species distribution in lowland tropical forests. Species occurrence along water availability gradients depends on their ability to tolerate drought. To identify species traits underlying drought-tolerance we excavated first year seedlings of 62 dry and moist forest tree species at the onset of the dry season. We evaluate how morphological seedling traits differ between forests, and whether functional groups of species can be identified based on trait relations. We also compare seedling traits along independent axes of drought and shade-tolerance to assess a hypothesised trade-off. Seedlings of dry forest species improve water foraging capacity in deep soil layers by an increased belowground biomass allocation and by having deep roots. They minimize the risk of cavitation by making dense stems, and reduce transpiration by producing less leaf tissue. Moist forest seedlings have large leaf areas and a greater above-ground biomass, in order to maximize light interception, and long, cheap, branched root systems, to increase water and nutrient capture. Associations among seedling traits reveal three major drought strategies: 1) evergreen drought-tolerant species have high biomass investment in enduring organs, minimize cavitation and minimize transpiration in order to persist under dry conditions; 2) drought-avoiding species maximize resource capture during a limited growing season and then avoid stress with a deciduous leaf habit in the dry season; 3) drought-intolerant species maximize both below- and above-ground resource capture to increase competitiveness for light, but are consequently precluded from dry habitats. We found no direct trade-off between drought- and shade-tolerance, because they depend largely on different morphological adaptations. Drought-tolerance is supported by a high biomass investment to the root system, while shade-tolerance is mainly promoted by a low growth rate and low SLA. We conclude that there are three general adaptation strategies of drought-tolerance, which seemingly hold true across biomes and for different life forms. Drought- and shade-tolerance are largely independent from one another, suggesting a high potential for niche differentiation, as species specialisation can occur at different combinations of water and light availability.

KEYWORDS

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

INTRODUCTION

Species composition of tropical forests changes considerably with water availability (Bongers et al. 2004, Ter Steege et al. 2006): on a large scale, patterns of species distribution change along rainfall gradients (Hall and Swaine 1981, Swaine 1996, Engelbrecht et al. 2007), as species vary in the annual precipitation, length of the dry period and cumulative water deficit at which they are most abundant (Bongers et al. 1999), on a smaller scale, species occurrence is affected by topographical variation in water availability, even in relatively wet ecosystems (Borchert 1994, Clark 1999, Valencia et al. 2004). Occurrence along these large- and small-scale gradients of water availability depends on a species ability to resist drought. While drought-intolerant species are associated with relatively wet slopes and valleys, more drought-resistant species are associated with dry elevated areas (Harms et al. 2001, Engelbrecht and Kursar 2003). Under wet, shady conditions, drought-resistant species are probably out-competed by drought-intolerant ones.

Climate change scenarios predict a decrease in annual rainfall, an increase in dry season length and greater inter-annual rainfall variability for the tropics (Bawa and Markham 1995, Hulme and Viner 1998). If we want to assess how species will respond to these changes in water availability, we need to understand how they are adapted to drought. There is a longstanding interest in the effects of water deficit on basic plant processes, especially in the agricultural literature (reviewed in Iljin 1957, Vaadia et al. 1961, Hsiao 1973). Some early work also includes classifications of plants based on their physiological response to water stress and ability to survive water shortages (e.g. Milthorpe and Spencer 1957, De Wit 1959). Nowadays two major strategies of species adaptation to drought can be identified, each with its specific suite of functional traits: 1) tolerating drought stress and 2) delaying drought stress. Drought-tolerance is promoted by a plant's continued physiological functioning at low water availability. Drought-tolerant species reduce the probability of xylem cavitation and maintain gas exchange, hydraulic conductance and cell survival at low water potentials (Engelbrecht and Kursar 2003, Tyree et al. 2003). Delaying drought stress can be achieved by deciduousness, i.e. shedding leaves in the dry season (Reich and Borchert 1984, Borchert 1994). Deciduousness is a strong predictor of seedling survival during drought (Poorter and Markesteijn 2008), but comes at the expense of a shorter growing season and regular biomass loss. Deciduous species are therefore often light-demanding (Eamus and Prior 2001) and highly efficient in reabsorbing nutrients before shedding their leaves (Aerts 1996, H. Paz, pers. comm.), which are cheap because of a low biomass investment per unit leaf area, but costly in terms of nutrient or carbon loss (Givnish 2002). Evergreen species can delay drought stress by maximizing their access to water, while minimizing transpirational water loss. Traits associated with this form of drought-delay include high biomass investments to the root system, high specific root lengths, small leaf area and strong stomatal control (cf. Paz 2003, Slot and Poorter 2007, Poorter and Markesteijn 2008).

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

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

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

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

allow them to maximize water capture and/or conservation, while minimizing transpirational water loss. Moist forest seedlings will show adaptations that enhance their light interception.

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

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

METHODS

Forest sites

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

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

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

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

Species and seedling selection

We selected a total of 62 species from 30 families; 34 species from the dry forest and 37 species from the moist forest, with 9 species in common between both sites (Table 4.2). The selection of the species was based on their relative abundance in each forest and together they represent more than 75% of all trees ≥ 10 cm dbh (M. Peña-Claros, unpublished data).

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

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

Seedling traits

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

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

The 21 traits presented are functionally important for the following reasons: seedling biomass serves as a proxy for relative growth rate over the first year. Leaf area and leaf mass fraction describe the plant level biomass investment in light intercepting tissue, while leaf size is important for the regulation of heat load. The specific leaf area and leaf area ratio indicate how efficiently plants display their leaves to intercept light. Stem density is an indicator of the stem vulnerability to cavitation (Preston et al. 2006), and the stem mass fraction and leaf area per unit stem area are important for biomechanical and hydraulic support. Rooting depth, area and volume indicate how much and what part of the soil volume is explored for nutrients and water. The root mass fraction indicates the biomass investment in belowground foraging, and the specific root length and secondary-to-primary-root-mass ratio indicate how efficient this biomass is used to create a large absorptive area. Root length, and root length per unit leaf area and per unit plant mass indicate the relative amount of hydraulic support. Root water content is an indicator for the construction costs of roots (how much root “volume” is created per unit of root dry mass), and the potential for water storage in the roots. Seedling traits and their abbreviations are summarized in Table 4.1.

Table 4.1

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

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

Species drought- and shade-tolerance

The 62 study species were ranked along independent axes of drought- and shade-tolerance. We used a ‘drought index’ (DI) as an ecological indicator of a species drought-tolerance (cf. Poorter and Markesteijn 2008). The DI corresponds to the species distribution along the rainfall gradient and was derived from the relative abundance of a species in the dry and the moist forest. The DI is calculated as: DI = 100(D_{dry} / D_{dry} + D_{moist}), where D_{dry} and D_{moist} are the mean stem densities (tree ha-1) of a given species in the dry and the moist forest site, respectively. Stem densities were calculated from the number of trees ($\geq$ 10 cm d.b.h.), for 32 one-hectare plots in the dry and 48 one-hectare plots in the moist forest (Peña-Claro et al., in prep.). It is important to keep in mind that the DI provides a simplified description of the actual species distribution, as it resulted from an analysis including two forests only. The DI thus provides a rough estimate of the actual species position along the rainfall gradient, as the species occurrence further up or down the gradient (in wetter or drier systems) could not be assessed. The DI among species varies from 0 to 100, where 0 indicates that a species is only found in the moist forest, and 100 indicates that the species is only found in the dry forest, while the remainders occur at both sites (0<DI<100) (Table 4.2). The DI is positively correlated with the seedling drought survival of evergreen species, as determined under standardised experimental conditions (Poorter and Markesteijn 2008).

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

Table 4.2

List of 62 species with scientific and family names and abbreviations as used in the graphs. The species drought index (relative distribution of species along the rainfall gradient) (DI) is given, as well as their juvenile crown exposure (CE). Values presented are the back-transformed species means of seedling biomass at harvest (BIOM) and seedling traits included in this study. Trait values were calculated at a standardized seedling size of 4.7 grams (see table 4.1 for the abbreviations).

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

Table 4.2 Continued

Species	Family	Code	DI	CE	BIOM g	LA cm^2	LS cm^2	SLA cm^2 g^{-1}	LMF g g^{-1}	LAR cm^2 g^{-1}	SD g cm^{-3}	SMF g g^{-1}	RD cm	RA cm^2	RV cm^3	RL cm	SRL cm g^{-1}	RWC g g^{-1}	RMF g g^{-1}	RLLA cm g^{-1}	RLPM cm g^{-1}	SPRMR cm cm^{-1}	LASA cm^2 mm^{-2}
MOIST FOREST																							
Alibertia verrucosa	Rubiaceae	Ali.v	1	1.35	2	50	16	214	0.51	112	0.72	0.27	14	0.56	1.66	22	269	0.64	0.19	0.45	50	1.15	25
Ampelocera ruizii	Ulmaceae	Amp.r	2	1.35	8	58	17	288	0.43	126	0.45	0.33	6	3.89	8.13	135	1288	0.57	0.22	2.34	295	1.48	17
Aspidosperma cylindrocarpon	Apocynaceae	Asp.c	82	1.75	4	42	10	174	0.45	79	0.48	0.24	4	0.72	2.09	26	309	0.61	0.17	0.63	50	1.29	13
Batocarpus amazonicus	Moraceae	Bat.a	6	1.35	4	49	13	302	0.36	100	0.36	0.32	10	0.16	0.46	30	282	0.67	0.25	0.60	60	1.10	17
Caesalpinia pluviosa	Fabaceae	Cae.p	94	1.87	5	23	5	339	0.16	52	0.74	0.38	8	0.89	2.04	28	141	0.46	0.44	1.17	62	1.07	7
Cariniana estrellensis	Lecythidaceae	Car.e	0	1.40	8	49	9	331	0.34	110	0.55	0.28	10	0.13	0.15	28	191	0.65	0.37	0.60	66	1.12	15
Cariniana ianeirensis	Lecythidaceae	Car.i	21	1.74	7	26	5	380	0.20	59	0.30	0.39	5	1.78	4.07	28	155	0.80	0.41	1.05	60	1.12	3
Casearia gossypiosperma	Flacourtiacae	Cas.g	93	1.83	7	59	11	316	0.43	132	0.66	0.23	9	0.21	0.62	69	513	0.59	0.31	1.17	155	1.35	25
Cavanillesia hylogeiton	Malvaceae	Cav.h	0	2.16	35	35	48	380	0.21	79	0.16	0.55	3	10.72	16.98	7	71	0.94	0.22	0.19	15	1.35	2
Cecropia concolor	Cecropiaceae	Cec.c	30	2.44	7	93	13	331	0.63	204	0.30	0.13	3	3.39	4.47	76	794	0.72	0.23	0.81	170	2.34	15
Cedrela fissilis	Meliaceae	Ced.f	33	1.98	11	129	66	724	0.39	282	0.21	0.31	4	46.77	346.74	60	513	0.81	0.27	0.47	135	2.40	19
Centrolobium microchaete	Fabaceae	Cen.m	95	1.94	7	33	10	389	0.23	76	0.58	0.37	7	0.06	0.17	18	107	0.58	0.38	0.54	40	1.05	10
Ficus boliviana	Moraceae	Fic.b	2	1.93	7	31	6	380	0.19	69	0.27	0.33	7	3.47	3.63	79	389	0.74	0.46	2.57	178	1.51	6
Gallesia integrifolia	Phytolaccaceae	Gal.i	58	1.84	3	35	12	316	0.25	76	0.43	0.43	4	1.20	1.23	138	1000	0.53	0.31	3.98	302	1.41	6
Heliocarpus americanus	Malvaceae	Hel.a	46	2.36	3	93	22	417	0.50	204	0.19	0.31	5	1.58	2.19	62	851	0.77	0.16	0.66	135	1.45	15
Hirtella triandra	Chrysobalanaceae	Hir.t	0	1.28	1	58	28	282	0.46	126	0.74	0.31	9	0.09	0.20	42	490	0.59	0.22	0.72	91	1.17	23
Hura crepitans	Euphorbiaceae	Hur.c	0	1.62	6	69	11	537	0.29	151	0.15	0.40	5	1.66	4.68	49	380	0.82	0.29	0.71	107	1.38	5
Jacaratia spinosa	Caricaceae	Jac.s	0	2.02	2	110	24	708	0.37	245	0.13	0.40	10	4.17	10.96	32	372	0.90	0.20	0.29	71	1.17	6
Licaria triandra	Lauraceae	Lic.t	0	1.35	4	38	9	214	0.40	85	0.49	0.32	16	2.51	5.13	44	372	0.66	0.27	1.15	98	1.26	11
Myrciaria sp.	Myrtaceae	Myr.	48	1.45	2	49	16	295	0.37	110	0.74	0.31	8	0.41	0.52	63	490	0.37	0.29	1.29	138	1.35	22
Ocotea sp.	Lauraceae	Oco1	0	1.37	4	45	10	224	0.44	98	0.46	0.31	3	4.17	9.55	52	501	0.68	0.23	1.17	115	1.70	13
Ocotea sp.	Lauraceae	Oco2	0	1.34	4	41	9	209	0.43	89	0.55	0.31	17	2.14	7.59	42	389	0.60	0.24	1.02	91	1.20	14
Pourouma cecropiifolia	Cecropiaceae	Pou.c	0	1.38	1	63	6	309	0.45	141	0.44	0.25	8	0.23	0.27	30	251	0.47	0.26	0.46	65	1.20	21
Pouteria macrophylla	Sapotaceae	Pou.m	0	1.55	3	39	15	204	0.42	85	0.58	0.26	4	3.89	15.14	26	178	0.58	0.31	0.66	56	1.12	17
Pouteria nemorosa	Sapotaceae	Pou.n	0	1.57	8	19	4	331	0.13	41	0.47	0.29	9	0.06	0.16	35	135	0.53	0.57	1.91	78	1.10	4
Pseudolmedia laevis	Moraceae	Pse.l	0	1.32	3	49	14	240	0.46	107	0.46	0.23	8	1.15	4.47	45	468	0.55	0.22	0.93	100	1.07	15
Sapindus saponaria	Sapindaceae	Sap.s	2	2.23	10	72	25	468	0.35	162	0.28	0.31	9	3.09	9.33	63	447	0.67	0.32	0.87	138	1.48	13
Sapium glandulosum	Euphorbiaceae	Sap.g	8	1.63	8	35	8	437	0.32	78	0.37	0.34	8	0.04	0.12	91	603	0.60	0.34	2.57	200	1.58	7
Schizolobium parahyba	Fabaceae	Sch.p	0	2.39	8	63	16	372	0.38	141	0.31	0.29	10	10.72	20.89	105	871	0.80	0.28	1.62	229	2.04	10
Spondias mombin	Anacardiaceae	Spo.m	48	1.95	3	26	10	479	0.17	56	0.29	0.22	6	0.13	2.24	20	78	0.79	0.62	0.78	44	1.10	6
Stylogyne ambigua	Myrsinaceae	Sty.a	0	1.46	2	54	18	229	0.52	120	0.40	0.23	6	0.20	0.37	41	389	0.71	0.23	0.76	91	1.35	13
Sweetia fruticosa	Fabaceae	Swe.f	78	1.91	9	54	19	407	0.31	120	0.65	0.23	13	0.00	0.00	16	79	0.56	0.45	0.30	35	1.02	28
Swietenia macrophylla	Meliaceae	Swi.m	0	1.62	7	78	17	380	0.44	170	0.30	0.31	5	0.11	0.28	18	191	0.57	0.21	0.23	40	1.05	17
Terminalia oblonga	Combretaceae	Ter.o	0	1.88	11	68	9	324	0.49	151	0.71	0.28	3	0.26	0.29	100	1047	0.34	0.22	1.48	224	1.35	25
Trema micrantha	Ulmaceae	Tre.m	0	2.52	5	81	17	380	0.49	178	0.32	0.23	4	7.24	10.23	117	1023	0.65	0.26	1.45	257	3.31	26
Urera caracasana	Urticaceae	Ure.c	7	1.99	9	100	21	479	0.47	224	0.26	0.12	5	0.89	5.13	178	1122	0.80	0.38	1.78	398	1.62	19

Do field data reflect inherent species differences or environmental differences?

When comparing functional seedling traits of species with data collected in the field, there is always the possibility that results are partly confounded by differences in environmental conditions under which seedlings were growing. To assess the magnitude of this problem we compared the species-specific trait values obtained for seedlings growing in the field with the values obtained from an independent common garden experiment, in which seedlings were grown at 10% of full irradiance (Poorter and Markesteijn 2008). For 31 species common to both studies we found that seedling trait values in the field and the greenhouse were highly correlated (Table 4.1): of the 13 traits compared 11 were positively correlated, 7 of which strongly ($0.60 \geq r \geq 0.87$; $P < 0.001$). Leaf area and leaf area ratio were unrelated between both studies, probably because they are strongly size-dependent and more prone to ontogenetic drift (no ontogenetic correction was done in the greenhouse study). The strong correlations between trait values obtained in the greenhouse and the field suggests that environmental heterogeneity in the field confounded the results only to a limited extent, and that sound generalisations can be made based upon this field study.

Data analysis

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

We tested for the effect of forest type, species and seedling biomass on traits with a two-way nested ANCOVA, with forest as fixed factor, species nested within forest as a random factor and $\log_{10}$-transformed seedling biomass as a covariate. The amount of variation explained by the forest, species and seedling size was calculated as the sum of squares of the effect divided by the total sum of squares of the model (η^2 * 100%). η^2 is equivalent to R^2. The model showed that there was a strong effect of seedling biomass on most traits, and that sometimes the slopes were not homogeneous (Table 4.3). To correct for ontogenetic effects in further cross-species analyses, the trait values for each species were recalculated at a standardized seedling biomass of 4.7 g, using species-specific regression equations. 4.7 g is the grand mean biomass for all species and individuals lumped.

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

Table 4.3

Two-way nested ANCOVA with the effect of forest (n=2) and species nested within forest (n=71) on seedling traits. Log-transformed seedling biomass was included a covariate to test its effect on seedling traits and interaction with forest (Forest * Biomass) and species (Species within forest * Biomass). F-values, significance levels (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$) and the amount of explained variation (η^2) of the effects are given. η^2 is an equivalent of R^2 and was calculated as the sum of squares of the effect relative to the total sum of squares (*100, in %). LMF, SMF, RMF and RWC arcsine transformed and the other traits were log$_{10}$-transformed prior to analysis. The means of the absolute seedling trait values of dry and moist forest species (n=34 and 37 respectively) are presented. See table 4.1 for the trait abbreviations.

Traits	Forest			Species within forest			Biomass			Forest * Biomass			Species within forest * Biomass			Means per forest	
	F	p	η^2	F	p	η2	F	p	η2	F	p	η2	F	p	η2	Dry	Moist
Total seedling biomass (g)	7	**	1	9	***	52										4.20	4.85
LA (cm^2)	156	***	3	17	***	19	3917	***	66	0	ns	0	2	***	3	34.8	54.0
LS (cm^2)	22	***	1	3	***	13	916	***	50	5	*	0	2	***	7	8.01	12.1
SLA (cm^2 g^{-1})	26	***	1	27	***	73	15	***	1	0	ns	0	2	***	5	309	333
LMF (g g^{-1})	134	***	6	18	***	60	73	***	4	0	ns	0	2	**	5	0.30	0.37
LAR (cm^2 g^{-1})	178	***	8	17	***	54	151	***	7	0	ns	0	2	***	7	80.4	111.0
SD (g cm^{-3})	224	***	7	29	***	67	114	***	4	1	ns	0	2	***	5	0.53	0.38
SMF (g g^{-1})	53	***	3	13	***	56	7	**	0	18	***	1	2	***	8	0.27	0.30
RL (cm)	11	***	0	17	***	46	745	***	28	1	ns	0	2	***	5	39.4	47.7
RD (cm)	122	***	10	5	***	21	399	***	33	0	ns	0	1	ns	4	15.3	12.6
RA (cm^2)	10	**	1	8	***	27	679	***	43	0	ns	0	1	*	5	12.3	17.8
RV (cm^3)	0	ns	0	6	***	18	948	***	55	0	ns	0	1	*	4	189	223
SRL (cm g^{-1})	130	***	4	23	***	47	984	***	30	5	*	0	2	***	4	253	354
RWC (g g^{-1})	82	***	5	11	***	50	8	**	1	0	ns	0	3	***	11	0.59	0.67
RMF (g g^{-1})	313	***	12	20	***	53	161	***	6	16	***	1	3	***	8	0.40	0.30
RLLA (cm cm-^{2})	25	***	1	11	***	44	271	***	16	0	ns	0	2	***	8	1.13	0.88
RLPM (cm g^{-1})	16	***	1	18	***	45	827	***	30	0	ns	0	2	***	5	91.5	97.3
SPRMR (g g^{-1})	137	***	9	12	***	52	0	ns	0	0	ns	0	2	**	7	1.14	1.32
LASA (cm^2 mm^2)	3	ns	0	17	***	64	1	ns	0	2	ns	0	2	***	7	11.5	12.3

RESULTS

Between forests and among species variation

Variation in seedling traits between forests and among species was evaluated with a nested ANOVA, including seedling biomass as a covariate. All traits but RV and LASA differed significantly between dry and moist forests, but the amount of explained variation was low (0.4-12%) in comparison to among species variation (13-73%) (Table 4.3). Seedling biomass significantly explained variation in all traits but SPRMR and LASA (0.4-66%). There was a significant biomass-forest interaction effect on four traits, but the magnitude of this interaction effect was small (0.2-1.1%). A greater portion of the total variation was explained by the interaction between seedling biomass and species within forests (3-11%). The interaction was significant for all traits except RD (Table 4.3), indicating that species follow species-specific ontogenetic trajectories.

The strongest differences between dry and moist forest seedlings were found for RMF, RD, SPRMR, LAR and SD (Table 4.3). Seedlings of dry forest species had a higher biomass fraction in roots than moist forest species. Dry forest species had deeper root systems whereas moist forest species showed more secondary, lateral roots (higher SPRMR) covering a larger soil area (larger RA) and had a larger total root length. Dry forest species generally make a primary root with little to no lateral extensions that is relatively short and thick, with a low SRL. Dry forest species showed a lower RWC, but a higher SD than moist forest species, had smaller leaves and a higher root length per unit leaf area (Table 4.3). Total rooting volume (RV) did not differ between forests. Furthermore seedlings of moist forest species invested more of their total biomass into their leaves (they had high LMF and LAR, and a large LA) and their leaves were relatively thin (high SLA) in comparison to dry forest seedlings. Moist forest seedlings had a higher stem mass fraction and more root length per unit plant biomass.

Trait associations and functional groups

We evaluated the associations among species traits with a principal component analysis (PCA). We included the 18 seedling traits together with seedling biomass, deciduousness and compoundness in the analysis. The first two axes together explained 48% of the variation, the first axis 28% (Fig. 4.1). Dry and moist forest species differed in their position along the first PCA axis (t-test; t = 2.7, d.f. = 66, P = 0.009), with moist forest species having higher axis scores. Species that invest biomass in aboveground light capture and have efficient root extension for belowground resource capture (a high root length per unit biomass invested) are found towards the right. Seedlings of these species have a high LAR and LMF, while they show relatively long and thin roots (high SRL) with more lateral branching (high SPRMR). Most species on this side of the axis are found in the moist forest (Fig. 4.2) with a clear cluster of pioneers marking the end of the gradient (Solanum riparium; Sol.r, Trema micrantha; Tre.m, Cecropia concolor; Cec.c, Urera caracasana; Ure.c, Heliocarpus americanus; Hel.a, Urera baccifera; Ure.b and Schizolobium parahyba; Sch.p). Species on the left side of the axis invest a greater portion of their biomass in their root system (high RMF, large RD) and stem (high SD and SMF). These species have a compound leaf habit (Fig. 4.1) and are mainly dry forest species and shade-tolerant moist forest species (Fig. 4.2). This axis corresponds with ‘persistence’, as it ranks species that can persist under low resource conditions at the left to ephemeral, short-lived species with a high resource demand at the right.

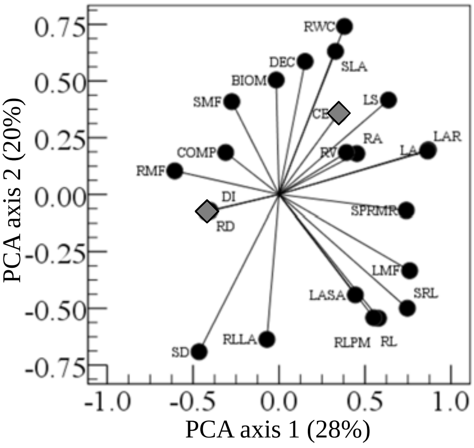

Figure 4.1

Principal component analysis (PCA) with the mean values of the seedling traits, of 62 tree species. Trait values were calculated at a standardized seedling size of 4.7 grams. The first two PCA axes are shown with the percentages of explained variation. Total seedling biomass at the time of harvest (BIOM) was included in the analyses as a continuous variable and deciduousness (DEC) and compoundness (COMP) were included as dummy variables (0,1). Species drought index (DI) and juvenile crown exposure (CE) were not included in the PCA, but plotted later based on their Pearson correlation coefficients with the first two axes.

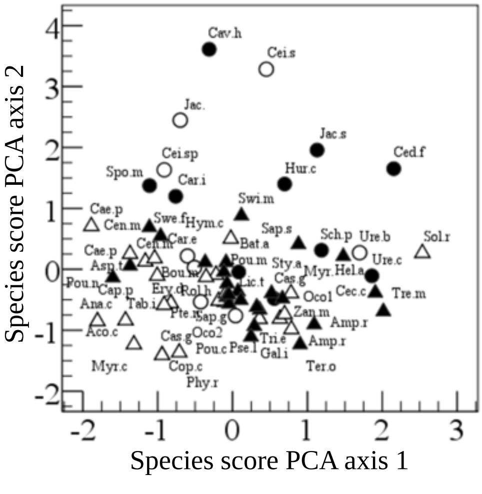

Figure 4.2

Species scores along the first two principal components. Species names are given as abbreviations (see Table 4.2). Different symbols indicate forest type and deciduousness. Open symbols represent dry forest species, closed symbol represent moist forest species. Dots represent deciduous species and triangles represent evergreen species.

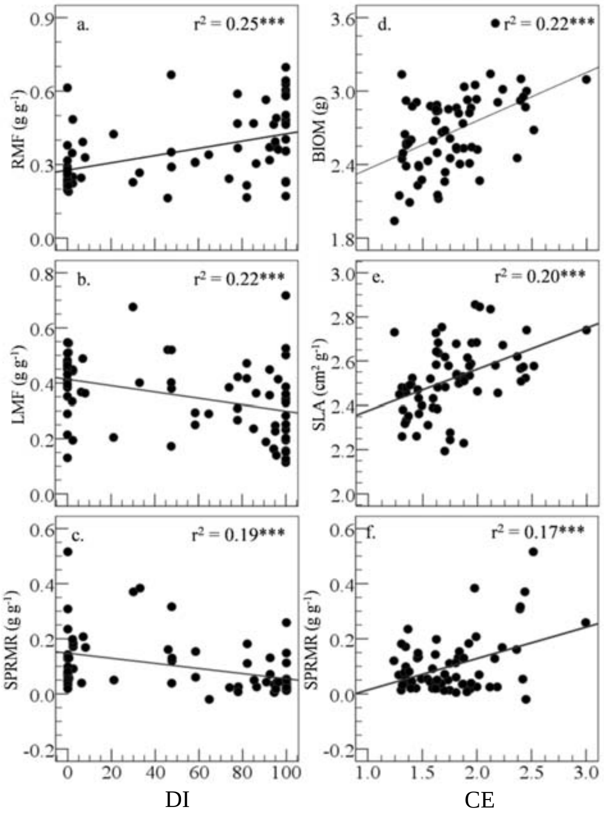

Figure 4.3

Associations between species drought index (DI; n=56), juvenile crown exposure (CE; n=59) and functional seedling traits. Trait values were calculated at a standardized seedling size of 4.7 grams. Not all 62 species were included in the analyses as we were unable to calculate the DI for six and CE for three species. a) root mass fraction (RMF; g g^{-1}), b) leaf mass fraction (LMF; g g^{-1}), and c) secondary to primary root mass ratio (SPRMR; g g^{-1}) with the DI, and d) seedling biomass (BIOM; g), e) specific leaf area (SLA; cm^{2} g^{-1}), and f) secondary to primary root mass ratio (SPRMR; g g^{-1}) with CE. Regression lines, coefficients of determination, and significance levels are shown. * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

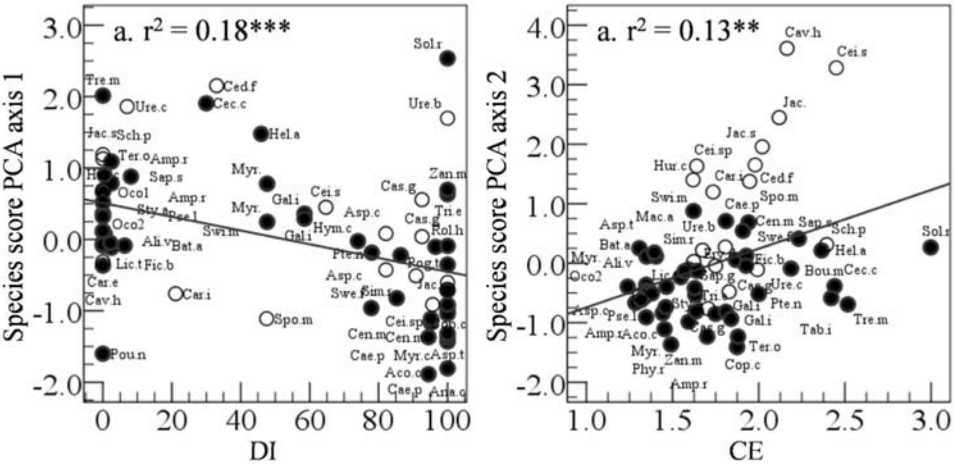

Figure 4.4

Association between species drought index (DI), juvenile crown exposure (CE) and the species scores along the first two principal components. a) DI with the species scores along the first principal component axis and b) CE with the species scores along the second principal component axis. Regression lines with coefficients of determination and significance levels are shown.

Table 4.4

Correlation among species traits. Traits were calculated at a standardized seedling size of 4.7 grams, the drought index (DI), juvenile crown exposure (CE) and the first two PCA axes of 62 tropical tree species. Pearson correlation coefficients are shown (2-tailed; n=62) at (Italic) p<0.05; (Bold) p<0.01; (Bold Italic) p<0.001. See Table 4.1 for trait abbreviations.

	BIOM	LA	LS	SLA	LMF	LAR	SD	SMF	RD	RA	RV	RL	SRL	RWC	RMF	RLLA	RLPM	SPRMR	LASA	DEC	COMP	DI	CE
LA	0.04																						
LS	0.03	***0.71***																					
SLA	*0.28*	**0.39**	**0.38**																				
LMF	*-0.25*	***0.71***	***0.44***	-0.19																			
LAR	-0.05	***0.96***	***0.75***	***0.45***	***0.71***																		
SD	**-0.35**	***-0.40***	**-0.37**	***-0.59***	-0.04	***-0.41***																	
SMF	0.15	-0.23	0.02	0.20	***-0.44***	-0.21	-0.09																
RD	-0.04	*-0.27*	*-0.26*	-0.04	-0.22	*-0.26*	**0.31**	0.13															
RA	0.13	0.17	0.18	**0.33**	0.07	0.22	***-0.40***	0.02	-0.17														
RV	0.15	0.13	0.15	**0.33**	0.04	0.16	**-0.36**	-0.02	-0.06	***0.98***													
RL	-0.04	*0.24*	-0.10	0.01	**0.32**	0.19	-0.05	*-0.28*	*-0.24*	*0.29*	*0.25*												
SRL	-0.11	***0.46***	0.12	-0.06	***0.61***	***0.41***	-0.11	-0.20	*-0.27*	*0.27*	0.22	***0.90***											
RWC	***0.39***	**0.34**	***0.40***	***0.49***	0.03	**0.31**	***-0.86***	0.17	-0.21	*0.28*	*0.27*	-0.04	0.05										
RMF	0.17	***-0.60***	***-0.46***	0.18	***-0.77***	***-0.57***	0.09	-0.14	0.15	0.02	0.07	-0.13	***-0.53***	-0.14									
RLLA	-0.11	***-0.45***	***-0.58***	-0.22	-0.16	***-0.44***	0.21	-0.13	-0.05	0.17	0.16	***0.74***	***0.51***	*-0.29*	*0.27*								
RLPM	-0.14	*0.24*	-0.07	0.09	**0.35**	*0.26*	-0.07	*-0.29*	*-0.25*	**0.34**	*0.29*	***0.95***	***0.86***	-0.08	-0.13	***0.75***							
SPRMR	0.17	***0.50***	0.22	0.20	***0.49***	***0.48***	*-0.30*	-0.17	**-0.37**	**0.37**	**0.32**	***0.55***	***0.64***	**0.27**	**-0.38**	0.18	***0.56***						
LASA	**-0.36**	***0.54***	***0.42***	-0.15	***0.66***	***0.57***	***0.40***	***-0.49***	-0.01	-0.12	-0.12	0.09	*0.24*	***-0.41***	***-0.39***	*-0.27*	0.13	0.14					
DEC	*0.25*	0.18	0.15	***0.43***	-0.20	0.14	***-0.47***	0.11	-0.22	0.15	0.15	0.01	-0.04	***0.55***	0.09	-0.12	-0.02	0.16	**-0.36**				
COMP	0.19	-0.10	-0.03	0.08	*-0.28*	-0.15	0.14	-0.05	0.02	-0.21	-0.16	*-0.26*	**-0.34**	-0.08	*0.26*	-0.17	*-0.30*	-0.13	-0.01	-0.02			
DI	-0.06	***-0.41***	*-0.30*	-0.18	***-0.44***	***-0.42***	**0.39**	-0.16	0.02	*-0.29*	*-0.28*	-0.16	**-0.37**	**-0.36**	***0.50***	0.11	-0.18	***-0.44***	-0.06	0.00	**0.39**		
CE	***0.47***	***0.40***	*0.29*	***0.45***	0.06	**0.34**	**-0.37**	-0.06	-0.23	0.16	0.14	0.16	0.14	**0.37**	-0.01	-0.15	0.10	***0.41***	-0.06	0.23	0.20	0.06	
PCA axis 1	-0.02	***0.87***	***0.64***	**0.33**	***0.76***	***0.86***	***-0.47***	*-0.27*	***-0.40***	***0.45***	***0.39***	***0.55***	***0.75***	**0.38**	***-0.61***	-0.07	***0.58***	***0.74***	***0.44***	0.15	*-0.31*	***-0.42***	**0.35**
PCA axis 2	***0.50***	0.20	***0.42***	***0.63***	**-0.33**	0.19	***-0.69***	***0.41***	-0.07	0.18	0.18	***-0.54***	***-0.50***	***0.74***	0.10	***-0.64***	***-0.54***	-0.07	***-0.44***	***0.59***	0.18	-0.13	**0.36**

heterogeneity leads to additional noise (Møller and Jennions 2002). However, given the fact that our field data and experimental data were strongly correlated (see Methods), this may also indicate that other factors than first year seedling morphology (e.g. seedling physiology, Engelbrecht et al. 2007) determine the assembly of dry and moist tropical forest communities. Within each forest, there was a surprisingly large inter-specific variation in seedling traits (average explained variation is 45%, range 13–73%, Table 4.3). This large variation may be important, because it possibly allows coexisting species to sort out along smaller-scale environmental gradients within each forest. Seedling size at the onset of the dry season had a strong effect on 16 out of 18 seedling traits and explained on average 23% of the variation (range 1-66%, Table 4.3). This strong ontogenetic drift indicates that many traits change when plants increase in size, and indicates that ontogenetic corrections, as done in this study, are important to avoid erroneous conclusions (cf. Evans 1972, Poorter and Pothmann 1992).

Overall, seedling morphology of dry and moist forest species differed in line with the hypothesis of Brouwer (1963) which predicts that, under a given regime of stresses, plants maximize their surface area for intake of the most limiting resource. In tropical dry deciduous forests water is the most limiting resource for plant growth and survival. Consequently, seedlings of dry forest species enhance water uptake through an increased RMF, a higher root length per unit leaf area and a greater RD, which allows them to forage more efficiently in deeper soil layers, where more water is available, especially in the dry season (Engelbrecht et al. 2005). Rooting volumes did not differ significantly between dry and wet forest seedlings. Foraging deeper underground, rather than increasing the volume of exploited soil, appears to be the preferred strategy when it comes to water acquisition in dry ecosystems. Rooting depths were indeed found to be greater in vegetations from dry ecosystems (Canadell et al. 1996, but see Schenk and Jackson 2002), in seedlings from forests with a long dry period (Paz 2003) and in species from dry sandy soils (Yamada et al. 2005). Dry forest seedlings had a smaller SRL, SPRMR, root length and rooting area than moist forest seedlings, in contrast to our hypothesis. In terms of water availability, dry forest species grow in a poorer resource environment than moist forest species. This may call for a conservative, rather than an acquisitive resource strategy. Dry forest species reduce water loss through a reduction of the amount of transpirational tissue (low LS, LA, SLA and LAR) and their seedlings have higher stem densities, which makes them less vulnerable to xylem cavitation. High stem densities mainly result from smaller vessels that have a higher resistance to embolism (Castro-Díez 1998, Hacke et al. 2001, Tyree and Zimmermann 2002). Cavitation reduces hydraulic conductance as vessels become (partly) dysfunctional once an embolism has formed (Tyree and Sperry 1989, Tyree and Zimmermann 2002). Such reduced hydraulic conductance limits photosynthesis (Santiago et al. 2004) and can ultimately result in the loss of entire stem sections.

We hypothesized that moist forest seedlings should show characteristics related to acquisition of light rather than water as dense vegetation casts deeper shades and reduces light availability, thus making light the most limiting resource. Moist forest species indeed increased their light interception by investing a large portion of their biomass in leaf tissue (high LMF) by making larger leaves, having a larger total seedling leaf area, and having higher SLA and LAR. The bigger seedling size of moist forest species at the onset of the dry season may both be the result of a longer growing season and of a higher relative growth rate, and can be advantageous to dry season survival as bigger seedlings are less susceptible to drought (Kobe *et al.* 1995, Poorter and Hayashida-Oliver 2000, Gilbert 2001). Moist forest species increased below-ground resource capture by producing long, branched root systems (high SPRMR), which at first sight seems in contradiction with our hypothesis. However, moist forest species may be more nutrient and water demanding, because of their greater photosynthetic capacity and higher inherent growth rates.

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

Trait associations and functional groups

Species separated along two major trait axes that reflected species variation in persistence and deciduousness, respectively. The persistence axis separated drought- and shade-tolerant species from water- and light-demanding species (Fig. 4.1 and Fig. 4.2). Persistent species show a conservative resource use strategy with high biomass investment in enduring plant organs (roots and stem) and little in leaf tissue. These species are generally slow-growing and forage for water in deeper soil layers. Their high stem densities suggest a lower risk of cavitation (Tyree and Sperry 1989, Tyree and Zimmermann 2002), a higher structural stability and smaller chance of damage by falling debris or herbivory. The water- and light-demanding species at the other end of the gradient allocate more biomass to their leaves, resulting in a larger total leaf area, which allows for increased light foraging, and thus more photosynthesis. In addition, they have long and branched root systems (cf. Huante *et al.* 1992) which increase the probability to encounter and exploit high nutrient pockets (Fitter 1985, Craine 2002, Raynaud and Leadley 2004) and fuel onward growth. These drought-intolerant species therefore follow an acquisitive resource strategy, maximising resource uptake to increase their competitiveness in relatively wet microhabitats.

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

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

Is there a trade-off between drought- and shade-tolerance? The underlying mechanisms revisited

Smith and Huston (1989) predicted a trade-off between drought- and shade-tolerance based on a trade-off in biomass allocation to roots versus shoot. We indeed found a strong trade-off between RMF and LMF ($r = 0.77$, $P < 0.001$). Still no trade-off between drought- and shade-tolerance was found, neither when all species were taken into account ($r = 0.06$, $P > 0.05$) (Table 4.4, Fig. 4.1), nor when analyzing evergreen species ($r = 0.26$, $P > 0.05$) and deciduous species ($r = -0.39$, $P > 0.05$) separately.

Evidence for the proposed biomass allocation trade-off is equivocal and the underlying mechanisms are not well understood. Root and leaf mass fraction affect below- and aboveground foraging capacity only to a minor extent (cf. Poorter and Nagel 2000). Moreover, a small biomass investment in roots (low RMF) can be compensated for by making cheap roots with a large root length per unit biomass invested (i.e. a high SRL). Likewise, a low biomass investment in leaves (low LMF) can be compensated for by realizing a large leaf area per unit leaf biomass invested (i.e. high SLA) (Poorter 2005), through the formation of thin or low density leaves (Witkowski and Lamont 1991). Our results partly support the latter idea. RMF and SRL are indeed negatively correlated ($r = -0.53$, $p<0.001$), which leads to an uncoupling of RMF and root length per unit plant mass ($r = -0.13$, $P > 0.05$). However, LMF is only marginally negatively correlated with SLA ($r = -0.19$, $p>0.05$), and therefore there is still a positive association between LMF and LAR at the whole-plant level ($r = 0.71$, $p < 0.001$) (Table 4.4, Fig. 4.1). Because of the compensation by SRL, and to a lesser extent SLA, this means that at the whole plant level there is no trade-off between the surface area for belowground (RLPM) and above-ground (LAR) resource capture per unit plant mass ($r = 0.26$, $p < 0.05$), and hence no trade-off between drought- and shade-tolerance (Table 4.4, Fig. 4.1).

The multiple regression analyses further showed that drought- and shade-tolerance were mainly determined by different suites of traits (see also Fig. 4.4). Our results thus support the idea that drought- and shade-tolerance are uncoupled and vary independently. This implies a high potential for species niche differentiation, because adaptations that favour drought-tolerance do not necessarily restrain species performance in the shade, nor do adaptations that favour shade-tolerance automatically imply that species are drought-intolerant (Coomes and Grubb 2000, Sack and Grubb 2002, Sanchez-Gomez et al. 2006).

We also reported on the correlations of morphological seedling traits with a DI in an experimental study (Poorter and Markesteijn 2008) and overall we found the same trends in the current study. RMF and compoundness were positively related and LAR, LMF and SMF were negatively related to the DI. Still a multiple regression analysis on that experimental data showed that the DI was mainly explained by different traits than in the current field study. Both studies have a large number of species in common ($n = 31$), but nine of the experimental species were not studied in the field and thirty-one species from this field study were not assessed in the experiment. Additionally, not all traits measured in the experiment were measured in the field, and several new traits that were not measured in the experiment were added in the field study. These methodological differences probably explain some discrepancies in results between both studies.

CONCLUSIONS

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

Jacaratia spinosa
(Caricaceae)

Chapter 5

Ecological and functional correlates of cavitation resistance among tropical dry forest tree species

Lars Markesteijn, Lourens Poorter, Horacio Paz, Lawren Sack and Frans Bongers

ABSTRACT

When drought occurs and soil water potentials drop, the pressure gradient in xylem vessels increases and they are more likely to become dysfunctional due to cavitation. It is thus crucial for dry forest tree species to protect their vascular system against excessive cavitation and secure hydraulic conductivity in the dry period. In this study we analysed vulnerability curves for saplings of 13 tropical dry forest tree species differing in life history strategy and leaf phenology. I examined how cavitation resistance (i.e. P_{50}) is influenced by stem and leaf traits and how it determines the leaf water potential in the field. Among species P_{50} values ranged from -0.8 to -6.2 MPa. Pioneer species were more vulnerable to cavitation than shade-tolerant species, but evergreen and deciduous species did not differ. P_{50} was negatively related with wood density and, against expectation; maximum vessel length had a negative additive effect. P_{50} was negatively associated with the Huber-value and LDMC, and positively with leaf size. We found a trade-off between cavitation resistance and hydraulic efficiency. Most species in the field were operating well above their hydraulic limit, but pioneers had smaller hydraulic safety margins than shade-tolerants

KEYWORDS

Cavitation resistance, Hydraulic conductivity, Wood density, Functional traits, Leaf water potential, Tropical dry forest, Bolivia

INTRODUCTION

It is widely supported that water is transported through the xylem of woody plants under negative pressure (Tyree 1997, Angeles et al. 2004, but see Zimmermann et al. 2004). When drought occurs, soil water potentials drop, the pressure gradient in the plants xylem increases and vessels are more likely to become dysfunctional due to cavitation. It is thus crucial for their growth and survival that trees from seasonally dry forests protect their vascular system against excessive cavitation and secure hydraulic conductivity in dry periods (Engelbrecht and Kursar 2003, Tyree et al. 2003, Santiago et al. 2004).

The extent to which species can resist cavitation or conduct water through their stems is thought to be determined by adaptations of the xylem vessels. Wide vessels for example have the advantage of a greater water transport capacity or hydraulic efficiency, as the Hagen-Poiseuille law predicts that hydraulic efficiency of a vessel increases with the fourth power of its diameter. For optimal hydraulic efficiency the length of the vessels is important as well. About 50% of the resistance in the hydraulic pathway is created at the pitmembranes that connect separate vessel elements (Zimmermann 1983) and as such a hydraulic pathway build up of fewer, longer vessels will be more efficient in transporting water than a pathway that stacks a lot of short vessels. Consequently evolution has driven plants towards wider and longer vessels (Tyree et al. 1994), but within limits.

As is the case with many adaptive traits that benefit the plant, there are associated costs involved (Givnish 1986). Wide, long vessels are not only more efficient in transporting water; they are also more vulnerable to drought-induced cavitation than narrow short vessels. Cavitation is the process of air being sucked into the xylem at which emboli are formed (Tyree & Sperry 1989), which can be triggered by two events. First of all cavitation occurs when the negative pressure in the xylem drops to the point that it becomes strong enough to break the cohesive bonds between water molecules and air is sucked through the largest pit pores (minuscule holes connecting separate vessels) into the vessel. This event is known as air-seeding (Zimmermann 1983, Sperry and Tyree 1988). Vulnerability to air-seeding may thus be related to the total pitted area of the xylem vessel and indirectly to the vessel length, as longer vessels are a greater chance to contain vulnerable pit pores (Tyree 1994, Sperry et al. 2005). Secondly, cavitation can occur when the pressure in the xylem drops to a point that the mechanical strength of the cell wall is compromised, the cell wall ruptures and collapses (Carlquist 1975, Tyree et al. 1994, Hacke et al. 2001, Brodribb and Holbrook 2005). Narrow vessels with relatively thick cell walls are better protected against this form of cavitation through vessel implosion (Hacke et al. 2001).

The xylem potential at 50% loss of hydraulic conductivity (P_{50}; in MPa) is the most widely used measure of cavitation resistance and varies widely among taxa. The most vulnerable species are found in wet tropical forest, where 50% loss of conductivity is reached at values as high as -0.18 MPa, while P_{50} values as low as -14.1 MPa were found for the most resistant dry forest species (reviewed in Maherali et al. 2004). Although there is a large overlap in P_{50} values between groups of species, conifers were found to be on average more cavitation resistant than angiosperms and shrubs were more resistant than trees (Maherali et al. 2004). One would also expect that evergreen species, that have to tolerate seasonal drought, are more cavitation resistant than deciduous species, which avoid drought by shedding their leaves in the dry season (Poorter and Markesteijn 2008, Markesteijn et al. 2009). Interestingly, this does not seem to be the case, as both groups were found to have similar P_{50} values (Maherali et al. 2004). As the authors themselves already pointed out this unexpected result was probably caused by the large number of winter deciduous species in their comparison. Studies that evaluate cavitation resistance of coexisting evergreen and deciduous tree species from dry ecosystems are rare and one of the goals set for the current study was to compare evergreen and deciduous tree species in more in detail.

As the risk of cavitation is greatest in dry ecosystems, where drought is a seasonally reoccurring event, it is expected that dry forest tree species will be well protected to resist cavitation, but also that this will come at the cost of a reduced hydraulic efficiency (Zimmerman 1983, Tyree et al. 1994). This trade-off will have pronounced effects on the ecological performance of dry forest tree species. Still, while hydraulic functioning of plants is relatively well understood, relatively few studies have made the link between cavitation resistance, leaf traits and species' life history strategies or ecological performance in the field.

The aim of this study was to examine cavitation resistance of 13 tropical dry forest tree species. We assessed how stem and leaf traits are associated with cavitation resistance and how cavitation resistance explains the minimum leaf water potential that species can tolerate in the dry season. The following questions were addressed; 1) How does resistance to cavitation differ between shade-tolerant and pioneer species and between deciduous and evergreen species?, 2) How is cavitation resistance affected by stem structural traits and associated with leaf traits?, 3) Are cavitation resistance and hydraulic conductivity associated?, and 4) How does cavitation resistance influence the leaf water potential that species can tolerate in the dry season?

METHODS

Study area

Fieldwork was carried out in a tropical dry forest in the eastern lowlands of Bolivia, near the town of Concepción, Santa Cruz. The forest site is part of the Chiquitano dry forest formation, situated on the Precambrian Brazilian shield (Cochrane 1973) at the transition of the Amazonian tropical lowland evergreen rain forest in the north and the thorn-shrub formations of the Gran Chaco region in the south (Killeen et al. 1998, Jardim et al. 2003). The forest is private property of a certified timber company (INPA Parket ltda.) and one of the long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF).

The study site (16°07'S, 61°43'W) has been classified as a tropical lowland dry deciduous forest, with a mean annual temperature of 24.3 ºC, a mean annual precipitation of 1160 mm (meteorological data from 1943-2005 from AASANA for Concepción at 40 km) and a dry period of three months (June - September) in which the potential evapotranspiration exceeds precipitation. The study area has a mean altitude of about 458 m with generally poor oxisol soils (Pariona 1996). The forest has a mean stem density of 420 trees ha^{-1}, a basal area of 18.3 m^2 ha^{-1}, and a species richness of 34 ha^{-1} (trees ≥ 10 cm diameter at breast height; M. Peña-Claros et al., unpublished). Average canopy height is 20 m and virtually all canopy trees shed their leaves in the dry season. The most dominant species in the area are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Salicaceae), and *Caesalpinia pluviosa* DC (Fabaceae).

Species and sapling selection

We studied cavitation resistance of thirteen tree species from nine different families (Table 5.1). Species were selected to differ in shade-tolerance and include seven shade-tolerant species and six pioneers. At the sapling stage species differ in their leaf habit; five species are drought-deciduous and, while eight species are evergreen.

Hydraulic conductivity

Sapwood-specific and leaf-specific hydraulic conductivity were determined on five saplings of each of the thirteen species. Selected saplings were between 150 and 200 cm tall and located along the roads and exposed to full or partial overhead light. Saplings were selected at high light availability as under these conditions saplings most likely experienced the largest vapour pressure deficits and the greatest water stress. Moreover, it is almost impossible to find short-lived pioneers under shady conditions. By sampling at full overhead light we are able to compare pioneers and shade-tolerants under similar growth conditions, thus reducing the effect of phenotypic variation in response to light.

The shoots of whole saplings were harvested and transported to a field laboratory for further processing. Lateral branches and leaves were cut from the main stem and wounds were sealed with instant adhesive glue. The stems were re-cut under distilled water to avoid the induction of new embolisms. Distal ends were trimmed with a razorblade to clear any accidentally blocked vessels and to secure a close fit about 1 cm of the bark at each side of the branch was removed. While submerged, the shaved end of the branch was wrapped in Parafilm (Pechiney Plastic Packaging, Chicago, USA) and connected to a manifold of hysteresis-resistant poly-tetra-fluor-ethane (PTFE) tubing, which held up to five stems simultaneously. With all stems in place the manifold was attached to a pressurised reservoir (150 kPa) filled with a flow solution of 10 mmol KCl dissolved in degassed and filtered (0.2 µm) distilled water. The stems were flushed for at least 30 minutes to remove embolism and connected to a second manifold attached to a hydraulic flow meter (Sperry et al. 1988). The flow meter consisted of an elevated water reservoir supplying the same flow solution to the stems at ~5 kPa, with the actual height and pressure quantified for each conductivity measurement. To hamper microbial growth in the reservoir and tubing the flow meter was frequently flushed with a 10% bleach solution and rinsed. Water flow through the stems was left to equilibrate for about 10 minutes after which flow rates were determined volumetrically with serological pipettes connected to the distal end of the stem. We measured the flow rates as the time (s) to fill 0.1 or 0.01 ml (in case of low flow) pipette volume. Hydraulic conductance (K_h; in m^3 s^{-1} MPa^{-1}) was calculated with the following formula;

$$K_h = \frac{\Delta V}{(\Delta P / \Delta X)} \qquad \text{(Eq. 1)}$$

where ΔV is the flow rate (m^3 s^{-1}) and (ΔP/ΔX) is the pressure drop across the stem segment of length X (MPa m^{-1}). We estimated the sapwood area as the stem cross-sectional area after bark removal, minus the area of pith, and calculated sapwood specific conductivity (K_S; kg m^{-1} s^{-1} MPa^{-1}) was calculated by dividing Kh with the sapwood area.

We determined total leaf area for the measured stems. The fresh mass of the leaves was measured in the field with a precision balance (0.01g) and leaves of a subsample of known fresh mass was digitised with a flatbed scanner (Canon Lide 50) and analysed using ImageJ software (http://rsbweb.nih.gov/ij/) to determine the leaf area. Total leaf area above the measured stem segment was estimated as the fresh mass of all the leaves over the fresh mass of the subsample, multiplied by the leaf area of the subsample. Leaf specific conductivity (K_L; mmol m^{-1} s^{-1} MPa^{-1}) was calculated as K_h divided by the total leaf area, hence multiplied with 18.02 (the molar mass of water).

Cavitation resistance

For 3 saplings per species the cavitation resistance was determined by estimating the xylem pressure at 50% loss of hydraulic conductivity (P_{50}) using the bench drying technique (Sperry et al. 1988). Saplings were harvested in the field, transported to the field station and hung upside-down on a sunny location to dehydrate. Per individual sapling five branches were measured in sequence of increasing dehydration. Two a-priori selected leaves per branch were bagged and covered in shade cloth to allow their leaf water potentials to equilibrate with that of the stem xylem. Upon measurement a branch was cut from the dehydrating sapling under distilled water to avoid cavitation of the xylem due to cutting. With a pressure bomb (SKPM 1405, Skye instruments Ltd. Powys, UK) we measured the water potential (ψ_l) of the equilibrated leaves, after which the branch was re-cut into a 10 to 12 cm long segment. The distal ends were trimmed with a razor blade. By first measuring the native conductance (K) and secondly the maximum conductance (K_{max}) after flushing the stem segment (at ~100 kPa pressure head for a minimum of 30 minutes) the percentage loss of hydraulic conductivity (PLC) was calculated, as;

$$\mathrm{PLC} = 100 * \frac{1-K}{K_{\max}} \qquad \text{(Eq. 2)}$$

Paired PLC measurements and mean xylem potential were plotted to create vulnerability curves for each of the 13 species (Fig. 5.1) by fitting an exponential sigmoid function (Pammenter and Vander Willigen 1998);

$$\mathrm{PLC} = \frac{100}{1 + \mathrm{e}^{a(\Psi - b)}} \quad , \qquad \text{(Eq. 3)}$$

where Ψ is the measured xylem potential, a is the slope of the curve (measures the species response to increasing xylem pressure) and b is the xylem potential at 50% loss of hydraulic conductivity (gives the point curve displacement along the x-axis (Fig. 5.1)). Curve parameters a en b were estimated with the non-linear regression procedure in SPSS 15.0 (SPSS Inc., Chicago, USA).

Stem and leaf traits

For a sample of each stem measured for conductivity we estimated the fresh volume without the bark using the water displacement method (Ilic et al. 2000). Samples were then oven-dried for 48 hours at 75°C after which we measured dry mass with a precision balance (±0.0001 g). Wood density (WD; g cm^{-3}) was calculated as the dry mass over the fresh volume.

Maximum vessel length (VL; cm) was determined by air injection (Ewers and Fisher 1989) for five saplings per species. Saplings were selected under the same conditions and in the same area as those measured for conductivity, cut at ground level and transported to the field station. The distal ends of the stem were trimmed with a razor blade to clear blocked vessels and the proximal end was attached to an air pump delivering ~100 kPa pressure. The upper end of the stem was submerged in water and cut back 1 cm at a time until air bubbles escaped. Subsequently the remaining length of the stem was taken as the length of the longest continuous vessel.

For each sapling we calculated the Huber-value (Hv; $cm^2\ cm^{-2}$) as the cross-sectional sapwood area of the upper end of the stem divided the total leaf area it supports. Subsamples of the leaf material collected to estimate the total leaf area were saturated overnight in moist paper towels in a refrigerator after which their fresh mass and average leaf size (LS; cm^2) were determined. The samples were then oven-dried at 65°C for 48 hours before the determination of dry mass. Leaf dry matter content (LDMC; $g\ g^{-1}$) was calculated as the leaf dry mass divided by the fresh mass. The specific leaf area (SLA; $cm^2\ g^{-1}$) was calculated as the leaf area divided by the dry mass. All hydraulic traits included in this paper are summarized in table 5.1.

Dry season leaf water potential

In the dry season of 2008 (April – October) the midday leaf water potential (ψ_l) on 5 individual saplings per species were measured. Saplings were selected from exposed conditions along the road. Mid-day leaf water potentials were measured with a pressure chamber (Model SKPM 1405, Skye instruments Ltd. Powys, UK). Fully expanded and exposed healthy leaves were selected, without signs of herbivory. Between 14.00 and 17.00h leaves were cut from the saplings, and immediately sealed into plastic bags. After cutting a leaf from a plant the ψ_l can decrease rapidly due to continue transpiration. To reduce the exchange of gasses the CO_2 and H_20 concentration of the air in the bags was raised by exhaling several times into them before sealing. The ψ_l measurements were made two months after the onset of the dry season (June) and before drought in this forest was at its peak (August-September; Markesteijn et al. 2008). In this way it was still possible to compare both evergreen and drought-deciduous species, before they shed their leaves.

Data analysis

Differences between pioneers and shade-tolerant species and deciduous and evergreen species were analysed with independent samples t-tests. Linear regression analyses were used to determine how P_{50} depends on structural stem traits (e.g. wood density and maximum vessel length) and how P_{50} in turn influences the dry season leaf water potential. A backward multiple regression analysis was used to evaluate which species traits best explained P_{50}. Pearson correlation analyses were used to examine the associations between P_{50} and leaf traits across species.

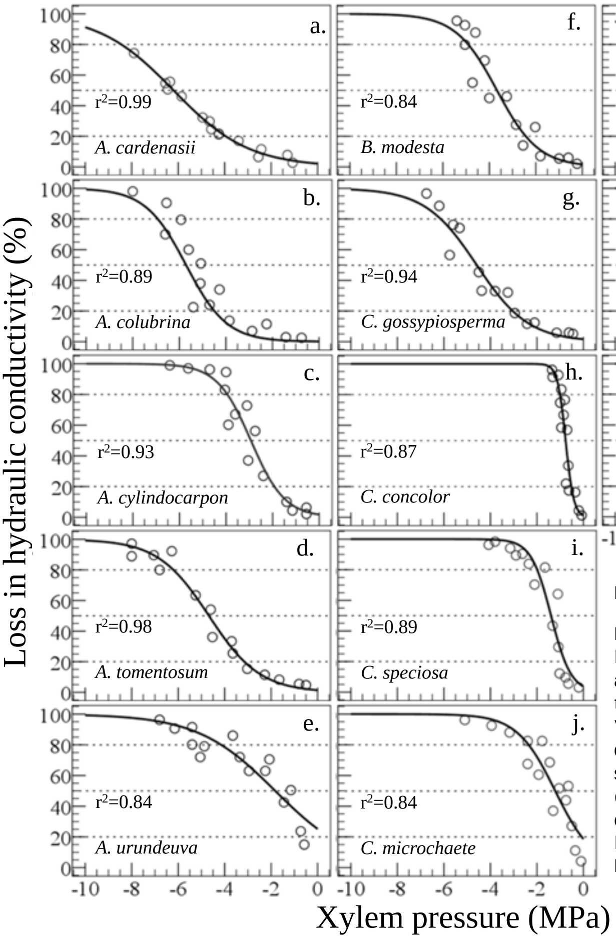

Figure 5.1

Relations between percentage loss of hydraulic conductivity and xylem potential for 13 tropical dry forest tree species. Vulnerability curves were estimated from 15 samples per species. Figures represent the different species, alphabetically organised. Horizontal dotted lines intersect with the curves at P_{20}, P_{50} and P_{80} respectively.

Table 5.1

Cavitation resistance of 13 tropical dry forest tree species. Species are grouped into pioneers and shade-tolerant species. Leaf habit (D; Deciduous, E; Evergreen), the slope of the vulnerability curves and the xylem potential at 20%, 50% and 80% loss of hydraulic conductivity (P_{20}, P_{50} and P_{80}) are given.

Species	Family	Leaf habit	Slope (% MPa^{-1})	P_{20} (MPa)	P_{50} (MPa)	P_{80} (MPa)
Pioneer species:						
Astronium urundeuva	Anacardiaceae	D	6.0	-0.5	-1.8	-4.2
Bougainvillea modesta	Nyctaginaceae	E	11.2	-2.4	-3.7	-4.9
Cecropia concolor	Urticaceae	E	57.7	-0.5	-0.8	-1
Ceiba speciosa	Malvaceae	D	23.3	-0.3	-1.4	-3.5
Centrolobium microchaete	Fabaceae	D	12.1	-0.1	-1.2	-2.4
Solanum riparium	Solanaceae	E	17.4	-1.3	-2.1	-2.9
Shade-tolerant species:						
Acosmium cardenasii	Fabaceae	E	6.2	-4	-6.2	-8.5
Anadenanthera colubrina	Fabaceae	E	11.4	-4.2	-5.7	-6.6
Aspidosperma cylindrocarpon	Apocynaceae	D	13.7	-1.9	-2.9	-3.9
Aspidosperma tomentosum	Apocynaceae	E	9.1	-3.2	-4.7	-6.2
Casearia gossypiosperma	Salicaceae	D	9.0	-3	-4.6	-6.1
Copaifera chodatiana	Fabaceae	E	6.9	-3.7	-5.7	-7.7
Trichilia elegans	Meliaceae	E	14	-2.5	-3.5	-4.5

Table 5.2

Differences in mean cavitation resistance between pioneers and shade-tolerant species and deciduous and evergreen species. ns, non-significant; **, P<0.01; ***, P<0.001.

	Pioneer (n=6)			Shade-tolerant (n=7)			t-test	
	mean	±	se	mean	±	se	t	p
P_{20}	-0.86	±	0.36	-3.20	±	0.31	-5.03	***
P_{50}	-1.83	±	0.41	-4.76	±	0.46	-4.66	***
P_{80}	-3.13	±	0.56	-6.22	±	0.61	-3.67	**
	Deciduous (n=5)			Evergreen (n=8)			t-test	
	mean	±	se	mean	±	se	t	p
P_{20}	-1.17	±	0.57	-2.71	±	0.46	-2.10	ns
P_{50}	-2.39	±	0.63	-4.04	±	0.68	-1.66	ns
P_{80}	-4.01	±	0.62	-5.28	±	0.88	-1.03	ns

On average, pioneer species had substantially higher P_{20}, P_{50} and P_{80} values than the shade-tolerant species (Table 5.2, Fig. 5.2, 5.4a.), but the slopes of the curves did not differ significantly (Fig. 5.3, Table 5.2). Deciduous species tended to have higher P_{20}, P_{50} and P_{80} values than evergreen species, although none of the differences were significant (Table 5.2, Fig. 5.4b). Species hardly showed any crossovers in the ranking of P_{20}, P_{50} and P_{80}. Between P_{50} and P_{80}, for instance, only four species shifted in rank, but never more than 2 ranks (Fig. 5.3), which suggests that the species ranking is maintained at different intensities of drought.

Although P_{80} is probably ecologically the most relevant estimator of species cavitation resistance, as most plants will resist up to 80% loss in hydraulic conductivity without severely compromising their survival (L. Sack, pers. comm.) In further analyses we

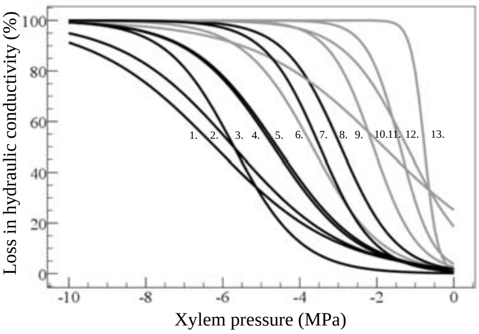

Figure 5.2

Vulnerability curves for 13 dry forest tree species. The graph shows the percentage loss of hydraulic conductivity at increasing xylem pressure, estimated from 15 samples per species. Species are numbered and sorted on increasing P_{50}; xylem potential at 50% loss of conductivity; 1. Acosmium cardenasii (Fabaceae), 2. Copaifera chodatiana (Fabaceae); 3. Anadenanthera colubrina (Fabaceae), 4. Aspidosperma tomentosum (Apocynaceae), 5. - Casearia gossypiosperma (Salicaceae), 6. Bougainvillea modesta (Nyctanginaceae), 7. Trichilia elegans (Meliaceae), 8. Aspidosperma cylindrocarpon (Apocynaceae), 9. Solanum riparium (Solanaceae), 10. Astronium urundeuva (Anacardiaceae), 11. Ceiba speciosa (Malvaceae), 12. Centrolobium microchaete (Fabaceae), 13. Cecropia concolor (Urticaceae). Black lines represent shade-tolerant species and gray lines pioneers.

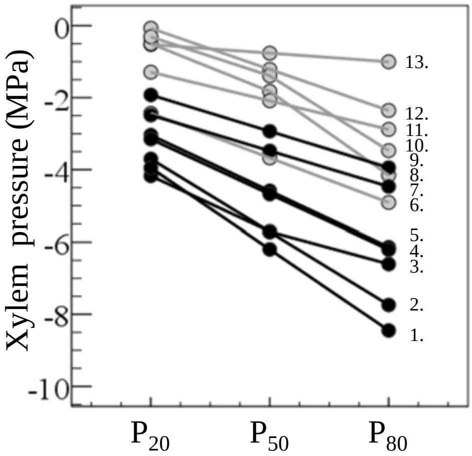

Figure 5.3

Crossovers of species ranking between estimators of cavitation resistance. 1. Acosmium cardenasii (Fabaceae), 2. Copaifera chodatiana (Fabaceae); 3. Anadenanthera colubrina (Fabaceae), 4. Aspidosperma tomentosum (Apocynaceae), 5. - Casearia gossypiosperma (Salicaceae), 6. Bougainvillea modesta (Nyctanginaceae), 7. Trichilia elegans (Meliaceae), 8. Astronium urundeuva (Anacardiaceae), 9. Aspidosperma cylindrocarpon (Apocynaceae), 10. Ceiba speciosa (Malvaceae), 11. Solanum riparium (Solanaceae), 12. Centrolobium microchaete (Fabaceae), 13. Cecropia concolor (Urticaceae). Black lines and dots represent shade-tolerant species and gray lines and dots pioneers.

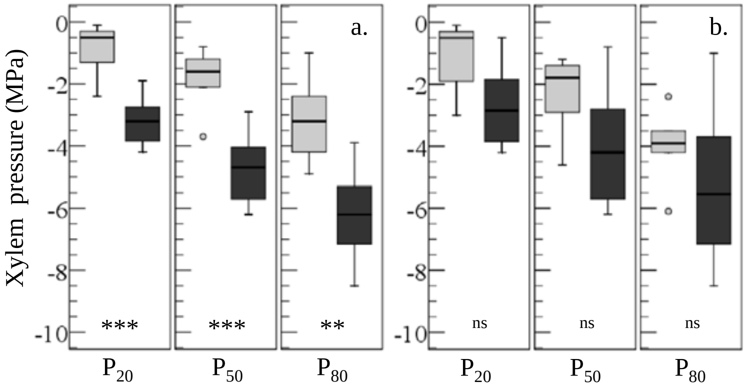

Figure 5.4

Differences in mean cavitation resistance between pioneers and shade-tolerant species (a.) and deciduous and evergreen species. ns, non-significant; **, P<0.01; ***, P<0.001. P20, P50 and P80 represent the xylem pressure at 20%, 50% and 80% loss in hydraulic conductivity respectively. Light boxes represent pioneers (a.) or deciduous species (b.) and dark ones shade-tolerant species (a.) and evergreen species (b.). Whiskers give the minimum and maximum values, boxes the first and third quartile, and the horizontal bar gives the median.

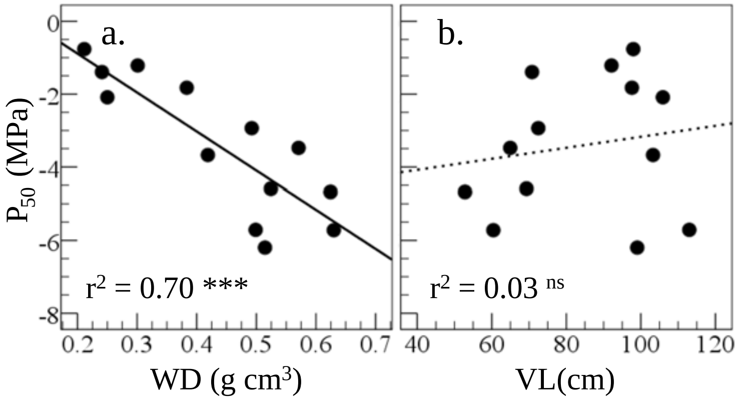

Figure 5.5

Regressions between cavitation resistance (P_{50}) and wood density (a.) and maximum vessel length (b.) of 13 dry forest species. Regression coefficients (r^2) and their level of significance are given. ns, non-significant; *, $P \leq 0.05$, **, $P \leq 0.01$; ***, $P \leq 0.001$.

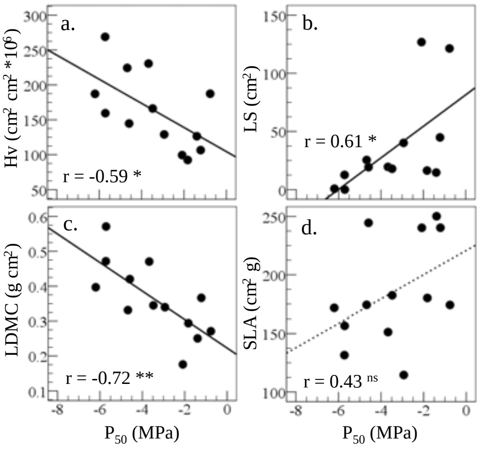

Figure 5.6

Associations between leaf traits and cavitation resistance (P_{50}) of 13 dry forest species. Pearson correlation coefficients (r) and their level of significance are given. ^{ns}, non-significant; *, $P \leq 0.05$, **, $P \leq 0.01$; ***, $P \leq 0.001$.

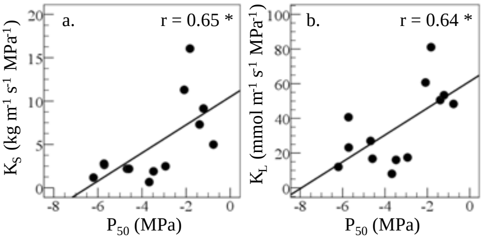

Figure 5.7

Relations between stem hydraulic conductivity (K_S; a.), leaf hydraulic conductivity (K_L; b.) and cavitation resistance (P_{50}) of tropical dry forest species. Pearson correlation coefficients and their level of significance are given. *, $P < 0.05$.

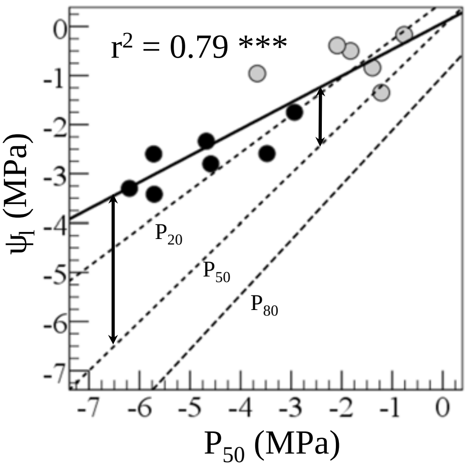

Figure 5.8

Regression between the dry season leaf water potential (ψ_l) and cavitation resistance (P_{50}) of 13 dry forest tree species. The regression coefficient and its level of significance are given. ***, $P < 0.001$. The dotted lines represent the theoratical relationship between cavitation resistance and midday leaf water potential where ψ_l equals P_{20}, P_{50} and P_{80}, respectively. The difference between the regression line and the 1:1 relationship (black arrows, where $\psi_l = P_{50}$) was defined as the hydraulic safety margin.

How is cavitation resistance affected by stem traits?

Species with a high wood density were more resistant to cavitation than species with a low wood density (Fig. 5.5a). WD is a variable that integrates various wood properties and is closely linked to mechanical support, water transport and (stem) storage capacity. Consequently WD plays a central role in the life history strategies of species. Species with a low WD often realise high diameter and height growth rates (Roderick 2000, Poorter 2008, Chave et al. 2009) while species with a high WD have slow growth rates, but survive drought and shade better (Alvarez and Kitajima 2007, Poorter and Markesteijn 2008).

Variation in WD results from the variation in size, shape, arrangement and frequency of cells (Hacke et al. 2001, Jacobsen et al. 2005) and dense wood in dry forest species can results from a suite of anatomical adaptations that minimise the risk of drought-induced xylem cavitation and secure water and nutrient transport through the stem. A high WD can result from narrower xylem vessels with thicker cell walls (Hacke et al. 2001). As narrow vessels are less efficient conductors than wide vessels, they tend to occur in higher densities (Sperry et al. 2008, Poorter et al. in press). Narrow and/or thick walled vessels have a higher cell wall to lumen area ratio which implies that they can withstand more negative pressures before collapsing (Hacke et al. 2001, Zanne et al. 2006) and thus narrow vessels are more resistant to cavitation (Salleo and Lo Gullo 1989, Lo Gullo and Salleo 1993, Hargrave et al. 1994, Hacke et al. 2001). An increased fibre wall area and a decreased fibre lumen area were also found to increase resistance to xylem cell wall implosion (Jacobsen et al. 2005) and will increase WD.

Vessel length is a somewhat neglected vessel dimension because its exact measurement is a labour-intensive job involving several technical problems (Comstock and Sperry 2000). The backward multiple regression showed that in addition to WD, VL significantly explained an additional 12% of the variation in P_{50} (Table 5.3). Interestingly the standardised regression coefficient (β) of VL in the multiple regression was negative (Table 5.3), which suggests that in addition to denser wood, longer vessels should lead to a higher cavitation resistance. This seems counterintuitive as earlier studies had found that VL should scale negatively to cavitation resistance (Ewers 1985), because in general vessel length scales positively to vessel diameter (Ewers 1985, Ewers et al. 1997, Hacke et al. 2006, Jacobsen et al. 2007). Longer vessels have a larger connection area with adjacent vessels, and are likely to contain more pit pores, which increases the probability of air-seeding from neighbouring embolised vessels (Hargrave et al. 1994, Tyree et al. 1994, Sperry et al. 2005, Hacke et al. 2006, Zanne et al. 2006, Choat et al. 2008). The negative relation between VL and P_{50} found in this study can mainly be attributed to two species, *Acosmium cardenasii* and *Anadenanthera colubrina*. These species have the greatest cavitation resistance in this study and combine a high WD with a large VL. Interestingly *A. cardenasii* and *A. colubrina* are also among the two most abundant tree species in this dry forest that together account for more than 40% of the stems over 10 cm dbh. This may suggest that these species can escape the trade-off between WD (i.e. cavitation resistance) and VL (i.e. hydraulic conductivity). Apparently these species follow a very feasible strategy in which they are both well protected against drought-induced cavitation and are relatively efficient in conducting the water through their stem. This may explain their dominant presence in this tropical dry forest.

How is cavitation resistance associated with leaf traits?

P_{50} was negatively associated with Hv and LDMC and positively with LS (Fig. 5.6). At a given amount of leaf area, species with a low Hv operate at a reduced investment in sapwood. Hv and WD were positively associated (Pearson r = 0.56, P=0.44). Hence, the cross-sectional sapwood area of these species is relatively small as it probably consists of fewer, larger diameter vessels that, according to the Hagen-Pouseuille law, are more efficient in transporting large quantities of water (Jacobsen et al. 2007). Among 40 dry forest tree species, low Hv species had a high stem hydraulic conductivity (K_S) (Markesteijn et al. submitted), which was also found among Australian rainforest species (Brodribb and Field 2000), but this high hydraulic efficiency comes at a reduced cavitation resistance and hence a negative association between Hv and P_{50} (Fig. 5.6a).

LS was positively associated with P_{50} (Fig. 5.6b), suggesting that small leaves are associated with drought-tolerance of dry forest tree species. Small leaves are characteristic for species from arid environments (McDonald et al. 2003). Small leaves have a smaller boundary layer resistance, which facilitates cooling of the convective area and thus assists the regulation of the heat load of the leaves to secure close to optimal temperatures for photosynthesis (Parkhurst and Loucks 1972). Smaller leaves as such do not necessarily lead to a reduction of transpiration, as often suggested. On the contrary, because of a thinner boundary layer, small leaved species actually suffer an increased evaporative demand (Parkhurst and Loucks 1972). To compensate for the reduced light interception of small leaves species produce them in bigger quantities and the advantage of small leaves in relation to drought-tolerance is that it is less expansive to reduce transpiration by shedding small individual leaves than big ones. Furthermore, the smallest leaves (leaflets) in this tropical dry forest are all found for species with compound leaves. Many of these species fold their leaflets at times of high evaporative demand (e.g. around noon) or towards the peak of the dry season.

LDMC was negatively related to P_{50} and among leaf traits explained most of its variation (Fig. 5.6c). LDMC is related the leaf´s modulus of elasticity, or stiffness, as leaves with higher LDMC form thicker and more rigid cell walls, which allows them to tolerate a lower leaf water potential without losing turgor (Cheung 1975, Zimmermann 1978, Monson and Smith 1982). This allows species with a high LDMC to acquire water from relatively dry soils, while minimising damage to the leaf cell structures and stay physiologically active under more extreme drought (Bowman and Roberts 1985, Engelbrecht and Kursar 2003, Tyree et al. 2003) In Panama Kursar et al. (2009) found that LDMC was closely related to the minimum seasonal leaf water potential species could tolerate, and that it was a good predictor of species drought performance in the field and their distribution across a gradient in dry season length.

Surprisingly, we did not find a clear relation between SLA and P_{50}, while SLA is in general considered to be the key trait that modulates leaf function in plants. Numerous studies have shown SLA to decrease with drought across species (Skarpe 1996, Cunningham et al. 1999, Fonseca et al. 2000). SLA can be calculated as (1/[leaf density * leaf thickness]). As such a low SLA can result from an increase in either one of both components. A low SLA that results from an increased leaf density will be well related to P_{50} for the same reasons as LDMC, because it lowers the modulus of elasticity. An increase in leaf thickness alone will not have the same effect and thus SLA can be uncoupled from leaf density and P_{50}. In this tropical dry forest it was LDMC and not SLA that was associated with species moisture requirements (Chapter 6).

How is cavitation resistance associated with hydraulic conductivity?

The negative relation between P_{50} and K_S and K_L (Fig. 5.7) represents a key ecological trade-off between hydraulic safety and hydraulic efficiency that land plants theoretically have to face (Zimmerman 1983, Tyree et al. 1994). Wood density is the principal stem trait around which this trade-off evolves and was the best predictor of both P_{50} (this study) and K_S and K_L across species (Chapter 6). Still it has recently been suggested that the relationship between cavitation resistance and hydraulic conductivity can be largely uncoupled, depending on the species included in the analysis (e.g. deciduous vs. evergreen angiosperms and conifers) (Maherali et al. 2004). In their meta-analysis Maherali et al. (2004) found little evidence of an evolutionary basis for the trade-off between P_{50} and K_S, but recognise that at smaller scales results can be different. Possibly, the trade-off between cavitation resistance and hydraulic efficiency is uncoupled when species from different communities are pooled together, while among species within communities the trade-off is stronger. The findings of this current study corroborates with several other studies that also found a trade-off between hydraulic safety and efficiency (Zimmerman 1983, Tyree et al. 1994, Hacke et al. 2006, Sperry et al. 2008).

As explained earlier P_{50} depends on structural wood anatomical adaptations that increase the xylem resistance against cell implosion and most of these adaptations increase the resistance in the flow pathway and thus constrain hydraulic efficiency. The importance of vessel dimensions for cavitation resistance remains a subject of debate, especially because air-seeding mainly depends on the pit membrane structure (Sperry 2000), which may vary independently from vessel size or length (Hacke and Sperry 2001)

How does cavitation resistance influence the leaf water potential that species can tolerate in the dry season?

P_{50} was found to strongly affect ψ_l across species (Fig. 5.8) and thus species with a greater cavitation resistance clearly tolerated lower midday leaf water potentials than species vulnerable to cavitation. This result corresponds to findings from dry Mexican (Bhaskar et al. 2007) and Mediterranean Chaparral vegetation (Jacobsen et al. 2007), Sonoran desert vegetation (Pockman and Sperry 2000) and a tropical dry forest (Brodribb et al. 2003).

The leaf water potential in general (not only the seasonal minimum) results from the balance between water supply (mainly soil water availability) and the atmospheric water demand (evaporative demand) and is largely determined by the interactions among several properties of the plant hydraulic architecture (reviewed in Bhaskar and Ackerly 2006). According to the cohesion-tension theory (Dixon 1894) the flow of water from soil to leaf takes place as a hydraulic continuum under negative pressure. When the pressure in the xylem becomes too negative (due to drought) and the xylem cavitates, plants lose their capacity to photosynthesise and access to atmospheric CO_2, which will lead to leaf desiccation and eventually branch, shoot and plant death (Tyree and Sperry 1988, Davis et al. 2002, Engelbrecht et al. 2005). Cavitation resistant species prevent this from happening through wood anatomical adaptations (summarized earlier), but at the cost of a reduced hydraulic conductivity. As a consequence cavitation resistant species cannot provide enough water to the leaf to buffer the leaf water potential and have to tolerate lower ψl than species with low cavitation resistance (Sperry et al. 2002). Hence the strong influence of P_{50} on ψ_l (Fig. 5.8).

We measured the midday leaf water potentials two months after the onset of the dry season (June 2008) and before drought in this forest was at its peak (normally in August-September; Markesteijn et al. 2008). Consequently, most species were operating well above their hydraulic limit, that we defined here as the xylem potential at 50% loss of conductivity (Fig. 5.8; 1:1 line). In fact for most species leaf water potentials corresponded to those expected close to 20% loss of hydraulic conductivity. It was argued that to maximise stomatal conductance and carbon gain species should reduce their cavitation resistance and operate as close as possible to their hydraulic limit, without risking complete cavitation (Sperry et al. 1998). Operating close to the hydraulic limit (closer to hydraulic failure) is a risky strategy that is not likely followed by all species. Fast growing pioneers benefit from taking high risks as this allows them to maximise photosynthesis and carbon intake (Poorter and Bongers 2006). Pioneers can probably also afford it as their increased carbon intake results in a positive carbon balance and reduces the (re)construction cost of tissues lost if hydraulic failure should occur. Notably drought- and shade-tolerant species follow a more conservative resource strategy with stricter limitations on carbon intake and they need to operate at safe distance from their hydraulic limit as long as possible. Our results support this idea as pioneers were less resistant to cavitation and had clearly smaller hydraulic safety margins than shade-tolerant species (Fig. 5.8).

Ficus boliviana
(Moraceae)

Chapter 6

Hydraulic niche partitioning among saplings of tropical dry forest species; coordination of species moisture and light requirements

Lars Markesteijn, Lourens Poorter, Horacio Paz, Lawren Sack and Frans Bongers

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ABSTRACT

The basic function of the plant hydraulic architecture has been the subject of many studies, but we know very little about how hydraulic properties are related to species' life history strategies, such as drought- and shade-tolerance. Prevailing theories seem to be contradictory. We measured sapwood- (K_S) and leaf-hydraulic conductivity (K_L) of 40 co-existing dry forest tree species in a Bolivian dry forest, and examined their association with functional stem and leaf traits and indices of species´ moisture and light requirements. Hydraulic properties varied substantially across species. Species' values for K_S and K_L were negatively correlated with wood density and positively with maximum vessel length. K_S values were negatively correlated with the Huber-value (stem cross-sectional area per leaf area) and leaf dry matter content. Species´ moisture and light requirements scaled similarly with hydraulic properties, with negative relationships to wood density and positive relationships to K_L. Hydraulic properties varied across species in line with the classical trade-off between hydraulic efficiency and safety, which results in coordinated moisture and light requirements across species and thus coordination of species´ drought- and shade-tolerance rather than the frequently hypothesised trade-off.

KEYWORDS

Tropical dry forest, niche partitioning, hydraulic conductivity, drought-tolerance, shade-tolerance, trade-offs, wood density.

INTRODUCTION

Several theories have been developed to explain the high biodiversity of tropical forests, including the balance between dispersal, speciation, immigration and extinction (reviewed in Wright 2002), but one of the most persevering ones is the niche differentiation theory. This theory postulates that different plant species can coexist by partitioning gradients in resource availability (Grubb 1977, Hutchinson 1978, cf. Tilman 1982) and by diverging in traits associated with high performance in given niches (Westoby et al. 2002, Poorter and Bongers 2006, Poorter 2007). This study aimed to determine the association of stem hydraulic traits with habitat requirements for a diverse tropical dry forest.

Traditionally, niche partitioning studies have mainly focused on light availability as the key factor determining species coexistence (e.g. Denslow 1987, Swaine and Whitmore 1988, Popma and Bongers 1991), partly because most of these studies were conducted in wet tropical forests, where light is the most limiting resource (Coomes and Grubb 2000, Asner et al. 2003, Lebrija-Trejos 2009). Tree species in wet tropical forest occupy rather similar light niches in the adult stage, but they differ strongly in their light niches in the regeneration stage (Poorter et al. 2006), to which they show clear physiological and morphological adaptations (cf. Grubb 1977, Poorter 2007).

Recently, interests have shifted toward increasing the understanding of the role of water availability as a factor for species coexistence. All tropical tree species have to cope with periodical water shortage at some point, and even in the wet tropics short dry spells can effect species survival in the field (Engelbrecht et al. 2006). On a macro-scale tree species distribution varies with precipitation (Bongers et al. 2004, Engelbrecht et al. 2007), while on a micro-scale species distribution varies along topographical gradients of soil water availability (Borchert 1994, Clark 1999, Valencia et al. 2004). Species partitioning along gradients in water availability will to great extent be determined by the ability of species to compete for water and tolerate drought. Species hydraulic architecture can be one of the major drivers of species partitioning in tropical forests.

All land plants potentially face the same fundamental trade-off to acquire sufficient water and maintain hydraulic conductivity to secure photosynthesis, while at the same time running the risk of (drought-induced) cavitation, which can lead to dysfunctional vessels, stomatal closure and eventually the abscission of leaves, shoots, and branches, and finally plant death (Tyree and Sperry 1988, Davis et al. 2002, Engelbrecht et al. 2005). This trade-off between hydraulic safety and efficiency has indeed been found (Zimmerman 1983, Tyree et al. 1994) and can be realised by structural adaptations of the stem anatomy. Examples of such adaptations are thinner and shorter vessels, thicker cell walls, a decreased total lumen area and smaller pit-pores, all of which can limit conductivity by increasing the resistance (Hacke 2001; Jacobsen et al. 2005, 2007). Although the basic mechanisms of plant hydraulic architecture are fairly well understood, we still know very little about how hydraulic properties are related to species' life history strategies, such as drought- and shade-tolerance (Tyree and Ewers 1991). Because of the trade-off between hydraulic efficiency and hydraulic safety it can be expected that species with high hydraulic conductivity are found in productive habitats with high water availability, while species that have lower conductivity are found in less productive habitats with low water availability (Carlquist 1975, Tyree and Zimmermann 2002).

Plants adapted to high light availability should have a high leaf specific conductivity, because light demanding species, relative to shade-tolerant species, achieve high growth rates through a greater photosynthetic capacity and leaf area (Poorter 2005, Poorter and Bongers 2006) and, as a consequence, they will have higher transpiration rates and a greater leaf level water demand. This calls for an increased water supply to the leaf and thus an increased stem- and leaf-specific conductivity. Preliminary studies suggest that light demanding species indeed possess such a high hydraulic conductivity (Tyree et al. 1998, Choat et al. 2005, Sack et al. 2005)

There are three alternative predictions on the association between shade- and drought-tolerance and the role of hydraulic architecture therein. First of all, the ecological consequence of the trade-off between hydraulic efficiency and hydraulic safety is that because of their high hydraulic efficiency, light-demanding species would be less drought-tolerant and should in their distribution thus be confined to relatively wet habitats. Likewise shade-tolerant species, with lower hydraulic efficiency, should be more drought-tolerant and able to persist at drier sites, where they can outcompete species that are more vulnerable to drought-induced cavitation. Such a pattern would contrast with a second prediction formulated by Smith and Huston (1989), who argued for a trade-off between drought- and shade-tolerance based on a trade-off in carbon allocation to belowground roots versus the aboveground shoot. Notably, recent studies suggested that hydraulic safety and hydraulic efficiency are not necessarily in trade-off. Depending on the set of species or the type of community assessed, hydraulic safety and efficiency can vary independently from one another (Maherali et al. 2004, Jabobsen et al. 2005, Choat et al. 2007). Such independence of hydraulic efficiency and safety is consistent with the findings of growth studies that have shown that drought- and shade-tolerance are also uncoupled across species and can vary independently from each other (Holmgren 2000, Sack and Grubb 2002, Sack 2004, Markesteijn and Poorter 2009).

To disentangle these contradictions we assessed how hydraulic architecture is associated with niche partitioning of tree species and we evaluated hydraulic properties and the moisture and light requirements of forty tropical dry forest species. We aimed to answer the following three questions; 1) How do stem hydraulic properties differ among tropical dry forest species?, 2) How is stem hydraulic conductivity related to key stem and leaf traits?, and 3) How are hydraulic properties related to moisture and light requirements of the species?

We predicted; 1) a large variation in hydraulic properties, as this would allow species to partition resources without outcompeting one-another and facilitate species coexistence, 2) that stem hydraulic conductance would be negatively associated with wood density and positively with maximum vessel length, reflecting the potential trade-off between hydraulic safety and efficiency, and 3) that stem and leaf hydraulic conductivity would be positively associated with light requirement, and potentially with moisture requirement of the species, as light demanding species have higher photosynthetic capacity, increased transpiration and an increased water demand at the leaf, as compared to shade-tolerant species. We thus predicted coordination, rather than trade-off, between drought- and shade-tolerance.

METHODS

Study area

Fieldwork was carried out in a deciduous tropical dry forest in the eastern lowlands of Bolivia, near the town of Concepción, Santa Cruz. The forest site is part of the Chiquitano dry forest formation, situated on the Precambrian Brazilian shield (Cochrane 1973) at the transition of the Amazonian tropical lowland evergreen rain forest in the north and the thorn-shrub formations of the Gran Chaco region in the south (Killeen *et al.* 1998, Jardim *et al.* 2003). The forest is private property of a certified timber company (INPA Parket ltda.) and one of the long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF).

The study site (16°07'S, 61°43'W) has been classified as a tropical lowland dry deciduous forest, with a mean annual temperature of 24.3 ºC, a mean annual precipitation of 1160 mm (meteorological data from 1943-2005 from AASANA for Concepción at 40 km) and a dry period of three months (June - September) in which the potential evapotranspiration exceeds precipitation. The study area has a mean altitude of about 458 m with generally poor oxisol soils (Pariona 1996). The forest has a mean stem density of 420 trees ha^{-1}, a basal area of 18.3 m^2 ha^{-1}, and a species richness of 34 ha^{-1} (trees $\geq$ 10 cm diameter at breast height; M. Peña-Claros *et al.* unpublished). Average canopy height is 20 m and virtually all canopy trees shed their leaves in the dry season. The most dominant species in the area are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Salicaceae), and *Caesalpinia pluviosa* DC (Fabaceae).

Species and sapling selection

We studied hydraulic properties of 40 tree species belonging to 37 different genera, 21 families and 12 orders (according to APG nomenclature).. The selected species include some of the most abundant in this type of forest and all together they represent more than 75% of those with stems over 10 cm dbh (IBIF, unpublished). We sampled ten species of Fabaceae, reflecting their dominance in this forest.

Species´ moisture and light requirements

To express species moisture and light requirements we used two independent indices; the dry season midday leaf water potential (ψ_l) and the juvenile crown exposure (CE_{juv}) of the species. These are qualitative, integrative indices, representing the resource supply available to the plant (and to the leaf tissues in the case of ψ_l), in its natural habitats; these indices are higher resolution, but similar in information to the rankings used to describe light or water requirements by Ellenberg (1991), or those compiled for temperate trees by Niinemets and Valladares (2006).

In the dry season of 2008 we measured ψ_l on 5 individual saplings per species. Saplings were selected from exposed conditions along the road. Mid-day leaf water potential was measured with a pressure chamber (Model SKPM 1405, Skye instruments Ltd. Powys, UK). We selected fully expanded and exposed healthy leaves, without signs of herbivory. Between 14.00 and 17.00 h leaves with cut from the saplings, and immediately sealed into plastic bags that were exhaled into for measurements were. The ψ_l measurements were made two months after the onset of the dry season (June) and before drought in this forest was at its peak (August-September; Markesteijn et al. 2008). In this way we were able to compare drought-avoiding deciduous species (a large component of the species pool); most of the deciduous species still have their leaves in the first half of the dry season. Because we wished to compare all species in their typical moisture requirement at the same time, we chose not to use the minimum leaf water potential (ψ_{min}) experienced annually as the index for moisture requirement, though this has been reported to be a good indicator for species distribution along moisture gradients (Pockman and Sperry 2000, Ackerly 2004, Bhaskar and Ackerly 2006, Jacobsen 2007, Kursar et al. 2009). Notably, previous work in other seasonally dry tropical forests has shown correlations across species among indices of physiological drought-tolerance and moisture supply, including among dry season mid-day leaf water potential, minimum seasonal leaf water potential, leaf water potential at 50% loss of stem conductivity, turgor loss point, and leaf water potential at 50% stomatal closure (Brodribb et al. 2002, 2003; Baltzer et al. 2008). In our dataset ψ_l was also strongly correlated with stem cavitation resistance (Pearson correlation analysis between P_{50} and ψ_l; r=0.89 ***, $P \leq 0.001$, n=13; L. Markesteijn et al., unpublished), which further underlines its value as a proxy of physiological moisture requirement.

Poorter and Kitajima (2007) provided an independent, objective and continuous measure of the regeneration light requirements of the species. An average of 523 individuals (range 16–9064) per species was measured over their whole size range for their height and crown exposure (CE; cf. Dawkins and Field 1978). Values of CE vary from 1 to 5 and indicate respectively that tree receives no direct light, lateral light only, overhead light on 10-90% of the vertical projection of the crown surface, overhead light on >90% of the vertical projection of the crown, and overhead light over the whole crown (emergent crown). CE measurements were repeatable (0.1±0.01SE average difference between two independent observers), and there is a good relation between CE and both canopy openness and incident radiation (Keeling and Phillips 2007). For each species CE was related to tree height, using a multinomial regression analysis (cf. Poorter et al. 2005, Sheil et al. 2006) and with the regression equation, the average population-level CE at a standardized height of two meters was calculated (CE_{juv}; juvenile crown exposure). Although similar sized individuals can occur under different light conditions, species with a low CE_{juv} will mainly regenerate in the shaded forest understory (shade-tolerant species), whereas species with a high CE_{juv} mainly regenerate in the high-light conditions of gaps (light-demanding pioneer species).

Hydraulic conductivity

Sapwood-specific and leaf-specific hydraulic conductivity were determined on 5 saplings of each of the 40 species. Selected saplings were between 150 and 200 cm tall and located along the roads and exposed to full or partial overhead light. The shoots of whole saplings were harvested and transported to a field laboratory for further processing. Any lateral branches and leaves were cut from the main stem and wounds were sealed with instant adhesive glue. The stems were recut under distilled water to avoid the introduction of new embolisms. Distal ends were trimmed with a razorblade to clear any accidentally blocked vessels and about 1 cm of the bark at each side of the branch was removed. While submerged, the shaved end of the branch was then wrapped in Parafilm (Pechiney Plastic Packaging, Chicago, USA) and connected to a manifold of hysteresis-resistant poly-tetra-fluor-ethane (PTFE) tubing, which held up to five stems simultaneously. With all stems in place the manifold was attached to a pressurised reservoir (150 kPa) filled with a flow solution of 10 mmol KCl dissolved in degassed and filtered (0.2 μm) distilled water. The stems were flushed for at least 30 minutes to remove embolism and connected to a second manifold attached to a hydraulic flow meter (Sperry et al. 1988). The flow meter consisted of an elevated water reservoir supplying the same flow solution to the stems at ~5 kPa, with the actual height and pressure quantified for each conductivity measurement. To hamper microbial growth in the reservoir and tubing the flow meter was frequently flushed with a 10% bleach solution and rinsed. Water flow through the stems was left to equilibrate for about 10 minutes after which flow rates were determined volumetrically with serological pipettes connected to the upper end of the stem. We measured the flow rates as the time (s) to fill 0.1 or 0.01 ml (in case of low flow) pipette volume. Hydraulic conductance (K_h; in m^3 s^{-1} MPa^{-1}) was calculated with the following formula;

$$K_h = \frac{\Delta V}{(\Delta P / \Delta X)} \qquad \text{(Eq. 1)}$$

where ΔV is the flow rate (m^3 s^{-1}) and (ΔP/ΔX) is the pressure drop across the stem segment of length X (MPa m^{-1}). We estimated the sapwood area as the stem cross-sectional area after bark removal, minus the area of pith, and calculated sapwood specific conductivity (K_S; kg m^{-1} s^{-1} MPa^{-1}) was calculated by dividing Kh with the sapwood area.

We determined total leaf area for the measured stems. The fresh mass of the leaves was measured in the field with a precision balance (0.01g) and the leaf area of a subsample of known fresh mass was digitised with a flatbed scanner (Canon Lide 50) and analysed using ImageJ software (http://rsbweb.nih.gov/ij/) to determine the leaf area. The total leaf area above the measured stem segment was estimated as the fresh mass of all the leaves over the fresh mass of the subsample, multiplied by the leaf area of the subsample. Leaf specific conductivity (K_L; mmol m^{-1} s^{-1} MPa^{-1}) was calculated as Kh divided by the total leaf area, hence multiplied with 18.02 (the molar mass of water).

Stem and leaf traits

Wood density (WD; g cm^{-3}) was determined for all 40 species. For a sample of each stem measured for conductivity we estimated the fresh volume without the bark using the water displacement method (Ilic et al. 2000). Samples were then dried in an oven for 48 hours at 75°C after which we measured dry mass with a precision balance ($\underline{+}$0.0001 g) and WD was calculated as dry mass / fresh volume.

Maximum vessel length (VL; cm) was determined by air injection (Ewers and Fisher 1989) for five saplings per species. Saplings were selected under the same conditions and in the same area as those measured for conductivity, cut at ground level and transported to the field station. The distal ends of the stem were trimmed with a razor blade to clear blocked vessels and the proximal end was attached to an air pump delivering ~100 kPa pressure. The upper end of the stem was submerged in water and cut back 1 cm at a time until air bubbles escaped. Subsequently the remaining length of the stem was taken as the length of the longest continuous vessel.

For each sapling we calculated the Huber-value (Hv; $cm^2\ cm^{-2}$) as the cross-sectional sapwood area of the upper end of the stem divided the total leaf area it supports. Subsamples of the leaf material collected to estimate the total leaf area were saturated overnight in moist paper towels in a refrigerator after which we measured their fresh mass and average leaf size (LS; cm^2). The samples were oven-dried at 65°C for 48 hours before the determination of dry mass. Leaf dry matter content (LDMC; $g\ g^{-1}$) was calculated as the dry mass divided by the fresh mass. The specific leaf area (SLA; $cm^2\ g^{-1}$) was calculated as the leaf area / dry mass. All hydraulic traits included in this paper are summarized in table 6.1.

Table 6.1

Abbreviations of measured traits with units.

Abbreviation	Trait	Units
ψ_l	Midday leaf water potential	MPa
CE_{juv}	Juvenile crown exposure	-
K_S	Sapwood-specific hydraulic conductivity	$kg\ m^{-1}\ s^{-1}\ MPa^{-1}$
K_L	Leaf-specific hydraulic conductivity	$mmol\ m^{-1}\ s^{-1}\ MPa^{-1}$
WD	Wood density	$g\ cm^{-3}$
VL	Maximum vessel length	cm
Hv	Huber-value (sapwood area per unit leaf area)	$cm^2\ cm^{-2}$ (*10^6)
LS	Mean leaf size	cm^2
LDMC	Leaf dry matter content	$g\ g^{-1}$
SLA	Specific leaf area	$cm^2\ g^{-1}$

Data analyses

Before analyses, hydraulic properties and species traits were ln-transformed to improve homoscedasticity and normality, except LDMC was arcsine-transformed, as a proportional trait. Among-species differences in hydraulic properties were assessed with one-way ANOVAs with species as a fixed factor. To estimate the total amount of variation explained by a given factor effect size we calculated η^2 (a functional equivalent of R^2) as the sum of squares of the factor of the model divided by the (corrected) total, x100%.

Pearson correlation analyses were used to determine how hydraulic conductivity related to the stem and leaf traits across species, their association with indices of moisture and light requirements (ψ_l and CE_{juv}). Forward multiple regressions were used to evaluate which traits were the most important correlates of hydraulic conductivity and which hydraulic properties best explained ψ_l and CE_{juv}.

Multivariate associations among hydraulic properties were analysed with a principal component analysis (PCA) of the mean species values for hydraulic properties and for other wood and leaf traits. The indices of moisture and light requirements (ψ_l and CE_{juv}) were not included in the initial analysis, but plotted a-posteriori against the PCA axes. Statistical analyses were performed using SPSS 15.0 (SPSS Inc., Chicago, USA).

Table 6.2

List of 40 species with scientific and family names and abbreviations, grouping into different guilds in relation to their shade-tolerance (short-lived pioneers (SLP), long-lived pioneers (LLP), Partial shade-tolerant (PST) and shade-tolerant (ST)) and leaf habit (deciduous (D) and evergreen (E)), indices of species´ moisture (ψ_l) and light requirements (CE_{juv}). The hydraulic properties and trait values presented are the untransformed species means (n = 5 per species) included in this study. See table 6.1 for the trait abbreviations.

Species	Code	Family	Guild	Leaf habit	ψ_l (MPa)	CE_{juv} (-)	K_S (kg m^{-1} s^{-1} MPa^{-1})	K_L (mmol m^{-1} s^{-1} Mpa^{-1})	WD (g g^{-1})	VL (cm)	Hv (cm^2 cm^{-2} $*10^6$)	LS (cm^2)	LDMC (g g^{-1})	SLA (cm^2 g^{-1})
Acosmium cardenasii	Aco.c	Fabaceae	ST	E	-3.3	1.4	1.2	12	0.51	99	187	0.8	0.40	172
Actinostemon concepcionis	Act.c	Euphorbiaceae	ST	E	-3.3	1.6	0.6	7	0.71	61	221	1.3	0.54	262
Ampelocera ruizii	Amp.r	Ulmaceae	PST	E	-1.3	1.6	3.6	19	0.55	95	99	42.8	0.34	161
Anadenanthera colubrina	Ana.c	Fabaceae	PST	E	-3.4	1.8	2.6	23	0.50	113	160	0.03	0.57	157
Aspidosperma cylindrocarpon	Asp.c	Apocynaceae	PST	D	-1.8	1.3	2.5	17	0.49	72	129	40.2	0.34	115
Aspidosperma tomentosum	Asp.t	Apocynaceae	PST	E	-2.3	1.3	2.2	27	0.62	53	224	25.5	0.33	174
Astronium urundeuva	Ast.u	Anacardiaceae	LLP	D	-0.5	2.4	16.0	81	0.38	98	92	16.4	0.29	180
Bougainvillea modesta	Bou.m	Nyctaginaceae	LLP	E	-1.0	2.2	0.7	8	0.42	103	231	19.5	0.47	151
Caesalpinia pluviosa	Cae.p	Fabaceae	PST	E	-1.2	1.8	7.6	75	0.61	102	179	1.2	0.47	174
Capparis prisca	Cap.p	Brassicaceae	ST	E	-2.5	1.6	0.6	4	0.53	61	140	73.0	0.34	109
Casearia gossypiosperma	Cas.g	Salicaceae	PST	D	-2.8	1.7	2.2	17	0.52	69	145	19.3	0.42	245
Cecropia concolor	Cec.c	Urticaceae	SLP	E	-0.2	2.4	5.0	48	0.21	98	187	121.3	0.27	174
Ceiba samaura	Cei.s	Malvaceae	LLP	D	-0.9	2.5	6.9	43	0.24	82	115	12.7	0.25	232
Ceiba speciosa	Cei.s	Malvaceae	LLP	D	-0.8	1.6	7.3	51	0.24	71	126	14.7	0.25	250
Centrolobium microchaete	Cen.m	Fabaceae	LLP	D	-1.4	1.9	9.1	53	0.30	92	107	44.9	0.37	240
Combretum leprosum	Com.l	Combretaceae	LLP	E	-1.3	.	5.4	33	0.43	85	112	223.7	0.39	139
Copaifera chodatiana	Cop.c	Fabaceae	PST	E	-2.6	1.9	2.8	41	0.63	60	269	12.6	0.47	132
Erythroxylum daphnites	Ery.d	Erythroxylaceae	ST	E	-2.0	1.6	0.7	11	0.75	54	311	8.2	0.54	152
Gallesia integrifolia	Gal.i	Phytolaccaceae	PST	E	-1.1	1.8	2.5	14	0.38	105	113	56.9	0.25	220
Hymenaea courbaril	Hym.c	Fabaceae	PST	E	-1.0	.	6.3	49	0.58	111	145	28.9	0.49	128
Machaerium acutifolium	Mac.a	Fabaceae	PST	E	-3.0	1.4	2.3	14	0.62	69	119	7.4	0.49	236
Machaerium scleroxylon	Mac.c	Fabaceae	LLP	D	-1.4	2.0	3.7	66	0.49	65	325	3.4	0.48	128
Manihot guaranatica	Man.g	Euphorbiaceae	SLP	D	-0.8	2.7	4.9	65	0.19	107	243	106.4	0.27	227
Myrciaria cauliflora	Myr.c	Myrtaceae	ST	E	-3.1	1.7	0.6	7	0.64	73	241	2.6	0.54	143
Neea cf. steinbachii	Nee.s	Nyctaginaceae	ST	E	-2.5	1.6	1.3	10	0.42	71	151	25.4	0.20	149
Ouratea sp.	Our.sp	Ochnaceae	ST	E	-0.8	1.8	0.6	5	0.52	58	137	69.4	0.53	103
Phyllanthus sp. nov.	Phy.sp	Euphorbiaceae	ST	E	-1.9	1.4	1.1	16	0.68	79	285	8.4	0.48	242
Phyllostylon rhamnoides	Phy.r	Ulmaceae	PST	E	-2.4	1.5	0.6	16	0.62	67	530	11.4	0.29	186
Pogonopus tubulosus	Pog.t	Rubiaceae	ST	D	-1.2	1.7	2.0	8	0.29	82	71	201.4	0.24	269
Psidium sartorianum	Psi.s	Myrtaceae	PST	E	-1.0	1.2	0.9	15	0.56	65	308	10.9	0.24	172
Pterogyne nitens	Pte.n	Fabaceae	LLP	E	-1.8	2.0	6.4	57	0.35	57	171	16.1	0.32	187
Schinopsis brasiliensis	Sch.b	Anacardiaceae	LLP	D	-1.1	.	2.3	18	0.51	66	138	2.5	0.40	177
Simira rubescens	Sim.r	Rubiaceae	PST	D	-2.6	1.6	4.1	34	0.52	61	154	59.5	0.38	161
Solanum riparium	Sol.r	Solanaceae	SLP	E	-0.4	3.0	11.3	61	0.25	106	99	126.8	0.18	240
Spondias mombin	Spo.m	Anacardiaceae	LLP	D	-0.7	2.4	8.1	59	0.22	80	133	35.3	0.23	215
Sweetia fruticosa	Swe.f	Fabaceae	PST	E	-1.5	1.7	8.2	36	0.61	97	79	6.3	0.44	196
Tabebuia impetiginosa	Tab.i	Bignoniaceae	LLP	E	-1.1	2.4	2.6	34	0.43	68	235	51.5	0.35	152
Trichilia elegans	Tri.e	Meliaceae	ST	E	-2.6	1.6	1.9	16	0.57	65	166	17.9	0.35	182
Zanthoxylum monogynum	Zan.m	Rutaceae	PST	E	-2.7	1.5	3.6	33	0.55	46	167	19.8	0.31	167

RESULTS

Species differences in hydraulic properties

Dry forest tree species differed considerably in all the studied hydraulic properties (Table 6.3). Species differences explained on average 83% of the total variation in traits (range 61 – 98%). Of all traits the amount of variation explained by species differences was greatest for K_S and K_L and LS, which differed respectively by 29 and 19-fold and more than 8000-fold across species. VL was least variable of the study traits and differed only 2-fold across species, from 46 to 118cm. The relatively narrow variation of VL may relate to the measurement of saplings of similar height.

Table 6.3

Among-species variation in hydraulic properties, including the results of one-way ANOVAs (df = 39): sum of squares (SS), mean sum of squares (MS), F and significance-values (P), and the total amount of explained variation (η^2; in %); and overall mean trait values (± se), the minimum (Min) and maximum trait values (Max) across species, and the ratio of the maximum value over the minimum value (Ratio) are given. ***, $P < 0.001$. See table 6.1 for the trait abbreviations.

	SS	MS	F	P	η^2	Mean	±	se	Min	Max	Ratio
Hydraulics											
ψ_l	22.6	0.58	44.1	***	92	-1.70	±	0.15	-3.42	-0.17	20.1
K_S	81.7	2.09	111	***	96	3.88	±	0.54	0.55	16.0	29.0
K_L	115	2.94	179	***	98	31.2	±	3.42	4.37	81.1	18.5
Wood traits							±				
WD	2.08	0.05	35.6	***	90	0.48	±	0.02	0.19	0.75	3.88
VL	11.3	0.29	6.44	***	61	78.4	±	2.94	46.3	113	2.44
Hv	34.8	0.89	15.7	***	79	183	±	13.9	70.9	530	7.48
Leaf traits							±				
LS	317	8.12	62.7	***	94	39.6	±	8.12	0.03	224	8053
LDMC	2.78	0.07	10.8	***	73	0.37	±	0.02	0.18	0.57	3.25
SLA	12.8	0.33	14.7	***	78	180	±	7.22	103	269	2.61

Hydraulic conductivity with stem and leaf traits.

K_S and K_L were strongly positively related (Table 6.4, Fig. 6.1). Both K_S and K_L were negatively correlated with wood density and positively with vessel length. Surprisingly, species with a lot of sapwood per unit leaf area (large Huber-value) had a lower K_S, such that K_L (= K_S/Hv) was less variable across species than K_S (29- and 18.5-fold respectively; Table 6.3). . K_S was negatively correlated with LDMC (Table 6.4, Fig. 6.1).

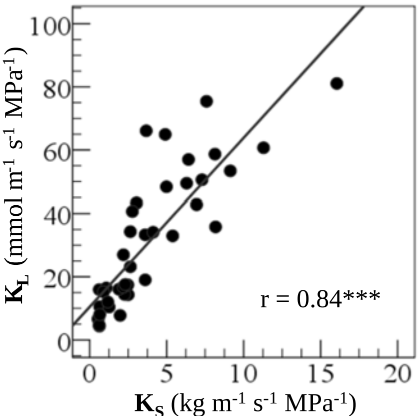


Figure 6.1

Relationship between stem and leaf specific hydraulic conductivity (K_S and K_L) of 40 tropical dry forest species. The Pearson correlation coefficient of the relationship and its level of significance are given. ***, $P < 0.001$.

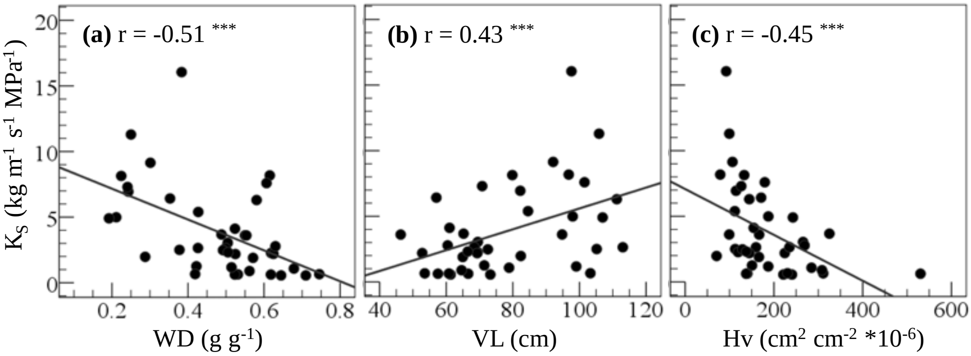


Figure 6.2

Relations between stem traits and sapwood-specific hydraulic conductivity (K_S) of 40 dry forest species. Pearson correlation coefficients and their level of significance are given. ***, $P < 0.001$.

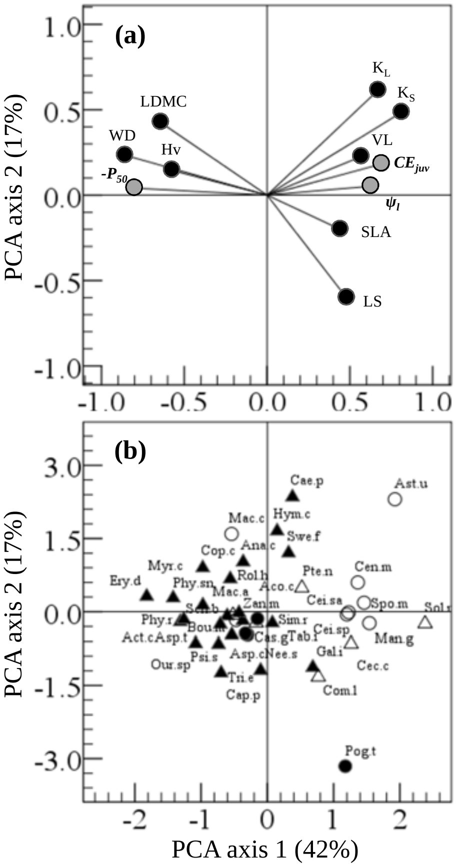


Figure 6.3

Principal component analysis (PCA) with the mean values of hydraulic properties of 40 tropical dry forest tree species. The first two PCA axes are shown with the percentages of explained variation. Species´ moisture requirements (ψ_{l},), light requirements (CE_{juv}) and cavitation resistance ($-P_{50}$, n=13) were not included in the PCA, but plotted later based on their correlation with the two axes (a). Different symbols in the species score plot (b) indicate deciduousness and shade-tolerance of the species. Open symbols are pioneers, closed symbols shade-tolerant species. Dots represent deciduous species and triangles evergreens. See table 6.1 for trait abbreviations and table 6.2 for species codes.

positively to K_S and K_L, maximum vessel length and leaf size and negatively with wood density. Notably, LDMC broke the pattern, being negatively related to Ψ_l but independent of CE_{juv} (Table 6.4, Fig. 6.4).

Forward multiple regression analyses showed that WD and K_L were the most important predictors of both ψ_l and CE_{juv}. For ψ_l the analyses resulted in a model in which WD was included first (β = -0.48, P = 0.002), explaining 38% of the variation and K_L (β = -0.30, P = 0.04) second, explaining an additional 7% of the variation. For CE_{juv} the resulting model appeared to be similar, it included WD first (β = -0.51, P < 0.001), explaining 49% of the variation, and K_L second (β = -0.37, P = 0.008), explaining an additional 10%. Notably, the similar association between traits and ψ_l and CE_{juv} might be the consequence of a strong association between both indices (Table 6.4, r = -0.89, $P \leq 0.001$).

Table 6.4

Bivariate relations between ψ_l and CE_{juv}, hydraulic properties and traits of saplings of 40 dry forest tree species. The table shows Pearson correlation coefficients and their significance. ^{ns}, non-significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. See table 6.1 for more detail on the traits.

	ψ_l	CE_{juv}	K_S	K_L	WD	VL	Hv	LS	LDMC
	n=40	n=36	n=40	n=40	n=40	n=40	n=40	n=40	n=40
Stress-tolerance									
ψ_l									
CE_{juv}	0.63 ***								
Conductivity									
K_S	0.53 ***	0.60 ***							
K_L	0.52 ***	0.63 ***	0.84 ***						
Wood traits									
WD	-0.62 ***	-0.70 ***	-0.51 ***	-0.48 **					
VL	0.36 *	0.48 **	0.43 **	0.32 *	-0.40 *				
Hv	-0.19 ^{ns}	-0.19 ^{ns}	-0.45 **	-0.12 ^{ns}	0.40 *	-0.32 *			
Leaf traits									
LS	0.38 *	0.39 *	0.12 ^{ns}	0.05 ^{ns}	-0.49 **	0.21 ^{ns}	-0.32 *		
LDMC	-0.42 **	-0.32 ^{ns}	-0.34 *	-0.25 ^{ns}	0.68 ***	-0.08 ^{ns}	0.20 ^{ns}	-0.36 *	
SLA	0.04 ^{ns}	0.18 ^{ns}	0.25 ^{ns}	0.10 ^{ns}	-0.33 *	0.18 ^{ns}	-0.21 ^{ns}	0.08 ^{ns}	-0.33 *

DISCUSSION

How do hydraulic properties differ among tropical dry forest tree species?

We found substantial differences across species in all hydraulic properties we studied and among species differences accounted for some 61% to 98% of the variation in traits. Especially the variation in hydraulic conductivity (K_S and K_L) and leaf size was large, which suggests that these traits may play a central role in the niche differentiation of tropical dry forest tree species.

How is hydraulic conductivity related to different stem and leaf traits?

We found strong correlations among functional traits. Wood density emerged as an especially strong correlate of hydraulic traits. Wood density is an easy to measure, low cost estimator that tells a lot about the hydraulic architecture of trees (Chave et al. 2009). In line with many other hydraulic studies, we found a negative relation between wood density and hydraulic conductivity (Bucci et al. 2004, Santiago et al. 2004) and it was the most important predictor of both K_S and K_L.

Dense wood should imply a denser cell packing, due to narrower vessel lumens, and cell wall thickness tends to be invariant with lumen diameter (Pittermann et al. 2006). Narrower vessels thus have a higher cell wall to lumen area ration, and a lower risk of vessel implosion when drought causes extremely negative xylem potentials (Hacke et al. 2001). Notably, lower pit air seeding pressures, a decrease in fibre lumen area or increase in fibre wall thickness could protect plants against cavitation without provoking a causal decline in hydraulic conductivity (Sperry 2000, Jacobsen et al. 2005). Wood density has other roles in the life history variation of trees, as species with low density wood have the potential to realise high growth rates (Roderick 2000, Poorter 2008, Chave et al. 2009) while high wood density increases drought and shade survival amongst evergreen species (Alvarez and Kitajima 2007, Poorter and Markesteijn 2008). Smaller vessels offer better protection against cavitation than bigger vessels, both within and among species (Salleo and Lo Gullo 1989, Lo Gullo and Salleo 1993, Hargrave et al. 1994, Hacke et al. 2001) but consequently have a reduced conductivity.

We also found that wood density related negatively to vessel length. Vessel length has received relatively little attention in studies of plant hydraulics because of various technical and theoretical reasons (Comstock and Sperry 2000). Still with simple means a reasonable estimation of the maximum vessel length in plants can be made (Ewers and Fisher 1989). We found a positive relationship between maximum vessel length and hydraulic conductivity, especially K_S. When water is transported in the stem major resistance in the flow pathway occurs at the pit-membranes that connect different vessel sections (Hacke and Sperry 2001, Sperry et al. 2002). The more often water has to pass from one vessel to the next the greater the resistance and the lower hydraulic conductivity (Hacke and Sperry 2001), the most efficient conducting vessel would be a pipe without any pit-membranes, explaining why species with greater maximum vessel length were more efficient conductors. However, long vessels come at a cost, as cavitation of long vessels would lead to embolism of a greater proportion of the flow pathway. To compensate for the higher cavitation risk of long vessels the typical length frequency distribution found among species is skewed towards shorter vessels (Ewers and Fisher 1989).

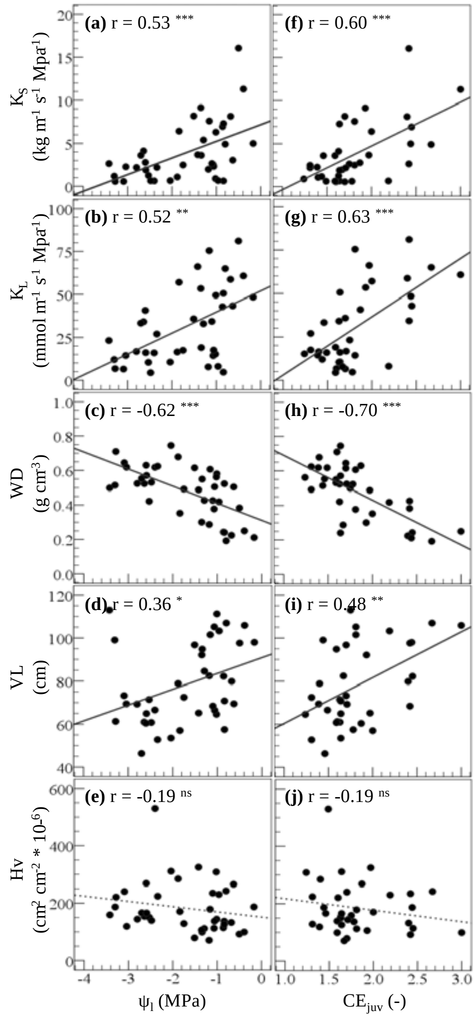


Figure 6.4

Relations between hydraulic conductivity, stem traits and indices of the moisture requirements (ψ_l) and light requirements (CE_{juv}) of 40 dry forest species. Pearson correlation coefficients and their level of significance are given. ^{ns}, non-significant; **, P < 0.01; ***, P < 0.001.

In general hydraulic conductivity was hardly related to leaf traits in this study. Contrary to our expectations, we did not find clear relations between hydraulic conductivity and SLA, where other studies tend to indicate a clear co-ordination of K_L with leaf photosynthetic traits as maximum assimilation rates, stomatal conductance and instantaneous water use efficiency (Santiago et al. 2004), all of which are known to relate well with SLA. Rather than SLA, LDMC is a more important hydraulic trait that is negatively related to conductivity. It allows species to resist low ψ_l and persist under dry conditions (Table 6.4, cf. Tyree et al. 2002, Tyree et al. 2003, Kursar et al. 2009). LDMC is also strongly positively correlated to wood density, indicating that species are geared for persistence by both investing in robust leaves and stems simultaneously.

How are hydraulic properties related to moisture and light requirements of the species?

In order to maintain relatively high leaf water potentials in the dry season, moisture requiring species have a high K_S and K_L. Hydraulic conductivity was facilitated by a low wood density, a large maximum vessel length and a reduced LDMC, which also explains why in the multiple regression analysis wood density is the best predictor for the moisture requirement of species. Our findings corroborate with those from Panamanian forests, where also a strong negative relation between leaf water potential and LDMC was reported (cf. Kursar et al. 2009). This study also reported that moisture requiring species had a greater stem hydraulic conductivity and that both ψ and LDMC were good predictors of species drought performance in the field and their distribution across a gradient in dry season length (cf. Kursar et al. 2009).

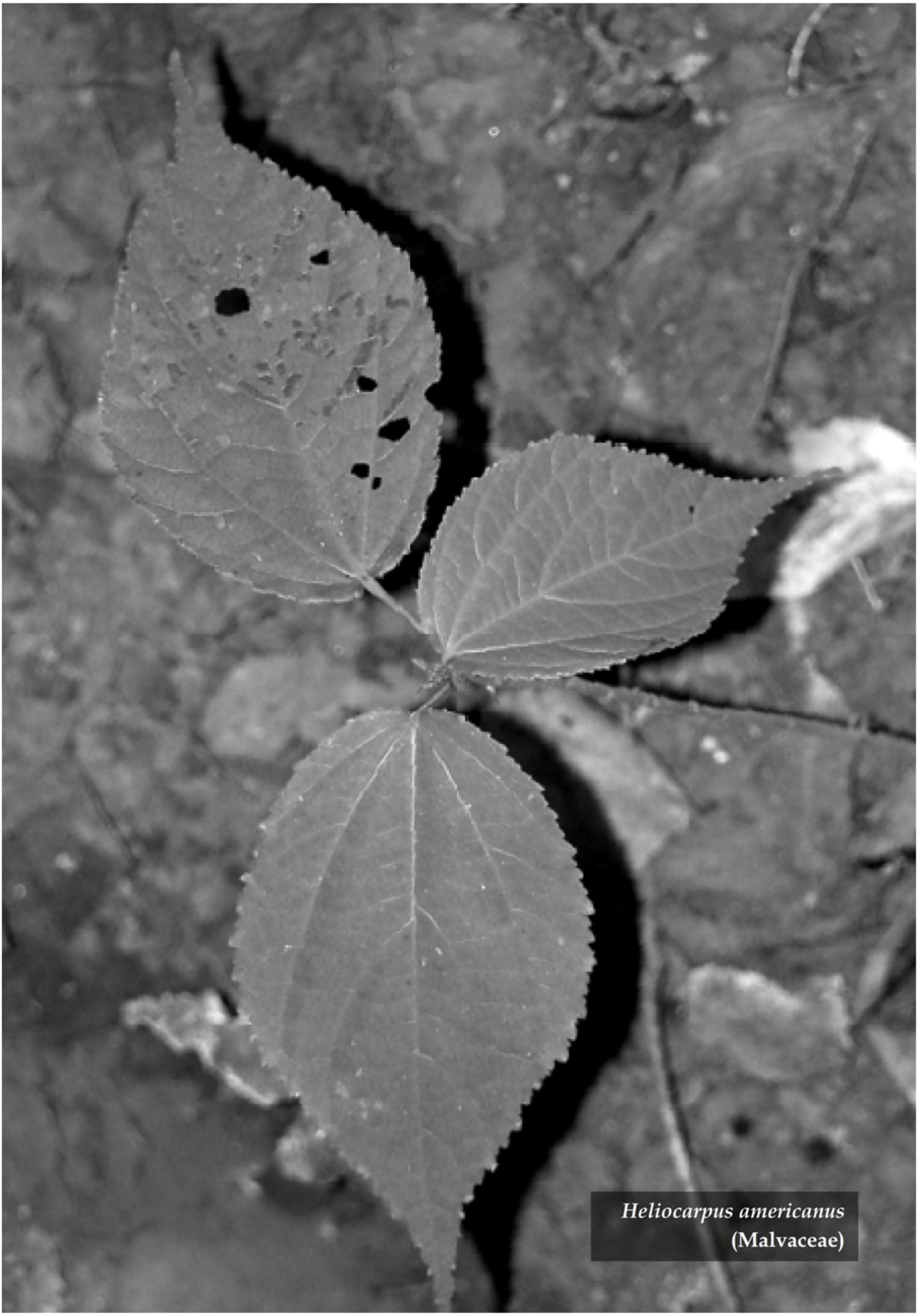
Light-demanding species are generally efficient, opportunistic light foragers that are geared to attain or maintain a dominant position in the canopy of regrowing vegetations (Whitmore 1989). They have high photosynthetic rates as to optimize their carbon gain and boost vertical growth (Ellis 2000, Poorter and Bongers 2006). A high photosynthetic capacity implies greater stomatal conductance and increased transpiration rates, which will have to be compensated for by an increased water flux to the leaves. In our study light-demanding species with a high CE_{juv} were found to have both a higher sapwood-specific and leaf-specific conductivity (Table 6.4, Fig. 6.4) which corroborates with other recent findings for tropical trees (Tyree et al. 1998, Sack et al. 2005).

As opposed to the more shade-tolerant species, light-demanders had a low wood density and a greater maximum vessel length, all geared to establish high hydraulic conductivity and optimize growth. Their low wood density will come at the cost of less structural and mechanical support and higher mortality rates (Poorter 2008, Chave et al. 2009).Thus these tropical dry forest species seemed to operate within the framework set by the growth-survival trade-off (Kitajima 1994) . LDMC and SLA vary often predictably with species shade-tolerance in evergreen wet tropical and humid temperate tree species

(Kitajima 1994, Walters and Reich 1999, Poorter and Bongers 2006), whereas in our dry forest community no such a relationship was found and LDMC and SLA showed to vary independently from CE_{juv} (Poorter 2009).

We found a positive correlation between the midday leaf water potential in the dry season and the juvenile crown exposure and multiple regression analyses showed that both indices were best explained by wood density in the first place and leaf-specific hydraulic conductivity in the second. Wood density is known to be a good estimator of species´ cavitation resistance (Salleo and Lo Gullo 1989, Lo Gullo and Salleo 1993, Hargrave et al. 1994, Hacke et al. 2001, L. Markesteijn et al., unpublished) and leaf hydraulic conductivity determines species´ hydraulic efficiency (Zimmerman 1983, Tyree et al. 1994). Our results thus show a strong coordination between species´ moisture and light requirements in this tropical dry forest, to the extent that habitat partitioning among species follows the classical trade-off between hydraulic efficiency and hydraulic safety (Zimmerman 1983, Tyree et al. 1994).

The results presented in this study do not support the hypothesis of Smith and Huston (1989) which states that there should be a trade-off between drought- and shade-tolerance on the basis of a trade-off in biomass allocation to above and below ground plant parts. From a plant hydraulic point of view, shade tolerant species can express drought-tolerance, and high light species may be constrained in their drought-tolerance due to the hydraulic safety versus efficiency trade-off. This implies coordination of drought- and shade-tolerance, with the ecological consequence that light-demanding species are more drought-intolerant and that their distribution will be restricted to productive habitats that combine both high light availability with high moisture availability, whereas shade-tolerant species are more drought-tolerant such that they will be the better competitors in both drier and shadier habitats. Notably, many species traits determine overall light and moisture requirements, and shade- and drought-tolerance, including hydraulic traits, leaf traits and whole plant traits. Our findings support the great potential of niche differentiation across the range of light and moisture levels in tropical dry forests, as was previously shown in growth experiments in tropical and temperate forests (Sack and Grubb 2002, Engelbrecht and Kursar 2003, Sack 2004, Baltzer et al. 2005, Quero et al. 2006), and that adaptation of hydraulic capacity is integrally linked with this niche differentiation.



Heliocarpus americanus
(Malvaceae)

Chapter 7

Seedling traits determine drought-tolerance of tropical tree species

Lourens Poorter and Lars Markesteijn

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ABSTRACT

Water availability is the most important factor determining tree species distribution in the tropics, but the underlying mechanisms are still not clear. In this study we compared functional traits of 38 tropical tree species from dry and moist forest, and quantified their ability to survive drought in a dry-down experiment in which wilting and survival were monitored. We evaluated how seedling traits affect drought survival, and how drought survival determines species distribution along the rainfall gradient. Dry forest species tended to have compound leaves, high stem dry matter content (stem dry mass over fresh mass), and low leaf area ratio, suggesting that reduction of transpiration and avoidance of xylem cavitation are important for their success. Three functional groups were identified based on the seedling traits; 1) drought avoiders with a deciduous leaf habit and taproots, 2) drought resisters with tough tissues (i.e., a high dry matter content) and a high stem density, and 3) light-demanding moist forest species with a large belowground foraging capacity. Dry forest species had a longer drought survival time (62d) than moist forest species (25d). Deciduousness explained 69% of interspecific variation in drought survival. Among evergreen species stem density explained 20% of the drought survival. Drought survival was not related to species distribution along the rainfall gradient, because it was mainly determined by deciduousness, and species with deciduous seedlings are found in both dry and moist forests. Among evergreen species drought survival explained 28% of the variation in species position along the rainfall gradient. This suggests that apart from drought-tolerance, other factors such as history, dispersal limitation, shade-tolerance and fire shape species distribution patterns along the rainfall gradient.

KEYWORDS

Biomass allocation, Bolivia, deciduousness, morphology, survival, tropical forest, water availability, wood density, wilting.

INTRODUCTION

Within the tropics, water availability is the most important environmental factor determining tree species richness (Gentry 1988, Poorter et al. 2004, ter Steege et al. 2006), composition (Hall and Swaine 1976, Bongers et al. 2004), and distribution (Bongers et al. 1999, Swaine 1996, Holmgren and Poorter 2007). Perhaps the most important component of water availability is the seasonality of its distribution. The length of the dry period may vary from a dry spell of a few days in perhumid wet forests, to a dry season of up to 8 months in dry monsoon forests (Walter 1985, Walsh 1996). Soil water potential at 20 cm depth can drop during this dry period to values below -2 MPa (Veenendaal et al. 1996), suggesting that plant water availability is very low. Seedlings and saplings are affected by this low water availability, and have a reduced leaf water potential and gas exchange (Wright et al. 1992, Tobin et al. 1999, Cao 2000), leading to a reduction in growth (Engelbrecht and Kursar 2003, Bunker and Carson 2005) and survival (Engelbrecht and Kursar 2003, Poorter 2005).

During the past decades tropical forests have experienced a dramatic decrease in annual rainfall, and an increase in dry season length and rainfall variability (Malhi and Wright 2004). Insight into the mechanisms of drought-tolerance is needed, if we want to understand and predict species responses to climatic change. The seedling stage is generally considered to be the most important bottleneck for successful regeneration in dry areas, as seedlings with their limited root system are most vulnerable to drought. To understand how species respond to drought, many experiments have been carried out in which seedlings have been exposed to fixed treatments of low or high levels of water availability (e.g., Burslem et al. 1996, Sack 2004). This may give insight how species partition microsites that differ consistently in water availability, such as wet valley bottoms and dry crests (Gunatilleke et al. 2006). However, it does not give insight into how species partition sites that differ in seasonality, such as wet and dry forests. In that case one should evaluate whether species are able to survive an extended period with little or no water at all (Veenendaal and Swaine 1998).

Species have basically three mechanisms to deal with drought; 1) drought avoidance by spending the dry season in a dormant state, 2) drought delay through an increase in water uptake and a reduction in water loss, and 3) physiological drought-tolerance by being physiologically able to maintain plant functioning at low cell water content. These mechanisms are closely linked to the functional traits of the species. Deciduousness is a trait that confers drought avoidance (Reich and Borchert 1984, Borchert 1994) but it has been more commonly found in the adult stage than in the seedling stage (Hall and Swaine 1981), probably because seedlings do not have sufficient carbohydrate reserves to replace every year a whole set of leaves. A high biomass investment in roots and a high specific root length enhance water uptake, and a low transpiring leaf area and strong stomatal control reduce water loss (Slot and Poorter 2007), both contributing to drought delay. Traits that allow plants to tolerate drought are osmotic regulation and the ability to withstand low leaf water potential (Bonal and Guehl 2001, Tyree et al. 2003). If we know how these species traits are correlated, then we can distinguish functional groups of species that respond in a same way to climate and climatic change (Díaz and Cabido 1997, Lavorel and Garnier 2002). Trait correlations give also gives insight whether there is a potential trade-off between drought-tolerance and shade-tolerance (Smith and Huston 1989, Sack 2004).

Here we compare seedling functional traits of 38 tropical tree species from dry and moist forest, and quantify the ability of 36 species to survive drought under standardized experimental conditions. Species are often classified as belonging to either wet or dry forests, but in reality they vary gradually and continuously in their distribution along the rainfall gradient (Bongers et al. 1999). Here we use a quantitative “drought index” to describe the position of the species along this rainfall gradient. We address the following questions: 1) how are seedling traits related to species position along the rainfall gradient? 2) how are seedling traits associated and what functional groups can be distinguished? 3) what is the drought survival of species under standardized conditions? and 4) what seedling traits are good predictors for drought survival and species distribution?

METHODS

Species and study sites

Thirty eight tropical tree species were selected for the study, of which 36 were included in the drought experiment (Table 7.1). Seeds of 24 species were collected from a moist semi-evergreen forest (La Chonta) and 16 species from a dry deciduous forest (Inpa) in lowland Bolivia. Two species, *Gallesia integrifolia* and *Spondias mombin* were collected from both sites. Species differed in their light requirements for regeneration, as indicated by the juvenile crown exposure (CE). The CE indicate the average, population-level light levels experienced by species when they are 2 m tall, and varies from 1 for species in the forest understory, 2 for species that receive, on average, lateral light, 3 for species that receive on average overhead light on part of their crown, and 4 for species that receive, on average, full overhead light on their whole crown (Poorter and Kitajima 2007).

Both forests are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF), and differ strikingly in climate, forest structure, species richness, and floristic composition (Peña-Claros et al. unpublished data). Inpa (16°6’S, 61°42’W), a dry deciduous forest, has an annual rainfall of 1160 mm with a distinct dry period (potential evapotranspiration > precipitation) of three months and a lowest dry season gravimetric soil water content at 10 cm depth of 4.6% ± 0.4 (SE) (L. Poorter, unpublished data). The forest has an average canopy height of 20 m, stem density of 437 ha^{-1}, basal area of 19.7

Table 7.1

List of 38 species (2 species were sampled at both sites) with scientific names, species abbreviations, density of stems > 10 cm diameter at breast height in dry and moist forest (D), drought index (DI), juvenile crown exposure (CE), survival time during drought (SurvT) and seedling traits. Seedling traits included are: leaf area ratio (LAR), specific leaf area (SLA), leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF), leaf dry matter content (LDMC), stem dry matter content (SDMC), root dry matter content (RDMC), stem density (SD), specific root length (SRL), root length per unit leaf area (RLLA), root length per unit plant mass (RLPM), compoundness (Comp), deciduousness (Dec) and taproot (Tapr). The latter three variables are dummy variables (1=yes, 0=no). Data on CE are from Poorter and Kitajima (2007), and data on tree density from IBIF. Some species have been sampled in the moist forest (e.g., *Aspidosperma cylindrocarpon*, *Hymenaea courbaril*), but are actually more abundant in dry forest, and have therefore a DI>50%.

Scientific name	Family	Code	Dmoist (/ha)	Ddry (/ha)	DI (%)	CE (-)	SurvT (d)	LAR (m^2/kg)	SLA (m^2/kg)	LMF (g/g)	SMF (g/g)	RMF (g/g)	LDMC (%)	SDMC (%)	RDMC (%)	SD (g/cm^3)	SRL (m/g)	RLLA (cm/cm^2)	RLPM (m/g)	Comp (-)	Dec (-)	Tapr (-)
moist forest																						
Alibertia verrucosa	Rubiaceae	Ali.v.	5.48	0.03	1	1.35	26	15.7	26.9	0.58	0.22	0.19	33	33	25	0.44	19.0	2.4	3.7	0	0	0
Aspidosperma cylindrocarpon	Apocynaceae	Asp.c.	2.00	9.28	82	1.75	27	4.4	15.0	0.30	0.26	0.44	33	43	23	0.34	5.3	5.2	2.2	0	0	1
Aspidosperma rigidum	Apocynaceae	Asp.r.	4.79	1.03	18	1.56	18	5.4	21.0	0.26	0.36	0.38	30	47	21	0.65	9.2	6.4	3.4	0	0	1
Batocarpus amazonicus	Moraceae	Bat.a.	1.38	0.09	6	1.35	20	11.4	35.0	0.32	0.33	0.35	34	35	32	0.37	6.4	2.0	2.2	0	0	1
Cariniana estrellensis	Lecythidaceae	Car.e.	1.25	0.00	0	1.40	21	7.2	25.6	0.28	0.21	0.51	40	40	42	0.56	1.3	1.0	0.7	0	0	0
Cariniana ianeirensis	Lecythidaceae	Car.i.	3.21	0.88	21	1.74	27	7.1	31.0	0.23	0.09	0.68	27	35	31	0.13	0.5	0.5	0.4	0	1	0
Cavanillesia hylogeiton	Bombacaceae	Cav.h.	0.67	0.00	0	2.16	-	7.4	33.2	0.22	0.50	0.28	17	21	16	0.14	1.3	0.5	0.4	0	1	0
Cedrela fissilis	Meliaceae	Ced.f.	0.31	0.22	41	1.98	24	7.6	61.1	0.13	0.34	0.53	19	26	27	0.19	1.8	1.4	0.9	1	1	0
Gallesia integrifolia	Phytolaccaceae	Gal.i.	2.06	2.91	58	1.84	22	4.5	26.1	0.17	0.50	0.33	30	45	37	0.42	30.5	22.3	10.0	0	0	0
Heliocarpus americanus	Tiliaceae	Hel.a.	2.21	1.88	46	2.36	20	6.5	35.9	0.18	0.45	0.37	23	28	17	0.28	35.8	22.6	13.0	0	0	0
Hymenaea courbaril	Fabaceae	Hym.c.	0.23	0.66	74	2.00	12	4.2	15.3	0.28	0.46	0.26	43	57	45	0.42	1.7	1.2	0.4	1	0	0
Jacaratia spinosa	Caricaceae	Jac.s.	2.73	0.00	0	2.02	-	10.1	58.3	0.17	0.61	0.22	13	12	8	0.14	11.3	2.5	2.4	0	0	0
Licaria triandra	Lauraceae	Lic.t.	9.92	0.00	0	1.35	14	9.9	22.6	0.43	0.34	0.23	40	43	33	0.38	7.6	1.8	1.7	0	0	0
Margaritaria nobilis	Euphorbiaceae	Mar.n.	2.67	0.00	0	1.84	18	8.9	35.3	0.25	0.43	0.32	25	38	25	0.46	25.5	10.0	8.1	0	0	0
Myrciaria sp.	Myrtaceae	Myr.s.	3.02	2.75	48	1.52	20	13.2	26.4	0.50	0.22	0.28	35	59	55	0.61	37.3	9.3	10.9	0	0	0
Pseudolmedia laevis	Moraceae	Pse.l.	87.29	0.00	0	1.32	17	11.4	26.7	0.43	0.22	0.35	39	30	27	0.35	12.9	3.9	4.4	0	0	0
Sapindus saponaria	Sapindaceae	Sap.s.	4.23	0.09	2	1.63	22	16.4	40.3	0.38	0.37	0.25	34	37	25	0.46	12.5	2.5	2.9	1	0	0
Sapium glandulosum	Euphorbiaceae	Sap.g.	2.79	0.25	8	2.23	20	19.9	45.8	0.43	0.34	0.23	18	17	13	0.23	23.8	2.9	5.5	0	0	0
Spondias mombin	Anacardiaceae	Spo.m.	1.10	1.00	48	1.95	134	9.4	54.4	0.17	0.22	0.61	17	28	21	0.26	3.1	2.0	1.8	1	1	1
Stylogyne ambigua	Myrsinaceae	Sty.a.	10.88	0.03	0	1.46	20	4.7	17.1	0.27	0.41	0.31	29	40	31	0.66	5.9	4.1	1.9	0	0	0
Swietenia macrophylla	Meliaceae	Swi.m.	0.69	0.00	0	1.62	14	9.1	27.5	0.33	0.42	0.25	36	43	31	0.40	5.9	2.0	1.6	1	0	1
Trema micrantha	Ulmaceae	Tre.m.	1.21	0.00	0	2.52	14	5.5	28.0	0.20	0.47	0.34	35	38	27	0.45	44.7	28.5	14.8	0	0	0
Triplaris americana	Polygonaceae	Tri.a.	0.17	0.00	0	1.90	9	14.8	30.6	0.48	0.16	0.36	29	45	56	0.28	10.8	2.7	3.8	0	0	0
Urera caracassana	Urticaceae	Ure.c.	12.35	0.94	7	1.99	-	8.6	31.6	0.27	0.38	0.35	25	19	22	0.27	26.8	11.0	9.4	0	0	0
average moist forest			6.78	0.92	19	1.78	25	9.3	32.1	0.30	0.35	0.35	29	36	29	0.37	14.2	6.2	4.4	0.21	0.17	0.21

Table 7.1 Continued

Scientific name	Family	Code	Dmoist (/ha)	Ddry (/ha)	DI (%)	CE (-)	SurvT (d)	LAR (m^2/kg)	SLA (m^2/kg)	LMF (g/g)	SMF (g/g)	RMF (g/g)	LDMC (%)	SDMC (%)	RDMC (%)	SD (g/cm^3)	SRL (m/g)	RLLA (cm/cm^2)	RLPM (m/g)	Comp (-)	Dec (-)	Tapr (-)
Amburana cearensis	Fabaceae	Amb.c.	-	-	100	-	180	3.2	42.8	0.07	0.25	0.67	26	42	23	0.32	0.3	0.7	0.2	1	1	1
Anadenanthera colubrina	Fabaceae	Ana.c.	0.00	17.97	100	1.75	23	7.7	30.6	0.25	0.13	0.62	51	51	43	0.79	10.3	7.8	6.2	1	0	1
Astronium urundeuva	Anacardiaceae	Ast.u.	0.00	1.34	100	2.42	21	5.8	34.7	0.17	0.10	0.74	28	49	36	0.13	2.2	2.8	1.6	1	0	0
Caesalpinia pluviosa	Fabaceae	Cae.p.	1.31	22.41	94	1.81	23	8.9	32.0	0.28	0.34	0.38	47	56	48	0.75	7.1	3.0	2.5	1	0	0
Ceiba samauma	Bombacaceae	Cei.s.	0.19	0.34	65	2.45	120	5.3	37.4	0.14	0.09	0.77	20	31	16	0.06	0.7	1.0	0.5	1	1	1
Centrolobium microchaete	Fabaceae	Cen.m.	0.85	16.84	95	1.93	-	5.9	35.1	0.17	0.35	0.48	31	47	37	0.49	3.3	2.6	1.5	1	0	1
Chorisia speciosa	Bombacaceae	Cho.s.	0.60	13.38	96	1.64	125	7.9	38.4	0.20	0.41	0.39	19	25	20	0.17	3.0	1.6	1.1	1	1	1
Gallesia integrifolia	Phytolaccaceae	Gal.i.	2.06	2.91	58	1.81	22	8.8	28.4	0.30	0.40	0.30	32	44	44	0.55	58.0	22.1	17.0	0	0	0
Guibourtia chodatiana	Fabaceae	Gui.c.	0.00	3.66	100	1.87	32	5.9	16.7	0.35	0.33	0.32	48	55	48	0.92	11.7	6.4	3.7	1	0	0
Platymiscium ulei	Fabaceae	Pla.u.	0.00	0.34	100	2.52	25	6.8	16.3	0.40	0.21	0.39	29	43	43	0.55	6.0	5.1	2.4	1	0	1
Pseudobombax marginatum	Bombacaceae	Pse.m.	0.04	0.03	43	-	120	3.6	43.3	0.08	0.24	0.68	21	26	25	0.13	0.4	0.8	0.3	1	1	1
Pterogyne nitens	Fabaceae	Pte.n.	0.06	0.22	78	2.00	21	7.0	24.9	0.29	0.13	0.59	39	54	33	0.61	10.6	9.4	6.2	1	0	0
Spondias mombin	Anacardiaceae	Spo.m.	1.10	1.00	48	2.40	149	8.4	50.5	0.17	0.20	0.63	16	27	19	0.26	4.6	3.6	2.9	1	1	1
Sweetia fruticosa	Fabaceae	Swe.f.	2.60	9.31	78	1.70	22	7.2	36.2	0.20	0.07	0.73	36	56	54	0.63	0.9	0.9	0.6	1	0	0
Tabebuia impeteginosa	Bignoniaceae	Tab.i.	0.00	0.78	100	2.42	22	6.6	38.4	0.17	0.15	0.68	36	43	28	0.40	5.2	5.6	3.5	1	0	1
average dry forest			0.59	6.26	85	2.06	62	6.4	33.8	0.21	0.23	0.56	34	44	35	0.45	8.5	5.9	3.6	0.94	0.31	0.63

m^2 ha^{-1} and species richness of 34 ha^{-1} (all data for trees > 10 cm diameter at breast height (Peña-Claros et al. unpublished data). Nearly all canopy trees are deciduous in the dry season. La Chonta (15°47'S, 62°55'W), a moist semi-evergreen forest, has an annual rainfall of 1580 mm with a distinct dry period of one month and a lowest dry season gravimetric soil water content at 10 cm depth of 11.9% ± 1.4. The forest has an average canopy height of 25 m, stem density of 368 ha^{-1}, basal area of 19.7 m^2ha^{-1} and species richness of 59 ha^{-1}. About a third of the canopy trees is deciduous in the dry season.

Seeds were germinated at ca. 15% of full sunlight in a nursery in Santa Cruz, Bolivia (16º30' S, 68º10'W) in trays with a 50:50 mixture of river sand and organic soil. Young seedlings were transplanted to 200 ml plastic tubes (3 cm wide, 12 cm long) containing 50% river sand, 25% topsoil from the dry forest, and 25% top soil from the moist forest. Seedlings were transferred to two shade houses, at IBIF. The shade houses were covered with a light-transparent roof, and both roof and walls were covered with neutral density shade cloth. Light level in the shade houses was ca.10% of full sunlight, which is typical for small forest gaps. This light level is sufficiently high for pioneers and shade tolerants to survive without problems, and to dry down the soil if no watering occurs. After an acclimation period of several weeks to months, an initial harvest was carried out.

Seedling traits

Five randomly selected seedlings per species were harvested at the start of the experiment. Height and diameter at the top and base of the stem were measured and leaves were counted. Seedlings were divided into roots, stem and leaves, and their fresh weight was determined. Leaves were digitalized with a desktop-scanner (Canon Lide 30), and their surface area (cm^2) was determined using pixel-counting software (Van Berloo 1998). Total root length was estimated using the line intersect method of Newman (1966). Roots were placed in a transparent water bath over a paper with a 2 x 2 cm grid system, and the number of intersection between the roots and the gridlines were counted. Subsequently, total root length was estimated as;

$$R = \frac{\pi.N.A}{2.H} \qquad \text{(Eq. 1)}$$

,where R is the total length of the root (cm), N is the number of intersections between root and gridlines, A is the area of the rectangle (cm^2) and H is the total length of the straight lines of the grid (cm) (Newman 1966). Afterwards, all plant parts were oven dried for 48 hours at 65ºC and weighed.

Based on the measurements, we calculated the leaf, stem and root dry matter content (LDMC, SDMC and RDMC; 100 x dry mass per unit fresh mass; %), and the leaf, stem and root mass fractions (LMF, SMF, RMF; dry mass per unit dry plant mass; g g^{-1}). We further calculated the specific leaf area (SLA; leaf area per unit dry leaf mass; m^2 kg^{-1}), leaf area ratio (LAR; leaf area per unit dry plant mass; m^2 kg^{-1}), specific root length (SRL; root length per unit dry root mass; cm g^{-1}), root length per unit plant mass (RLPM; cm g^{-1}) and root length per unit leaf area (RLLA; cm cm^{-2}). Stem density (SD) was determined as dry stem mass per unit stem volume (g cm^{-3}). The stem volume (V; cm^3) was calculated assuming the shape of a cone;

$$V = \frac{\pi . L}{12}\left(D_{top}{}^{2} + D_{top} . D_{base} + D_{base}{}^{2}\right) \qquad \text{(Eq. 2)}$$

, where L is stem length (cm), D_{top} is the diameter at the top of the stem (cm), just under the growth meristem, and D_{base} the diameter at the base of the stem, just above the root. The stem density is probably slightly lower than the wood density, as it includes both the bark and the pith. Finally we scored whether the species showed a deciduous leaf habit in the drought experiment, whether species had simple or compound leaves, and whether species showed a thickened tap root.

Drought experiment

Forty seedlings per species were used for the drought experiment, twenty seedlings per shadehouse. Seedling height and leaf number were measured at the start of the experiment, and seedlings were assigned in such way to the two shade houses that they did not differ significantly in seedling size. Average seedling height of the species at the start of the experiment was 16.2 cm (range 4.5-32.1). Tubes containing the seedlings were watered up to field capacity after which plants did not receive additional water. With this experiment, we, thus present a worst-case scenario in which seedlings restricted to a limited volume of soil are exposed to sudden drought. Such sudden, short dry spells have also been shown to affect seedling survival in the field within a few days (Engelbrecht *et al.* 2006). The progressive impact of drought on seedlings was assessed from the start of the experiment by monitoring leaf wilting and seedling survival every other day up to 36 days. Thereafter observations were made every two weeks, because the few remaining species showed little change in wilting behaviour. We adapted Engelbrecht and Kursar's (2003) five visual wilting stages based on leaf angle, leaf rolling and necrosis (Table 7.2). We included "deciduous" as an additional wilting stage (Table 7.2). These wilting stages are closely related to the gas exchange and water potential of seedlings of seedlings during progressive drought (Tyree *et al.* 2003, Slot and Poorter 2007). The drought survival experiment was done for 8 species in August 2004 and for 28 species in November 2005. There were no significant differences in average drought survival time of the species between the two years (t-test, t=0.3, P=0.77, df=34), and the results were therefore pooled.

Table 7.2

Characterization of different wilting stages, based on visual leaf and stem characteristics (adapted from Engelbrecht and Kursar 2003).

Wilting stage		Characteristics
0	Normal	No signs of wilting or water stress
1	Slightly wilted	Slight leaf angle changes, but no folding rolling or changes in leaf structure
2	Intermediately wilted	Strong leaf angle change or visible change of leaf surface structure, but no cell death
3	Severely wilted	Very strong leaf angle change or change of leaf surface structure with beginning leaf necrosis
4	Nearly dead	All leaves dead, but stem still alive; distinguished by color and elasticity
5	Deciduous	All leaves actively shed, but stem still alive; distinguished by color and elasticity
6	Dead	All above ground parts dead

Data analysis

A principal component analysis (PCA) was carried out to evaluate how seedling traits were associated amongst each other. The PCA was carried out using 15 traits of 40 species. Deciduousness, compound leaves, and the presence of taproots were included as dummy variables (present=1, absent=0). The drought index, drought survival time and juvenile crown exposure were not included in the analysis, but later correlated with the species scores along the first and second PCA axis.

A survival analysis was carried out to evaluate differences in survival times amongst species in the drought experiment. For this analysis the seedlings from both shadehouses were pooled. In 2004 the monitoring period was confined to 2 months. For two species (Ceiba samauma and Pseudobomax marginatum) not all seedlings had died by the end of the evaluation period, and these data were right-censored in the survival analysis. However, more than 50% of the seedlings were still alive after 4 months of drought (L. Poorter, pers. obs.), and the average survival time of these species was therefore arbitrarily set at 120 days.

The position of species along the rainfall gradient was quantified using a "drought index". The drought index (DI) is based on the relative abundance of a species in the dry and wet forest site, and calculated as;

$$DI = 100\left(\frac{D_{dry}}{D_{dry} + D_{moist}}\right) \qquad \text{(Eq. 3)}$$

, where D_{dry} and D_{moist} are the mean stem density (tree ha^{-1}) of a given species in the dry forest and moist forest respectively. Stem densities were calculated from the number of trees >10 cm diameter at breast height per ha, for 32 1 ha plots in the dry forest and 48 1 ha plots in the wet forest (Peña-Claros et al. unp. data). Of the 38 species, ten species occurred only in the moist forest (i.e., they had a DI of 0), seven species occurred only in the dry forest (i.e., they had a DI of 100), while the remainder occurred at both sites (having a DI between 0 and 100). It must be noted that the drought index provides a simplified description of the actual distribution of the species, as it was derived from two forests only. It therefore provides a conservative estimate of the actual species position along the rainfall gradient, as species that have a DI of 0 are likely to occur in even wetter forests, whereas species with a DI of 100 are likely to occur in even drier forests. Relationships between seedling traits, survival time, and drought index were evaluated with a Pearson correlation. A forward multiple regression was done to evaluate which of the 15 seedling traits are good predictors of the drought survival and the drought index of the species. All statistical analyses were done using SPSS 12.0.1.

RESULTS

Species traits versus drought index

An initial harvest was carried out at the start of the experiment to evaluate how species differed in their functional traits, and whether these traits are good predictors for species position along the rainfall gradient. Species position along the rainfall gradient was expressed by the drought index. RMF, RDMC, SDMC, compoundness and presence of a thickened taproot were positively correlated, and LAR, LMF and SMF were negatively correlated with the drought index (Table 7.3, Fig. 7.1). A multiple regression was carried out to evaluate which of the 15 seedling traits were the best predictors of the drought index. Compoundness was first included in the analysis, and explained 48% of the variation in drought index (standardized regression coefficient beta =0.52, $P<0.001$). SDMC (beta=0.28, $P=0.013$) and LAR (beta=-0.26, $P=0.019$) were included as second and third variable in the analysis, and explained an additional 10 and 6% of the variation.

Trait associations

A principal component analysis (PCA) was carried out to evaluate how species traits are associated amongst each other (Fig. 7.2a). The first and second axis explained respectively 33 and 25% of the trait variation. Three clusters of traits can be distinguished, related to deciduousness, dry matter content, and resource capture. On the right hand of the first axis are species with compound deciduous leaves with a high SLA, a high biomass fraction in roots (RMF) and a taproot. On the top of the second axis are species with high dry matter

Table 7.3

Pearson correlation between functional traits of seedlings of tropical tree species, their survival time during drought (SurvT), survival time during drought for evergreen species only (STever), juvenile crown exposure (CE) and drought index (DI). The n varies from 36-40 species (except for correlations with STever, for which n varies from 27-31). For trait abbreviations see Table 7.1. Correlations in bold are significant at the P<0.05, correlations in bold and italcs are significant at P<0.01.

Trait	SurvT	STever	DI	CE	LAR	SLA	LMF	SMF	RMF	LDMC	SDMC	RDMC	SD	SRL	RLLA	RLPM	Comp	Dec
DI	0.27	0.53																
CE	0.26	0.02	0.36															
LAR	-0.24	-0.14	-0.51	-0.26														
SLA	0.52	-0.09	-0.06	0.28	0.22													
LMF	-0.5	-0.06	-0.39	-0.48	0.72	-0.47												
SMF	-0.19	-0.23	-0.36	-0.04	-0.01	0.02	-0.05											
RMF	0.48	0.23	0.54	0.36	-0.49	0.3	-0.65	-0.73										
LDMC	-0.52	0.17	0.31	-0.39	-0.14	-0.57	0.24	-0.19	-0.02									
SDMC	-0.41	0.11	0.51	-0.20	-0.28	-0.59	0.14	-0.31	0.15	0.79								
RDMC	-0.45	0.01	0.34	-0.24	-0.06	-0.48	0.29	-0.32	0.05	0.68	0.83							
SD	-0.43	0.44	0.23	-0.33	-0.05	-0.55	0.32	-0.03	-0.2	0.69	0.7	0.62						
SRL	-0.33	-0.04	-0.21	0.07	0.24	-0.14	0.26	0.36	-0.46	0.04	0.01	0.08	0.2					
RLLA	-0.28	0.02	0.06	0.27	-0.21	-0.19	-0.13	0.31	-0.15	0.24	0.17	0.1	0.21	0.81				
RLPM	-0.33	-0.03	-0.08	0.16	0.1	-0.15	0.13	0.28	-0.3	0.14	0.09	0.11	0.23	0.96	0.91			
Comp	0.43	0.25	0.69	0.33	-0.31	0.25	-0.41	-0.35	0.55	0.17	0.29	0.16	0.08	-0.51	-0.28	-0.41		
Dec	0.85	-	0.08	0.23	-0.22	0.53	-0.49	-0.16	0.46	-0.58	-0.45	-0.42	-0.59	-0.41	-0.36	-0.41	0.3	
Tapr	0.56	0.15	0.41	0.13	-0.33	0.14	-0.37	-0.24	0.43	-0.04	0	-0.2	-0.12	-0.4	-0.17	-0.31	0.47	0.33

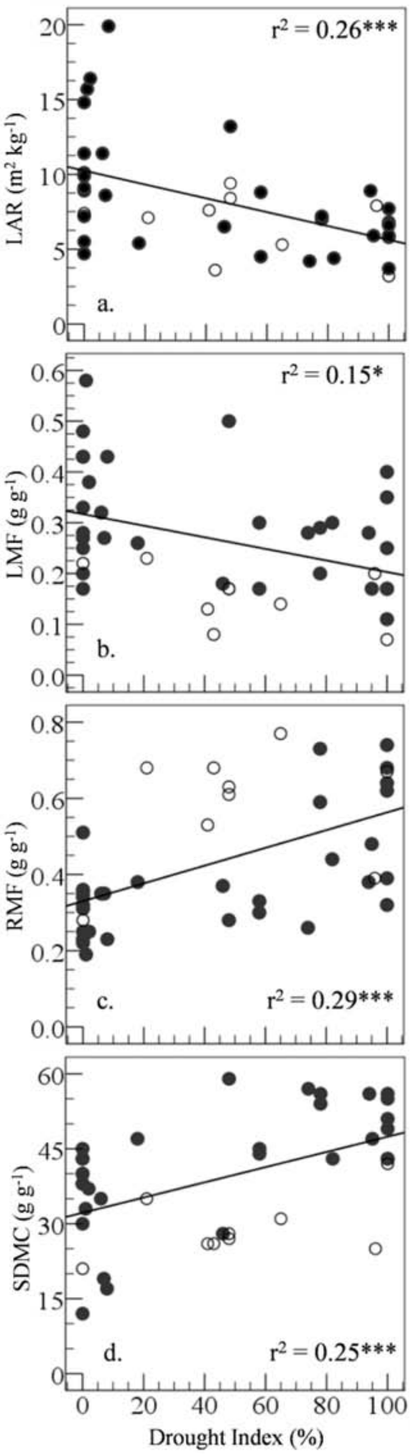

Figure 7.1

Relationship between functional traits and drought index of 38 tropical tree species (2 species were sampled at both sites) . Evergreen species are represented by filled symbols, deciduous species by open symbols. a) leaf area ratio (LAR), b) leaf mass fraction (LMF), c) root mass fraction (RMF), d) stem dry matter content (SDMC). Regression lines, coefficients of determination, and significance levels are shown. * $P<0.05$; **: $P<0.01$; ***: $P<0.001$

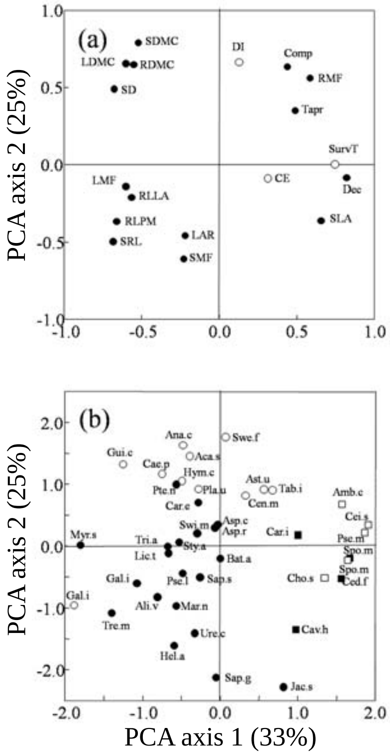

Figure 7.2

Principal component analysis of 15 seedling traits of 40 tropical tree species. The loading plots for the first axis (explained variation is 33%) and second axis (explained variation is 25%) are shown. Survival time during drought (SurvT), drought index (DI) and juvenile crown exposure (CE) were not included in the PCA analysis, but later correlated with the PCA axes (indicated by open symbols). Trait abbreviations are given in Table 7.1. b) Species loadings. Species abbreviations are given in Table 7.1. Moist forest species are indicated by filled symbols, dry forest species by open symbols, evergreen species by circles and deciduous species by squares.

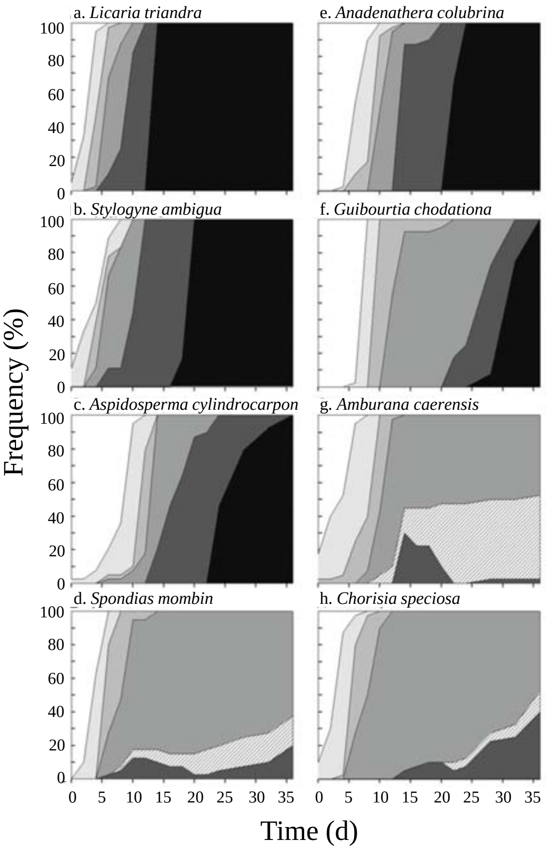

Figure 7.3

Time course of wilting of moist forest (left panels) and dry forest (right panels) tree species exposed to experimental drought. a) Licaria triandra, b) Stylogyne ambigua, c) Aspidosperma cylindrocarpon, d) Spondias mombin, e) Adenanthera colubrina, f) Guibourtia chodatiana, g) Amburana cearensis, h) Chorisia speciosa. Forty seedlings per species were exposed to drought. Different shading refers to different wilting stages: white: normal, dotted: slightly wilted, grey: intermediately wilted, dark grey: severely wilted, very dark grey: nearly dead, hatched: deciduous, black: dead.

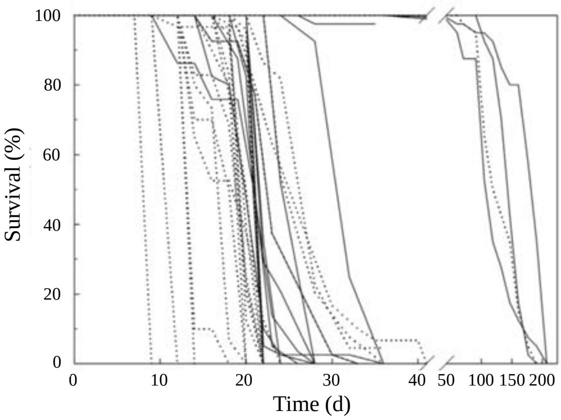

Figure 7.4

Survival curve of seedlings (n=40 per species) of 21 moist forest species (dotted lines) and 15 dry forest species (continuous lines) exposed to experimental drought.

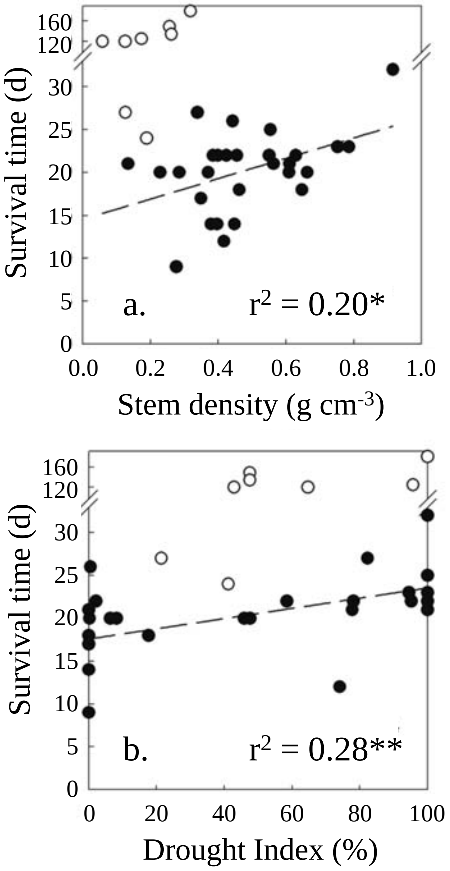

Figure 7.5

Drought survival time of seedlings of 36 tropical tree species versus a) stem density, and b) drought index. Evergreen species are represented by filled symbols, deciduous species by open symbols. The regression line has been fitted for the evergreen species only. Coefficients of determination, and significance levels are shown. * $P<0.05$; **: $P<0.01$; ***: $P<0.001$

Species from drier forests may enhance water capture by investing more biomass in roots, and by making thin roots with a high SRL, thus increasing the root length per unit plant mass. Species from drier forests were indeed characterized by a higher RMF (cf. Hoffmann and Franco 2003), but did not have a higher SRL or RLPM (Table 7.3). Foraging a large soil volume for water makes probably little sense in dry forests, as in the dry-season the water content in the top soil falls to uniformly low levels. Instead, trees may store water in a large root system (high RMF), consisting of a thick taproot with a low SRL. Similarly, in Australia, woody species from low rainfall areas have a lower SRL than species from high rainfall areas, which probably enhance the ability of roots to penetrate dry soil (Wright and Westoby 1999, Nicotra et al. 2002). In natural environments, soil water availability increases strongly with depth in the soil, especially so in the dry season (Engelbrecht et al. 2005). Species may therefore explore the moister deeper soil layers by making deep roots (Poorter and Hayashida-Oliver 2000). We did not evaluate rooting depth in our experimental setup, but other studies found that seedlings from drier forests make deeper roots than species from wetter forests (Paz 2003, Nicotra et al. 2002, Markesteijn and Poorter unp. data), by investing more biomass in the primary root axis, and diverting less biomass to lateral roots (Nicotra et al. 2002).

Perhaps the most surprising result was the strong correlation between stem dry matter content and the drought index. Similarly, Wright and Westoby (1999) found that species from drier areas had higher plant dry matter content than species from wetter areas. The SDMC represents the ratio of woody stem biomass over stem fresh mass. The fresh mass also includes water present in the symplast, vessels, and extracellular spaces. Tree species with a high SDMC are therefore likely to have narrow vessels with thick cell walls (Castro-Diez et al. 1998), and it is especially these stem traits that make trees less vulnerable to xylem cavitation (Hacke et al. 2001). Xylem cavitation is generally considered to be the most important cause of tree mortality in dry habitats (Cavender-Bares et al. 2004). A high SDMC may also enhance plant resistance to fire, wind, and grazing, which are other important causes of plant mortality in drier and more open plant communities.

The multiple regression indicated that dry forest trees are best characterized by compound leaves, stems with a high dry matter content, and low LAR, suggesting that reduction of transpiration and avoidance of xylem cavitation are important elements for the success of dry forest species. Not only the dry season performance, but also wet season performance might be important for the success of dry forest species. Many of the compound-leaved dry forest species belong to the Fabaceae (Table 7.1) which are nitrogen fixers. They are characterized by higher leaf nitrogen concentrations and a higher photosynthetic potential than the non-fixing species. This allows them to photosynthesize at high rates when water is available and accumulate carbon reserves for new foliage production after drought (cf. Eamus and Prior 2001).

Drought survival

The survival analysis showed that species show a large variation in dehydration and survival responses to drought (Fig. 7.3, Fig. 7.4). This varied from sudden dehydration and death within 9 days for the most extreme moist forest species, to leaf abscission and survival up to 6 months for the most extreme dry forest species. Dry forests had a drought survival time that was on average twice as long as that of moist forest species, indicating that they can bridge a longer dry season. Dry season survival under field conditions may be much higher than in our experiment, because seedlings in the field grow in an unlimited soil volume and benefit from incidental rains. The difference in survival time between dry and moist forest species is likely to be much more marked under field conditions, as especially the dry forest species are able to survive with the little water that is left in the soil. In a moist forest in Panama (2600 mm rain per year), Engelbrecht and Kursar (2003) evaluated the drought survival of seedlings of 28 species in the forest understory. Fifty seven percent of the species showed increased mortality in response to drought, but as many as 43% of the species could easily withstand 5.5 months of drought, suggesting that they are well-adapted to the seasonal drought in the area.

Species traits and drought survival; the importance of deciduousness and tough tissues

The multiple regression analysis showed that under extreme dry conditions drought avoidance through leaf abscission is the best strategy to survive drought, and that the presence of a thickened taproot is important as well. In fact, most deciduous species have a taproot, and water stored in the taproot may allow deciduous plants to support evaporational water loss through the bark, and maintain sufficient high cell water content to keep metabolic processes going, and flush again at the onset of the rainy season. If deciduous species were excluded then stem density became the best predictor of drought survival, probably because of its close link with resistance to xylem cavitation. The principal component analysis showed that dry forest species follow the same two strategies; drought avoidance through deciduousness, and drought resistance through tough and dense tissues (Fig. 7.2b). These two strategies were also found among drought-adapted Californian chaparral shrubs (Ackerly 2004), suggesting that they represent common avenues of plant adaptation to dry habitats (cf. Eamus and Prior 2001).

A third strategy is followed by the light-demanding pioneers from the moist forest (Fig. 7.3b). They were characterized by an extensive root system, with fine roots with a high SRL and high root length per unit plant mass (cf. Paz 2003). Such pioneers may not only forage for water, but especially for nutrients to meet the high nutrients requirements that come along with fast growth rates and high turnover rates of leaves and roots (cf. Ryser 1996, Reich et al. 1998, Poorter and Bongers 2006).

We evaluated seedling traits related to biomass allocation, morphology, and phenology. Tyree et al. (2003) found that drought-tolerance is also closely related to physiological traits; species that can tolerate low leaf water contents and leaf water potentials are the ones that show the best survival under dry conditions. Hence, the physiological ability of cells and meristems to remain alive under dry conditions is also an important component of drought survival.

The drought survival of evergreen species is linked to species position along the rainfall gradient, with species that have a longer survival time having higher abundances in drier forests (Fig. 7.5b). Similarly, in Panama the drought survival of seedlings was a good predictor of species position along local and regional gradients in water availability; species with a high drought survival had a higher abundance on the dry plateau, and in drier forests (Engelbrecht et al. 2005, 2007).

Is there a trade-off between drought-tolerance and shade-tolerance?

Smith and Huston (1989) hypothesized that there is a trade-off between species' ability to tolerate shade and drought. Species from dry habitats should allocate more biomass to roots to capture water and species from moist and shaded habitats should allocate more biomass to leaves to capture light. For the Bolivian tropical tree species, such a trade-off between shade and drought-tolerance has indeed been found; the correlation between drought index and juvenile crown exposure (the inverse of shade-tolerance) was 0.36 ($n=37$, $P=0.03$, Table 7.3). A similar trade-off has been found for a large set of temperate tree species (Niinemets and Valladares 2006). The underlying trade-off in biomass allocation to leaves and roots was also found ($r=-0.65$, $n=40$, $P<0.001$), and species from moist habitats had indeed a large LMF and species from dry habitats a high RMF (Fig. 7.1). Yet, Smith and Huston's paradigm does not fully apply; the high biomass fraction in leaves enables moist forest species to capture more light, but a high biomass fraction in roots does not enable dry forest species to capture more water, because their thick taproots are not very efficient in water uptake (cf. Craine et al. 2003) and do not result in a higher root length per unit plant mass (Table 7.3). Instead, roots of dry forest species may have a storage function for water to overcome the dry season, or a storage function for carbohydrates to resprout after fire (Hoffmann et al. 2003).

CONCLUSIONS

In this study we evaluated how seedling traits affect whole-plant performance under dry conditions, and how drought survival, in turn, determines the distribution pattern of tree species. Three functional groups were identified based on the seedling traits; 1) drought avoiders with a deciduous leaf habit and taproots, 2) drought resisters with tough tissues and a high stem density, and 3) light-demanding moist forest species with a large foraging capacity for belowground resources. Until recently it was thought that drought survival of seedlings mainly depends on physiological traits (e.g., Tyree et al. 2003), but this study indicates that phenological and morphological traits are important as well. Deciduousness explained to a large extent (69%) interspecific variation in drought survival. Apparently there is a cost associated to such a drought avoiding mechanism, because only 22% of the studied species are deciduous in the seedling stage. Among the evergreen species stem density explained most variation in drought survival best (20%), but 80% of the variation remained unexplained. This suggests that physiological traits and trait characteristics of later ontogenetic stages co-determine the drought-tolerance of this large group of evergreen species.

Drought survival in itself could not explain species distribution along the rainfall gradient, because it was mainly determined by deciduousness, and species that are deciduous in the seedling stage are found in both dry and moist forests (Fig. 7.5b). Among the evergreen species the drought survival was a reasonable but modest predictor (28%) of species position along the rainfall gradient. This predictive power might be enhanced once better and more refined estimates of species position along the rainfall gradient become available (e.g., Bongers et al. 1999) than the rather simple drought index that we used in this study. Nevertheless, it also suggest that, apart from drought-tolerance, other factors such as biogeographic history (Killeen et al. 2005), dispersal limitation (Daws et al. 2005), shade-tolerance and fire tolerance (Hoffmann 1999) shape the distribution patterns of tree species along the rainfall gradient.

Cavanillesia hylogeiton
(Malvaceae)

Chapter 8

Summary & Synthesis

Tropical forests occur under rainfall regimes that vary greatly in the rainfall pattern and frequency and intensity of drought. Consequently water availability is one of the most important environmental factors influencing community structure, species composition, species abundance, species richness and plant functioning across the rainfall gradient (Medina 1999, Ter Steege et al. 2006, Engelbrecht 2007), as well as species distribution along small scale gradients within tropical forests (Webb and Peart 2000, Comita and Engelbrecht 2009). Climate change models for the tropics predict considerable shifts in precipitation patterns involving both reductions in the total amount of annual precipitation as longer dry seasons and a greater year to year variability (Malhi and Wright 2004, Margin et al. 2007). The relative success of tree species to establish along small and large scale gradients of water availability and their success in dealing with future changes in water availability will depend on how they are adapted to tolerate drought.

Drought-tolerance can be defined as the ability of species to survive desiccation and minimise reductions in growth and fitness (Larcher 2003, Engelbrecht and Kursar 2003). Still, studies that examine drought-tolerance on a large number of tropical tree species are rare and tend to focus on comparative analyses of only few species from distinct groups at the extremes of life history gradients (e.g. pioneer vs. shade-tolerant species or deciduous vs. evergreen species). This implies that generalizations and the up-scaling of species-specific processes to the level of the forest community are difficult to make.

Across tropical forests water may be the most important limiting factor to plant growth and survival, but it is surely not the only limiting factor. Water and light availability, for instance, vary predictably; as dry forests are more open and have a higher light availability than wet forests that are dense and cast deeper shades (cf. Coomes and Grubb 2000, Parker et al. 2005). This trade-off between water and light availability can also be expected within forests where the vegetation on dry spots (e.g. crests) will be more open than on wet spots (e.g. valley bottoms). Species distribution along these gradients will thus largely depend on their ability to tolerate both drought and shade and a trade-off between drought- and shade-tolerance can thus exist if adaptations that enhance species drought-tolerance constrain their survival under low light conditions or the other way around. Although the existence of this trade-off is in theory quite plausible, it remains controversial as empirical evidence is inconsistent (e.g. Niinemets and Valladares 2006, Sack and Grubb 2002) and drought- and shade-tolerance have been found to show a trade-off (Niinemets and Valladares 2006) or to vary independently (Holmgren 2000, Sack and Grubb 2002, Sack 2004).

In this dissertation I applied a multi-species, multi-trait approach to give detailed information on the mechanisms of drought-tolerance of a large set of tropical tree species. New insights into the drivers that shape species distribution should be of great value as they can both help explain patterns of local and regional biodiversity in the present as well as predict the vulnerability of communities to current and future environmental change.

The following four questions were addressed; 1) How do dry and moist forests differ in soil water availability?, 2) How are dry and moist forest species adapted to drought and what different drought-strategies can be distinguished?, 3) Is there a trade-off between drought- and shade-tolerance?, and 4) How do drought- and shade-tolerance determine local and regional tree species distribution? In the following paragraphs I will first give a summary of the main findings of chapters 2 to 7 after which I will come back to each of the four research questions to answer them in a synthesis.

LIGHT-RELATED LEAF TRAIT PLASTICITY IN A TROPICAL DRY FOREST

Our understanding of leaf acclimation of tropical trees in relation to irradiance is mainly based on research involving wet forest species. In CHAPTER 2 I studied sun-shade plasticity of 24 morphological, anatomical and chemical leaf traits of 43 tree species in the dry forest site. To assess plasticity for each species, leaves were taken from five intermediate-sized trees with the most and five trees with the least illuminated crowns. I examined leaf trait variation in response to light and addressed (1) how leaf trait plasticity differs among functional species groups, (2) how plasticity relates to regeneration light requirements, adult stature, or ontogenetic changes in crown exposure of species and (3) how leaf trait plasticity differs among tropical dry, moist and wet forests.

Leaf trait variation was mainly determined by differences among species and to minor extent by light availability. Among species differences explained on average 77% of the leaf trait variation (range 34–95, Table 2.3), differences between light treatments explained considerably less (mean 3.4%, range 0.2–10). The largest sun shade plasticity was found for anatomical traits.

Short-lived pioneer species had the highest trait plasticity (Table 2.4) probable because they grow in more heterogeneous habitats (Strauss-Debenedetti and Bazzaz 1996), but this is in contrast with results from other studies (Sims and Pearcy 1989, Popma *et al.* 1992, Kitajima 1994, Rozendaal *et al.* 2006).

Overall plasticity was modest and rarely associated with regeneration light requirements, adult stature, or ontogenetic changes in crown exposure between saplings and adult trees (Table 2.4, Fig. 2.1). Maybe ontogenetic changes in crown exposure are related to ontogenetic plasticity, rather than the sun-shade plasticity as derived from trees of similar age.

I compared leaf trait plasticity from the dry forest site with a study from the moist site (Rozendaal *et al.* 2006) and a wet forest (Bongers and Popma 1988). Dry forest tree species had a lower light-related plasticity than wet forest species (Table 2.5, Fig. 2.2), probably because wet forests cast deeper shade year round. With light being a more limiting resource wet forest species may need stronger trait response. In dry forests, where light availability is less limiting, low water availability can constrain leaf trait plasticity in response to light.

SOIL AND PLANT WATER AVAILABILITY IN TROPICAL FORESTS

Heterogeneity in soil water availability codetermines species distribution in tropical forests, but studies that actually quantify the variation in soil water availability in tropical forests are rare. In CHAPTER 3 I determined seasonal variation in soil matric potentials (ψ_{soil}) along a topographic gradient and how this varies with soil depth in a tropical dry and moist forest.

In both the dry and moist forest ψ_{soil} tracked the variation in rainfall and declined during the dry season, but the drop in ψ_{soil} was more extreme in the dry forest than in the moist forest (Fig. 3.1), in spite of relatively small differences in monthly precipitation. This suggests that other factors than precipitation can have considerable effect on soil water availability, such as differences in evaporative demand, atmospheric water deficit, or soil texture.

Within the moist and the dry forest topography had a clear effect on soil water availability and on average valleys and slopes were relatively wet compared to crests (Fig. 3.3). This corroborates with the findings of several other studies (e.g. Becker et al. 1988, Daws et al. 2002) and underlines the importance of topography in redistributing soil water over the landscape. In the dry forest the top soils were drier than deep soils in the dry season, while the reverse was found at the start of the wet season (Fig. 3.3). This implies that deep rooting species have better access to soil water in the dry season, while shallow rooting species are the first to exploit water in the top soil after the first rains of the season.

I also evaluated the consequences of seasonal drought for the leaf water potential of tree saplings. Predawn leaf water potential (ψ_{pd}) turned out to be a good indicator of the actual water availability to a plant as it expresses the water potential of the soil immediately next to the root at any given moment in time. Overall ψ_{pd} tracked temporal variation in ψ_{soil}, and monthly precipitation.

If their morphological and physiological adaptations permit species to successfully compete for water at different topographical locations, or to tap the water from different soil layers or do so at different moments in time, then a variety of species may potentially coexist. Heterogeneity of soil water availability could therefore be a key contributing to the high biodiversity of tropical forest in general and seasonally dry forests in specific.

SEEDLING MORPHOLOGY OF DRY AND MOIST FOREST TREE SPECIES

Water availability is the main determinant of species distribution in lowland tropical forests and species occurrence along water availability gradients will depend on their ability to tolerate drought. To identify species traits underlying drought-tolerance I excavated first year seedlings of 62 dry and moist forest tree species at the onset of the dry season. In CHAPTER 4 I evaluated how morphological seedling traits differed between dry and moist forest tree species, whether functional strategies of species could be identified, and whether there was a functional basis for a trade-off between drought and shade-tolerance.

Overall, seedling morphology of dry and moist forest species differed in line with the hypothesis of Brouwer (1963) which predicts that, under a given regime of stresses, plants maximize their surface area for intake of the most limiting resource. Seedlings of dry forest species indeed had a higher water foraging capacity in deep soil layers by increasing biomass allocation to belowground tissue (high RMF) and by producing deep roots compared to moist forest species (Table 4.3). Dry forest seedlings had high stem densities, probably to minimise the risk of drought-induced cavitation, and reduced transpiration by investing less to leaf tissue (smaller leaf are, SLA, LAR) (Table 4.3). Moist forest seedlings had large leaf areas and a greater above-ground biomass allocation, thus enhancing light interception. In a light-limited environment, surprisingly moist forest species produced long, cheap and heavily branched root systems.

A principal component analysis on seedling traits showed that species sorted out along a ´persistence´ axis and a ´deciduousness´ axis and revealed three major drought strategies (Fig. 4.1, 4.2); 1) Evergreen drought-tolerant species had a high biomass investment in enduring organs and minimized cavitation and transpiration in order to persist under dry conditions. 2) Drought-avoiding species evaded drought stress with a deciduous leaf habit in the dry season and maximized resource capture during a limited growing season. 3) Drought-intolerant species maximized both below- and above-ground resource capture to increase competitiveness for light, water and nutrients and were consequently precluded from dry habitats.

I found no direct trade-off between drought- and shade-tolerance, because they depended largely on different morphological adaptations. Drought-tolerance was supported by a high biomass investment to the root system, while shade-tolerance was mainly promoted by a low growth rate and low SLA. Although across species I found a strong trade-off between the biomass invested in roots versus leaves (Table 4.4), it did not result in a trade-off between drought- and shade-tolerance (Fig. 4.1). Plants may compensate for a low RMF by producing relatively cheap roots with a large specific root length (SRL) and compensate for a low LMF by making cheap leaves with a large specific leaf area (SLA) (Poorter 2005). Such compensation possibilities may imply that the trade-off theory of Smith and Huston (1989) does not necessarily hold and that drought- and shade-tolerance can be uncoupled (Table 4.4).

CAVITATION RESISTANCE OF DRY FOREST TREE SPECIES

When drought occurs and soil water potentials drop, the pressure gradient in xylem vessels increases and they are more likely to become dysfunctional due to cavitation. It is thus crucial for dry forest tree species to protect their vascular system against excessive cavitation and secure hydraulic conductivity in the dry period. In CHAPTER 5 I analysed vulnerability curves (i.e. relation between percentage loss of hydraulic conductivity and xylem potential) for saplings of 13 tropical dry forest tree species differing in shade-tolerance and leaf phenology. I examined how cavitation resistance (i.e. P_{50}, the xylem pressure at 50% loss of hydraulic conductivity) is influenced by stem and leaf traits and how it determines the leaf water potential in the field.

Among species P_{50} values ranged from -0.8 to -6.2 MPa. Pioneer species were more vulnerable to cavitation than shade-tolerant species (Fig. 5.3), while evergreen and deciduous species did not differ in their cavitation vulnerability, in contrast to the expectation (Fig. 5.3).

Species with high wood density were more resistant to cavitation than species with a low wood density (Fig. 5.5a) probably because high density species have narrow and thick walled vessels. Longer vessels also implied higher cavitation resistance, in contrast to the general belief. P_{50} was positively associated to leaf dry matter content (Fig. 5.6), which is a good predictor of species drought survival in the field and their distribution across the rainfall gradient (Kursar et al. 2009). P_{50} was negatively associated with hydraulic conductance (Fig. 5.7), which represents an important ecological trade-off that land plants in theory have to face; the hydraulic safety versus hydraulic efficiency trade-off (Zimmerman 1983, Tyree et al. 1994). Most species were operating well above their hydraulic limit, defined here as the xylem potential at 50% loss of conductivity (Fig. 5.8), but pioneers had smaller hydraulic safety margins than shade-tolerants (Fig. 5.8). Pioneers are opportunistic light foragers that probably need to take greater risks in order to be competitive. Subsequently, their high photosynthetic capacity, high stomatal conductance and increased carbon intake may reduce the (re)construction cost of lost tissues should hydraulic failure accidentally occur.

HYDRAULIC CONDUCTIVITY OF DRY FOREST TREE SPECIES

Little is known about how hydraulic properties are related to species' life history strategies, such as drought- and shade-tolerance and prevailing theories seem to be contradictory. In CHAPTER 6 I measured hydraulic conductivity (K_S and K_L) of saplings of 40 co-existing dry forest tree species and evaluated how it was related to plant traits, and the moisture and regeneration light requirements of the species.

Hydraulic properties varied substantially across species. Differences among species especially explained a large amount of variation in K_S and K_L (96% vs. 98%).

In line with many other studies (Bucci et al. 2004, Santiago et al. 2004), we found that high hydraulic conductivity was related to low wood density (WD) and long (maximum) vessel length (VL) (Fig. 6.2). Low wood density results from wider vessels that are more efficient in transporting water than narrow vessels (Tyree 1994), but they are also more vulnerable to cavitation (Hargrave et al. 1994, Hacke et al. 2001) About 50% of the hydraulic resistance is caused when water passes through the pit membranes that connect separate vessel elements (Zimmerman 1983). Stems with long vessels have less hydraulic resistance as the number of pit-membranes is smaller.

Species´ moisture (ψ_l; defined as the midday dry season water potential) and light requirements (CE_{juv}) scaled negatively to WD and positively to K_L (Fig. 4) and thus varied in line with the theoretical trade-off between hydraulic safety and efficiency. This results in coordination between moisture and light requirements across species and hence coordination between species´ drought- and shade-tolerance, instead of the hypothesised trade-off. The ecological consequence of this positive relation is that light-demanding species are more drought-intolerant and that their distribution will be restricted to habitats that combine both high light and high moisture availability. Shade-tolerant species will be more drought-tolerant and better competitors in both drier and shadier habitats.

SEEDLING DROUGHT SURVIVAL IN RELATION TO DROUGHT-TOLERANCE

Water availability is the most important factor determining tree species distribution in the tropics, but underlying mechanisms are not well understood. In CHAPTER 7 I compared functional traits of 38 dry and moist forest tree species and quantified their ability to survive drought in a dry-down experiment I examined how seedling traits are related to species position along the rainfall gradient, what functional groups can be distinguished, and what seedling traits are good predictors for drought survival and species distribution.

Species position along the rainfall gradient (from wet to dry) was positively related to leaf compoundness and stem dry matter content, and negatively to leaf area ratio (Fig. 7.1), suggesting that reduction of transpiration and avoidance of xylem cavitation are most important for the success of species in drier ecosystems, while increasing light interception per unit plant biomass determines the relative success of species in moist ecosystems.

Three functional groups were identified based on the seedling traits; 1) drought avoiders with a deciduous leaf habit and taproots, 2) drought resisters with tough tissues (i.e., high dry matter content) and a high stem density, and 3) light-demanding moist forest species with a large belowground foraging capacity (Fig. 7.2).

Species varied greatly in the way they dehydrated and in drought survival responses (Fig. 7.4). Dry forest species survived longer (62 days) than moist forest species (25 days). Deciduousness explained 69% of interspecific variation in drought survival and the presence of a taproot an additional 5%.

Species drought survival did not directly explain their distribution along the rainfall gradient, mainly because deciduousness was such an important factor contributing to species drought survival, while deciduous species are well represented in both dry and moist forests (Fig. 7.5). Among evergreen species drought survival explained 28% of the variation in species position along the rainfall gradient (Fig. 7.5), which shows that drought-tolerance is an important factor shaping the species distribution of evergreen tree species, but also that other factors such as site-history, dispersal limitation, shade-tolerance and fire-occurrence can codetermine species distribution along the rainfall gradient.

SYNTHESIS

How do dry and moist forests differ in soil water availability?

In this dissertation I demonstrated that, regardless of the rather similar monthly precipitation in both forests, dry season soil water availability was clearly lower in the dry site than in the moist site. This suggests that other factors than precipitation, as soil texture, evaporative demand and atmospheric water deficit, can have considerable effect on soil water availability. More interesting I found that both sites, but especially the dry forest, show a lot of temporal and spatial variation in soil water availability. Temporal variation in soil water availability largely depends on the annual cycle of precipitation. Spatial heterogeneity is two-dimensional. Firstly there is horizontal heterogeneity in which soil water availability varies between and within forest with topography and ranges from relatively dry at elevated crests to wet on slopes and in low valleys. Secondly, there is spatial variation on the spot due to the vertical redistribution of the water with soil depth. When combining the three dimensions time, topography and soil depth, a very complex mosaic of soil water availability emerges that shows a great potential for niche partitioning among species at various levels. A variety of species may be allowed to coexist, if their morphological and physiological adaptations permit them to successfully compete for water at different topographical locations, tap their water from different soil layers and / or do so at different moments in time. Hence the heterogeneity of soil water availability should be considered as an important factor contributing to the high biodiversity of tropical forest in general and more specifically in seasonally dry forests.

How are dry and moist forest species adapted to drought and what different drought-strategies can be distinguished?

Coexisting tree species show a range of morphological, anatomical and physiological adaptations to drought. Differences among species in seedling morphology show that dry forest species have evolved mechanisms that enhance their access to water in deep soil layers, increase drought-induced cavitation resistance and increase water conservation. Moist forest species show adaptations that improve their light foraging capacity and increase nutrient and water acquisition (Chapter 4). Morphological divergence along the first mayor axis of species differentiation (´persistence´) sorts dry and moist forest species from drought-tolerant to drought-intolerant (Fig. 8.1). One of the main morphological traits that determines this axis is wood density (Chapter 4 & 7), which is a morphological expression of structural adaptations of the stem anatomy. Through stem anatomy wood density is directly linked to drought-induced cavitation resistance (P_{50}) (Chapter 5) and stem hydraulic conductivity (K_S) among species (Chapter 5 & 6). Wood density underlines therefore the hydraulic safety vs. hydraulic efficiency trade-off (Chapter 5 & 6). At the same time wood density was the most important trait determining drought survival among evergreen species (Chapter 7) and there is general agreement that wood density steers the trade-off between species growth and survival (Fig. 8.1). Both these trade-offs play an important role along the first strategy axis (Fig. 8.1). ´Deciduousness´ forms a second strategy axis, orthogonal to the persistence axis (Fig. 8.1) and separates the evergreen drought-tolerant and drought-intolerant species from the drought-avoiding species on deciduousness and correlated traits (Chapter 4 & 7). Deciduous and evergreen species did not differ in cavitation resistance (Chapter 5), but even so deciduousness was the main factor explaining drought survival among species (Chapter 7). Apparently, drought-avoiding species have the ability to survive drought, without having a high cavitation resistance. Consequently, they do not suffer the negative consequences of a high cavitation resistance, as a reduction of hydraulic efficiency and growth. Hence, drought-avoiding species can realise relatively high growth rates, which allows them to be relatively good competitors for light as well. This explains why deciduous species have a relatively high abundance in both dry and moist forests. A negative consequence of a drought-avoiding strategy is probably that at some point the leafless, dormant period will limit competitiveness for water (upper left corner of Fig. 8.1) and light (upper right corner of Fig. 8.1). That is why deciduous species are rare in extremely dry and wet ecosystems.

The findings of this dissertation suggest that instead of the two strategies suggested in the introduction (desiccation tolerance and desiccation delay) a third strategy emerges in the form of drought avoidance. Thus I propose that there are three mayor drought strategies among tropical tree species, I) physiological drought-tolerance, II) drought-intolerance and III) drought-avoidance (Fig. 8.1).

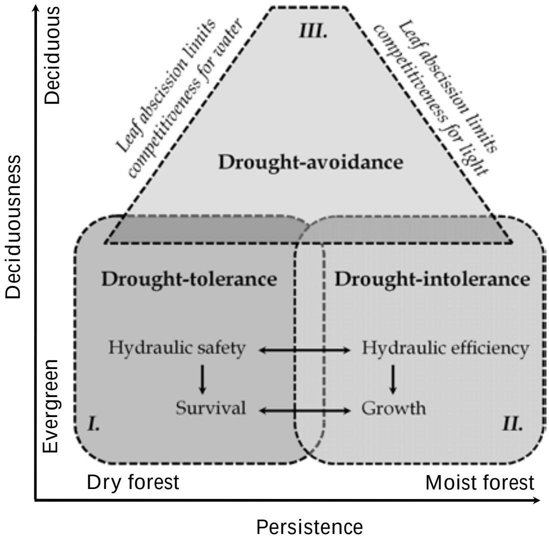

Figure 8.1

Hypothetical framework of the three drought-strategies that emerge among dry and moist forest tree species. Species sort along two strategy axis that are defined by suites of traits related to ´persistence´ (horizontal axis) and ´deciduousness´ (vertical axis). The persistence axis sorts species from dry to moist forests, the deciduousness axis sorts species from evergreen to deciduous species. Along the persistence axis two functionally linked trade-offs contribute to species separation; the physiological trade-off between hydraulic safety and hydraulic efficiency, and the trade-off between (drought) survival and growth. Three functional drought strategy that emerge are; I) drought-tolerance, II) drought-intolerance, and III) drought-avoidance. Instead of discreet clusters, these strategy spaces represent the extremes of continuous gradients as there is some overlap between them. Drought-avoiding species can largely escape the trade-offs along the first axis, but leaf abscission limits competitiveness for water at the driest extreme of the gradient (upper left) and for light at the wettest extreme (upper right).

This scale-related discrepancy may depend on the extent to which water and light, as limiting resources, play a role in the natural selection in both forest types. From an evolutionary point of view drought or shade adaptations can only be selected for if drought and shade are to large extent predictable and reoccurring events (cf. Stuefer 1996). Because of stronger seasonality, selection for drought and shade adaptations might have occurred in the dry forest, because water is limiting in the dry season and light becomes limiting in the wet season. This allows for selection of convergent traits to tolerate both drought and shade, as was shown by the similar relations between hydraulic properties and shade- and drought-tolerance of dry forest species (Chapter 5 & 6). In moist forests shade is definitely a predictable event and a selective force, but the dry season might just not be severe (or predictable) enough to allow for strong trait selection by drought. This implies that across moist forest species there is a bias towards adaptations that contribute to shade-tolerance and that real drought-adaptations are lacking or less pronounced. As a consequence drought- and shade-tolerance may vary independently among moist forest species. Pooling species from different forests into one analysis could have as a net result that (strong) intra-forest relationships are compromised and that drought- and shade-tolerance are uncoupled (Chapter 4).

How do drought- and shade-tolerance determine local and regional tree species distribution?

Drought- and shade-tolerance have clear effects on the local (within forest) and regional (across forest) distribution of tropical tree species (cf. Fig. 1.1). Within forest I found a large inter-specific variation in morphological and physiological species traits (Chapter 4 & 6), which is important, as it could facilitate species coexistence in different microhabitats of water availability (e.g. with topography and soil depth; Chapter 3) or light availability (e.g. from understory to gaps). In the dry forest I showed that hydraulic adaptation of species is integrally linked with niche differentiation. Hydraulic coordination of drought- and shade-tolerance implies that light-demanding species will be restricted to high resource habitats that combine high light availability with high moisture availability, whereas shade-tolerant species will be the better competitors in both drier and shadier habitats. Associations between hydraulic properties and drought- or shade-tolerance were very similar (Chapter 6), but all relationships were strongest with shade-tolerance. This shows that within this dry forest drought-tolerance is an important factor explaining the distribution of species, but also that shade-tolerance plays a more important role than initially expected. It would be controversial to suggest that shade-tolerance is contributing more to species distribution along water gradients in tropical dry forest than drought-tolerance; still the findings in this dissertation do seem to suggest it.

At the regional scale species distribution across forests was associated with several species traits (e.g. root mass fraction, rooting depth, LAR) that are related to either drought-or shade-tolerance. Still the traits that best explained species distribution were mainly related to drought-tolerance (Chapter 4 & 7). The occurrence of species at the dry end of the rainfall gradient depends on their ability to tolerate drought, but the assumption that species occurrence at the moist end of the rainfall gradient should depend on their shade-tolerance seems erroneous. If any it is the capacity of species to efficiently forage for light and acquire large amounts of resources that determines their distribution towards the wet end of the rainfall gradient, instead of their capacity to tolerate shade. This also explains why drought-avoiding species are relatively well presented in both dry and moist forests. Their main adaptive trait (deciduousness) allows drought-avoiding species to be specialist drought survivors, but most other species traits suggest that they are also good competitors for light and nutrients when they are fully functional in the wet season. Drought-avoiders as such escape the growth survival trade-off related to drought (Fig. 8.1). At local scales, within forest type, species distribution along water gradients may depend therefore on the interaction between species drought- and shade-tolerance while at larger scales distribution of (evergreen) species is determined by their drought-tolerance.


Sapindus saponaria
(Sapindaceae)

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Ocotea sp.
(Lauraceae)

Samenvatting

Tropische bossen komen voor bij regenval regimes die sterk van elkaar verschillen in neerslag patroon en de frequentie en intensiteit van droogte. Waterbeschikbaarheid is daarom een van de belangrijkste factoren die de structuur en soortensamenstelling van bossen beinvloedt en het functioneren en voorkomen van planten langs de regenvalgradient en op kleinere schaal langs hellingsgradienten binnen bossen bepaalt. Het succes van boomsoorten om zich te vestigen en te handhaven langs gradienten in waterbeschikbaarheid en hun succes in het omgaan met toekomstige veranderingen in waterbeschikbaarheid zal voor een groot deel afhangen van hoe soorten zijn aangepast om met droogte om te gaan.

In dit proefschrift vergelijk ik functionele kenmerken van een groot aantal tropische boomsoorten met behulp van zowel veldstudies als gecontroleerde experimenten, om gedetailleerde informatie te geven over de mechanismen die droogte tolerantie bepalen. De volgende onderzoeksvragen worden beantwoord; 1) Hoe verschillen tropisch droog en nat bos in bodem waterbeschikbaarheid?, 2) Hoe zijn droog en nat bos soorten aangepast aan droogte en welke verschillende droogte strategieën kunnen worden onderscheiden?, 3) Is er een trade-off tussen droogte en schaduw tolerantie?, en 4) Hoe bepalen droogte en schaduwtolerantie de lokale en regionale verspreiding van boomsoorten?

In het droogseizoen is de bodem waterbeschikbaarheid in het droog bos duidelijk lager dan in het nat bos. Ook is er vooral in het droog bos veel variatie in de bodem waterbeschikbaarheid. Temporele variatie in waterbeschikbaarheid hangt vooral af van de jaarlijkse neerslagcyclus. Ruimtelijk is deze heterogeniteit twee-dimensionaal; 1) de beschikbaarheid van water varieert namelijk met de topografie van het landschap; heuveltoppen zijn relatief droog in vergelijking met lage hellingen en dalen, en 2) in de bodem vinden we een verticale gradient in water beschikbaarheid met in het droge seizoen meer water in diepere bodemlagen terwijl in het natte seizoen de meeste water wordt aangetroffen in de toplaag. Wanneer we deze temporele en ruimtelijke dimensies combineren, ontstaat er een complex mozaïek van waterbeschikbaarheid in tropische bossen en blijkt dat er veel potentie is voor niche-partitionering tussen soorten, wanneer althans soorten zijn aangepast om deze variatie goed te benutten.

Zaailingen van droog bos soorten zijn beter aangepast om water uit diepe grondlagen te halen, om weerstand te bieden aan cavitatie veroorzaakt door droogte en om zuiniger om te gaan met water. Zaailingen van nat bos soorten hebben aanpassingen die duiden op een verbeterde invang van licht en een verhoogde inname van nutriënten en water. Uit de relaties en trade-offs tussen functionele kenmerken van soorten blijkt dat tropische boomsoorten drie belangrijke droogte strategieën volgen. Soorten zijn 1) fysiologisch droogte tolerant, 2) droogte intolerant, of 3) droogte ontwijkend.

Er is geen overtuigend bewijs voor een directe trade-off tussen droogte en schaduw tolerantie gevonden, omdat de relatie tussen droogte en schaduw tolerantie voornamelijk wordt bepaalt door de schaal van waarnemen. Op kleine schaal, binnen het droog bos, zijn droogte en schaduw tolerantie positief gerelateerd, omdat hydraulische eigenschappen van soorten integraal verbonden zijn met niche-differentiatie voor zowel licht als water. Dit betekent dat in hun verspreiding lichtminnende soorten zullen worden beperkt tot habitats die een hoge lichtbeschikbaarheid combineren met een hoge waterbeschikbaarheid. Schaduw tolerante soorten zullen beter concurreren in droge en schaduwrijke habitats. Op grotere schaal, tussen bossen, is er een sterke trade-off tussen boven- en ondergrondse biomassa allocatie. In theorie zou dit moeten leiden tot een trade-off tussen droogte tolerantie en schaduw tolerantie, maar in de praktijk gebeurt dit niet. Planten kunnen een lage biomassa investering in wortels compenseren door relatief goedkope wortels te vormen met een grote specifieke wortel lengte. Een lage investering in bladbiomassa kan zo ook worden gecompenseerd door het maken van goedkope bladeren met een groot specifiek bladoppervlakte. Droogte en schaduw tolerantie zijn dus grotendeels afhankelijk van verschillende morfologische kenmerken en kunnen worden ontkoppeld.

De verspreiding van soorten langs de regenvalgradient is niet direct te verklaren door droogte overleving van soorten, voornamelijk omdat bladverlies de belangrijkste factor blijkt die droogte overleving bepaalt. Bladverliezende soorten zijn goed vertegenwoordigd in zowel droge en natte bossen. De verspreiding van groenblijvende soorten in drogere bossen hangt voornamelijk af van droogte gerelateerde kenmerken als een hoge houtdichtheid en een grote biomassa investering in diepe wortels. De verspreiding van groenblijvende soorten in nattere bossen wordt voornamelijk bepaald door kenmerken die verband houden met lichtminnendheid, zoals een hoge blad biomassa fractie en lange, fijn vertakte wortelsystemen. Zo kom ik tot de conclusie dat op kleine schaal, binnen de bossen, de verspreiding van soorten langs watergradienten afhankelijk is van een positieve interactie tussen droogte en schaduw tolerantie, terwijl op grotere schaal deze relatie niet opgaat en de verspreiding van (groenblijvende) soorten voornamelijk wordt bepaald door droogte tolerantie.

Resumen

Los bosques tropicales aparecen bajo regímenes de precipitación con una gran variación en el patrón de la precipitación y la frecuencia e intensidad de la sequía. Por consiguiente la disponibilidad hídrica es uno de los factores medioambientales más importantes influenciando la estructura de la comunidad, la composición de especies y el funcionamiento de las plantas a lo largo del gradiente de precipitación a gran escala y el gradiente topográfico a una menor escala dentro bosques. El éxito relativo de las especies arbóreas en establecerse a lo largo de estos gradientes de disponibilidad hídrica y su éxito tratando con los futuros cambios en la disponibilidad hídrica dependerá en cómo están adaptados a tolerar la sequía.

En esta tesina, yo he aplicado un enfoque con múltiples especies y múltiples características en estudios de campo y un experimento controlado para dar información detallada de los mecanismos de tolerancia a la sequía de un numeroso conjunto de especies del bosque tropical seco y del bosque tropical húmedo. Las siguientes preguntas de investigación fueron tratadas; 1) ¿Como el bosque seco y húmedo difieren en la disponibilidad hídrica del suelo?, 2) ¿Como están adaptadas las especies arbóreas en los bosques secos y húmedos a la sequía?, y ¿cuáles son las diferentes estrategias a la sequía que pueden ser diferenciadas?, 3) ¿Hay un trade-off entre la tolerancia a la sequía y la tolerancia a la sombra?, y 4) ¿ Cómo la tolerancia a la sequía y a la sombra determinan la distribución de especies arbóreas a nivel local y regional?

La disponibilidad hídrica en la estación de sequía es claramente menor en el bosque seco que en el bosque húmedo. Especialmente en el bosque seco hay mucha variación temporal y espacial en la disponibilidad hídrica del suelo. La variación temporal depende del ciclo anual de precipitación. La heterogeneidad espacial es bidimensional; 1) la disponibilidad hídrica varía con la topografía del paisaje; cimas elevadas están secas en comparación con las pendientes y los valles, y 2) el agua del suelo esta redistribuido verticalmente con la profundidad del suelo; en la estación seca, mayor cantidad de agua esta disponible en las capas profundas del suelo mientras que en la estación húmeda, la mayor cantidad de agua se encuentra en la capa superior del suelo. Cuando se combinan las dimensiones temporales y espaciales, aparece un mosaico complejo de disponibilidad hídrica del suelo, el cual muestra un gran potencial para la división del nicho ecológico entre especies a diferentes niveles, si las especies están adaptadas para explotar esta variación.

Las plántulas de las especies del bosque seco han evolucionado mecanismos que mejoran su acceso al agua en capas profundas del suelo, aumentan la resistencia a la cavitación inducida por la sequía y aumentan la conservación de agua. Las plántulas de

especies del bosque húmedo muestran adaptaciones que mejoran su capacidad de búsqueda de luz y aumenta la adquisición de nutrientes y agua. Las asociaciones entre características funcionales muestran que hay tres principales estrategias para combatir la sequía entre especies arbóreas tropicales, 1) tolerancia a la sequía fisiológica, 2) intolerancia a la sequía y 3) evitación de la sequía.

No fue encontrada una evidencia concluyente de trade-off directo entre especies tolerantes a la sequía y especies tolerantes a la sombra. La asociación entre tolerancia a la sequía y tolerancia a la sombra esta principalmente sujeto a la escala de observación. A menor escala, dentro el bosque seco, la tolerancia a la sequía y la tolerancia a la sombra están relacionadas positivamente, como las propiedades hidráulicas de las especies están relacionadas íntegramente con la diferenciación de nichos ecológicos para ambas luz y agua. Esto implica que en su distribución, las especies heliófitas serán restringidas a hábitats que combinan elevada luz con elevada humedad disponible, mientras que las especies tolerantes a la sombra serán los mejores competidores en hábitats más secos y con mas sombra. A mayor escala fue encontrado un fuerte trade-off en asignación de biomasa entre la parte aérea y la parte subterránea del suelo, el cual en teoría debería de haber resultado en un trade-off entre tolerancia a la sequía y a la sombra, pero en la práctica no fue así. Las plantas pueden compensar por una baja fracción de biomasa de raíces produciendo raíces relativamente baratas con una gran longitud de raíz específica y compensar la baja fracción de biomasa de hoja produciendo hojas baratas con una gran área foliar específica. La tolerancia a la sequía y la tolerancia a la sombra de esta manera dependen en gran medida de los diferentes grupos de características morfológicas y estas pueden ser desacopladas.

La distribución de especies a lo largo del gradiente de precipitación no fue directamente explicado por la supervivencia a la sequía de las especies, principalmente porque la caducifoliedad fue el factor más importante en contribuir a la supervivencia y las especies caducifolias están bien representadas en ambos bosques, secos y húmedos. La aparición de especies perennifolias en el extremo seco del gradiente de precipitación en gran parte depende de características relacionadas con la sequía, como una alta densidad de madera y una gran asignación de biomasa a las raíces profundas. La aparición de especies en el extremo húmedo del gradiente de precipitación fue principalmente determinada por características relacionadas con la demanda de luz, como una elevada fracción de masa foliar y unos sistemas radicales largos y ramificados. En conclusión, yo propongo que a menores escalas, entre bosques, la distribución de especies a lo largo de gradientes hídricos depende en la interacción entre la tolerantica a la sequía y tolerantica a la sombra, mientras que a mayor escala la distribución de especies (perennifolias) está determinada principalmente por su tolerancia a la sequía.

Pouteria nemorosa
(Sapotaceae)

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Swietenia macrophylla
(Meliaceae)

Short biography

Lars Markesteijn was born in Dordrecht, the Netherlands on October 2, 1979. As the grandson of a farmer, the outdoors was and continues to be a constant factor in his life. Lars had his classical Pre-university education from 1992 to 1998 at the Johan de Witt-gymnasium in Dordrecht, where he was Abactis (secretary) of the student association Vossius in his fifth year. He studied Tropical Land Use at Wageningen University (WU) and wanted to become a development worker, interested in international food security and sustainable development in the tropics.

As a student Lars´ academic interests shifted from social sciences towards environmental sciences and specifically towards tropical forest ecology. After the propedeuse (initial academic year at Dutch Universities) Lars compiled a free educational program to comply with his shifted interests. In 2001 he went to Chiapas, Southern Mexico, for his first thesis, entitled "Seed rain and soil seed bank along a chronosequence of tropical lowland rainforest in Chiapas, Southern Mexico". This project was conducted as a joined operation between the Forest Ecology and Forest Management group (FEM) and the Centro de Investigaciones en Ecosistemas (CIEco) of the Universidad Nacional Autónoma de México (UNAM). In 2002 Lars became a student-assistant at FEM. After defending his first thesis he went to Santa Cruz, Bolivia for the first time in 2003 for a second thesis project in cooperation with the BOLFOR project and successively the Instituto Boliviano de Investigación Forestal (IBIF). This project resulted in two theses, entitled; "Functional leaf traits; Morphological (1), and anatomical (2) adaptations to different light environments and functional groups in a Bolivian dry forest". Early 2005 Lars graduated from his studies with honours (Cum Laude).

After working as a research assistant at the Forest Ecology and Forest Management group of Wageningen University in 2005, Lars started as a PhD candidate in October that year at the same department and four years and three weeks later he handed in the final draft of this dissertation.

Lars professional interests are related to tropical forest ecology, functional ecology, ecophysiology, tree species coexistence and diversity and stress tolerance, with of course a special interest in drought-tolerance of (tropical) trees. On the personal note Lars is interested in nearly everything related to human and natural history. He enjoys a good read and likes to cook and he is a spirited, though not very talented, musician. Lars is definitely a dog person.

Ceiba boliviana
(Malvaceae)

Publications

Published / accepted papers

Markesteijn L, Iraipi J, Bongers F, Poorter L. (2010). Seasonal variation in soil and plant water potentials in Bolivian tropical moist and dry forests. Journal of Tropical Ecology (Accepted for publication)

Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. Journal of Ecology 97: 311-325

Markesteijn L, Poorter L, Yanguas-Fernández E (2008) La disponibilidad hídrica estacional y topográfica en un bosque seco y húmedo tropical y la variacion en la morfologia de las plántulas arbóreas. Revista Boliviana de Ecologia y Conservación Ambiental 24: 27-42

Poorter L, Markesteijn L (2008) Seedling traits determine drought-tolerance of tropical tree species. Biotropica 40: 321-331

Markesteijn L, Poorter L, Bongers F (2007) Light-dependent leaf trait variation in 43 tropical dry forest tree species. American Journal of Botany 94: 515

Papers under peer-review

Markesteijn L, Poorter L, Paz H, Sack L, Bongers F. Hydraulic niche partitioning among tropical dry forest saplings; coordination of species moisture and light requirements. (New Phytologist)

Onoda Y, Westoby M, Adler PB, Choong AML, Clissold FJ, Cornelissen JHC, Díaz S, J. Dominy N, Elgart A, Enrico L, Fine PV, Howard JJ, Jalili A, Kitajima K, Kurokawa H, Lucas P, Markesteijn L, McArthur C, Peeters PJ, Perez-Harguindeguy N, Poorter L, Richards L, Santiago LS, Sosinski Jr EE, Van Bael SA, Warton DI, Wright IJ, Wright JS, Yamashita N. Global patterns of leaf mechanical properties. (Proceedings of the Nacional Academy of Sciences)

Book chapters:

Sterck FJ, Couralet C, Nangendo G, Wassie A, Sahle Y, Sass-Klaassen U, Markesteijn L, Bekele T, Bongers F. Juniperus procera (Cupressaceae) in afromontane forests in Ethiopia: from tree growth and population dynamics to sustainable forest use. In F Bongers et al., eds, Degraded forests in Eastern Africa: Management and Restoration. (Accepted for publication)

Hura crepitans
(Euphorbiaceae)

Affiliation of co-authors

FRANS BONGERS

Forest Ecology and Forest Management Group
Centre of Ecosystem studies
Wageningen University
Wageningen, the Netherlands

LOURENS POORTER

Forest Ecology and Forest Management Group
Centre of Ecosystem studies
Wageningen University
Wageningen, the Netherlands

JOSÉ IRAIPI

Instituto Boliviano de Investigación Forestal
Santa Cruz de la Sierra, Bolivia

HORACIO PAZ

Laboratorio de Ecología Funcional y Restauración Ecológica
Centro de Investigaciones en Ecosistemas
Universidad Nacional Autónoma de México
Morelia, Michoacán, México

LAWREN SACK

Department of Ecology and Evolutionary Biology
University of California
Los Angeles, California, United States of America

Simira rubescens
(Rubiaceae)

Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

The C.T. De Wit Graduate School PE&RC
PRODUCTION ECOLOGY & RESOURCE CONSERVATION

Review of Literature (4.2 ECTS)
- Drought-tolerance of tropical tree species; presented at the PhD discussion group on Forest and Conservation Ecology (2005)

Laboratory Training and Working Visits (4.3 ECTS)
- Hydraulics of tropical dry forest tree species; working visit to Bolivia with experts from Wageningen University (WU), University of California (UCLA), and Universidad Nacional Autónoma de México (UNAM) (2008)

Post-Graduate Courses (4.2 ECTS)
- Ecophysiology of plants; FE (2007)
- Linear mixed models; PE&RC (2009)
- Generalized linear models; PE&RC (2009)
- What's up in Tropical Forest Community Ecology?; PE&RC (2009)

Competence Strengthening / Skills Courses (3.8 ECTS)
- PhD Competence assessment; WGS (2006)
- Project- and time management course; WGS (2006)
- Writing grant proposals; WGS (2009)

Discussion Groups / Local Seminars and Other Scientific Meetings (7 ECTS)
- Production Ecology and Resource Conservation; PE&RC discussion group (2005-2006)
- Weekly chair group presentations; Forest Ecology and Forest Management group (2005-2009)
- ARC NZ Research network for vegetation function; workgroup 38; leaf biomechanics (incl. presentation); Macquarie University, Sydney, Australia (2008)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.8 ECTS)
- PE&RC Introduction weekend (2006)
- PE&RC One-day symposium (2007)
- Annual PhD meeting Tropical Ecology; UvA (incl. presentation) (2008)
- Annual PhD meeting Tropical Ecology; UvA (incl. presentation) (2009)

International Symposia, Workshops and Conferences (10.3 ECTS)
- 3rd National Forest Research Meeting; Santa Cruz de la Sierra, Bolivia (incl. oral and poster presentation) (2006)
- ATBC Annual meeting in Morelia, Michoacán, Mexico (incl. oral paper in symposium: functional ecology of tropical plant communities) (2007)
- NERN Annual meeting; Lunteren, the Netherlands (2008)
- NERN Annual meeting; Lunteren, the Netherlands (2009)
- Annual meeting of the Association of Tropical Biology and Conservation (ATBC) in Marburg, Germany (incl. oral paper in symposium: climate effects on regeneration dynamics) (2009)

Courses in which the PhD candidate has worked as a teacher (5 days)
- Ecological methods 1; REG, FEM