Lianas and trees in tropical forests in south China

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Lianen en bomen in tropisch bos in zuid China

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Chapter 1

General introduction

Lianas, woody vines, are an important but understudied growth form common to most forests throughout the world, particularly in the tropics. Lianas play a vital role in many aspects of forest dynamics. This role includes suppressing tree regeneration, increasing tree mortality, providing a valuable food resource for animals, physically linking trees together, thereby providing canopy-to-canopy access for arboreal animals (Putz and Mooney 1991, Schnitzer and Bongers 2002). Additionally, lianas are widely used by people (Bongers et al. 2002, 2005, Liu et al. 2004).

Recent studies on lianas have focused on the significant contribution of this life-form to the overall density and species diversity of tropical forests (Mascaro et al. 2004, Rice et al. 2004), mechanisms by which lianas alter the tropical forest diversity and regeneration (Schnitzer and Carson 2001), harming some shade-tolerant species while promoting some pioneer species (Schnitzer et al. 2000, Toledo-Acewes and Swaine 2007), and the significant contribution of lianas to whole-forest transpiration and carbon sequestration (Restom and Nepstad 2001, Schnitzer and Bongers 2002). Because lianas are favored by forest disturbances and are more diverse in warmer environments, human-induced disturbances and global warming are likely to promote liana abundance. These environmental modifications are already responsible for the reported increase in the growth rates and abundance of large diameter lianas in tropical forests (Phillips et al. 2002, Wright et al. 2004), although more data are needed to evaluate this trend and its possible causes. Our current understanding of the ecology of lianas and their role in forest dynamics, however, has lagged well behind that of most other vascular plant groups (Schnitzer and Bongers 2002), and many aspects of liana ecology await investigation. This thesis addresses lianas and trees in Xishuangbanna, southern China. It describes liana communities in three dominant forest types, analyses morphological and physiological differences, and resulting growth patterns, between lianas and trees, and, finally, it studies the effect of light, maybe the most important differentiating environmental factor in tropical forest, on seedling growth for one liana and for six tree and shrub species.

Lianas as a life form

Lianas have long attracted naturalists and story-tellers, yet despite the contributions of Darwin (1867) and other 19th Century biologists to the study of lianas, it wasn’t until fairly recently that ecologists turned their attention to this important group of plants (Schnitzer and Bongers 2002). The climbing habit has apparently evolved numerous times in the plant kingdom. There are lianas among such diverse taxa as gymnosperms (e.g., *Gnetum*), various palms (e.g., *Calamus*), and other monocotyledons (e.g., bamboo). Flowering plant families are particularly rich in climbing species (e.g., Vitaceae, Leguminosae, Menispermaceae, and Hippocrateaceae). Some genera mainly consist of lianas (e.g., *Vitaceae*) whereas others include lianas as well as shrubs and trees (e.g., *Bauhinia*, *Embelia*). There are also numerous species that grow as lianas when crowded, but are free-standing shrubs or trees if they fail to encounter mechanical supports (e.g., species of *Croton*, Gallenmúller et al. 2001).

Lianas climb by using other plants for support. This characteristic of not being self-supporting allows liana stems to be narrow, flexible and capable of phenomenal rates of growth in height or length. Liana seedlings often escape notice as being lianas, even from experienced ecologists, because they are self-supporting and resemble tree seedlings. Taxonomic uncertainties abound as it is a challenge to learn to identify all of them (Putz and Mooney 1991, Schnitzer and Bongers 2002). Lianas display a large diversity of climbing mechanisms, such as scrambler, twiner, hook climber, root climber, and tendril climber. Many species have specialized structures for grabbing supports. The most familiar prehensile apparatus is the tendril, but tendrils come in various sizes and evolutionarily derived from a variety of structures (Putz and Mooney 1991). Species with stem-derived tendrils tend to be able to successfully grasp larger diameter trellises than those with other sorts of tendrils, but all lianas except the root climbers are limited to climbing fairly narrow supports (Schnitzer and Bongers 2002). The scarcity of suitable supports that reach from near the ground up to the canopy is a major limitation for most climbing plants. Failure to locate and attach to trellises is the fate of most vine stems, other than root climbers, which are rare among tropical lianas. When a climbing plant reaches the top of its host, further height growth requires the location of a taller support of the appropriate diameter. If they encounter a suitable support and successfully attach to it, their progress towards the canopy continues. If they fail to find a support, they fall over and are replaced by another shoot (Putz 1984). The inter-support spanning capacities of different species are important for predicting which lianas are likely to be stalled on their way to the canopy. Most lianas that make it to the canopy do so with the help of a succession of taller supports.

Distribution of lianas

Lianas are found in forests from the tropics to the boreal zones of both the northern and southern hemispheres, and in deserts as well as rainforests. However, they are most diverse in tropical forests near the equator (Gentry 1991, Schnitzer and Bongers 2002). The high diversity and wide distributions of lianas is now widely recognized, thanks to efforts of researchers around the world (e.g., Asia: Putz and Chai 1987, Campbell and Newbery 1993, Muthuramkumar and Parthasarathy 2001, Reddy and Parthasarathy 2003, Parthasarathy et al. 2004, DeWalt et al. 2006), Africa (Balfour and Bond 1993, Parren and Bongers 2001), Australia (Chalmers and Turner 1994), Latin-America (Putz 1984, Burnham 2002, Solorzano et al. 2002, Mascaro et al. 2004, Rice et al. 2004). Liana abundance generally increases with forest disturbance, but also varies with other abiotic factors (total rainfall, seasonality of rainfall, soil fertility, and disturbance) (Campbell and Newberry 1993, Schnitzer and Bongers 2002, Schnitzer 2005). For example, lianas seem to increase their abundance with increasing seasonality (Schnitzer 2005). During forest succession after disturbance, lianas typically increase at first and then decrease in abundance, but due to growth of the individuals that persist, liana biomass tends to remain a constant fraction of the total forest biomass (DeWalt et al. 2000, Capers et al. 2005).

Liana vs. trees – Stem characteristics and leaf physiology

Lianas differ from trees by possessing large diameter vessels and abundant soft tissues in the xylem (Carlquist 1991), although some species are very tree-like in their stem cross-section. Having large vessels, lianas are thought to have high xylem conducting capacities, high sap flow and transpiration rates compared to trees (Ewers et al. 1991). Consequently, per unit cross-section area, liana stems can hydraulically support much larger total leaf areas than trees. This difference in allometry helps explain how in tropical forests, where lianas contribute only 5% to total above-ground biomass, liana leaves may constitute 40% of the total forest leaf area (Schnitzer and Bongers 2002). The abundance of soft tissues in liana stems (except for seedlings of some liana species) adds to their flexibility, helps them to avoid mechanical damage, and speeds the rate of recovery when damage does occur (Fisher and Ewers 1989, Putz and Holbrook 1991). This flexibility increases the likelihood of survival when they fall with their host trees. Consequently, many lianas that proliferate in treefall gaps are resprouts from lianas that survived the fall. The soft parenchyma tissues of liana species must have other physiological consequences, but these have apparently not been studied.

Lianas typically have a very high canopy:stem ratio, which results in a higher proportion of photosynthetic biomass than is present in most woody plants. Photosynthetic differences are expected to contribute to the competitive advantage of lianas over trees in productive habitats, and may be linked to the greater hydraulic capacity of vessels, enabling lianas to maintain higher stomatal conductance and therefore sustain higher transpiration rates. Lianas have similar stomatal conductance and leaf-level photosynthesis to trees in the wet season (Castellanos 1991, Ewers et al. 1990, Zotz and Winter 1996). However, lianas are reported to have a higher N concentration per unit leaf mass and lower leaf mass ratio (LMA) than supporting trees or shrubs (Castellanos et al. 1989, Kazda and Salzer 2000). A lower LMA in the leaves of lianas may improve the relationship between photosynthesis and nitrogen through relatively higher nitrogen allocation towards photosynthetic compounds and this may positively influence carbon fixation due to lower internal diffusion limitations (Evans 1999). Another possible difference between lianas and trees is a possibly different efficiency of resorption of nutrients from leaves before shedding. Nutrient resorption is the process in which nutrients are withdrawn from leaves prior to abscission and are re-used in developing tissues (such as leaves or reproductive structures such as seeds), or stored for later use. The absorption of nutrients (mainly N and P) from senescing leaves may be a key component of adaptive mechanisms that conserve limiting nutrients (Killingbeck 1996). Nutrients which are not resorbed, however, will be circulated through litterfall in the longer term (Aerts 1996). The degree of nutrient resorption affects litter quality, which consequently affects decomposition rates and soil nutrient availability (Aerts and Chapin 2000). Although nutrient resorption has been shown not to differ greatly between growth forms (e.g. shrubs, grasses, forbs and trees) (Aerts 1996), its relative importance among plant functional groups is still highly controversial (Richardson et al. 2005). Lianas support substantially more leaves per unit basal area than do trees (Putz 1983, Gerwing and Farias 2000) and the amount of liana leaf litter as a proportion of total litter production has generally increased in tropical forests (Wright et al. 2004). However, we still do not know the difference in the resorption of nutrients between lianas and trees.

Liana vs. trees – growth and responses to abiotic factors

Lianas are expected to have higher growth rates than trees (Putz and Mooney 1991, Schnitzer 2005), mainly because they need to invest less biomass in stems and thus can allocate more biomass to leaves (Darwin 1867, Putz 1983, Castellanos et al. 1989).

However, to date few whole-plant growth studies have been carried out to test this.

In tropical rain forests, resource availability (light, water, and nutrients) varies over spatial and temporal scales. Plant species may differ in their ability to use and conserve limited resources, which are patchily distributed. Spatial and temporal differences in resources availability within plant communities have led to the evolution of a variety of plant strategies (Schulze and Chapin 1987, Poorter 2005). Plant performance is enhanced through morphological and physiological adaptations to the abiotic environment. Lianas have been shown to have high plasticity to changes in light availability (Avalos and Mulkey 1999, Salzer et al. 2006) and elevated atmospheric CO_2 concentrations (Granados and Korner 2002, Zotz et al. 2006). Moreover, experiments revealed that lianas generally colonize nutrient-rich patches of soil much more quickly and with much less investment in root biomass than trees (Hättenschwiler 2002). Under natural conditions, the plant morphological and physiological behaviors are affected by continuously changing environmental variables, such as sunlight, water availability, and temperature (Mittler 2006). The seasonal change in rainfall is arguably the most important factor responsible for the distribution of plant species throughout the tropics (Swaine 1996, Bongers et al. 1999). Most organisms decrease in abundance with decreasing mean annual precipitation and increasing seasonality (Gentry 1982), except for lianas, which increase in abundance with increasing seasonality (Schnitzer 2005). Several characteristics common to lianas may enable them to compete particularly well during seasonal droughts, including: deep and well developed root systems (Tyree and Ewers 1996, Restom and Nepstad 2004), good stomatal control and high water-use efficiency (Andrade et al. 2005), low leaf construction costs per unit photosynthetic area (Castellanos 1991), and rapid vegetative growth rates (Schnitzer et al. 2004, 2005, Schnitzer 2005). Currently, evidence supporting the dry season growth advantage hypothesis is lacking.

Plant potential height

Plant height reflects strategy for securing carbon profit via light capture (Westoby et al. 2002). As taller plants shade shorter plants, competition favors additional expenditure on stems, opening an evolutionary arms race for light (Falster and Westoby 2003). However, not all plants are equally tall. In tropical vegetation, for instance, species potential (or maximum) height ranges from 1 to over 50 m (Foster and Janson 1985). Consequently, much of the emphasis in recent work has been on understanding the trade-offs associated with increased height that allow shorter species to persist in vegetation (e.g. Thomas 1996, Thomas and Bazzaz 1999, Sterck et al. 2001, Poorter et al. 2003, 2005). Potential height has been proposed as one of several traits capable of summarizing substantial variation among species' ecologies (Westoby et al. 2002). Potential height alone, however, cannot fully express a species' strategy for light capture, because it does not distinguish between the contrasting strategies in early vs. late successional situations (Thomas and Bazzaz 1999, Poorter et al. 2003, 2005).

Tropical woody species may partition these vertical height and horizontal light gradients (Richards 1952). Species that partition the vertical height gradient are small-sized understory species (like shrubs, small trees and small lianas) and large-sized canopy species (like canopy trees and big, high climbing lianas). Species that occupy different positions along these gradients are expected to possess different traits. Maximal tree stature and light demand are thought to capture the major variation in functional traits found among tropical rain forest tree species (Thomas 1996, Poorter et al. 2005). Unfortunately, such work has not been done yet for lianas. At any moment in the successional process, being taller than neighbors confers competitive advantage through prior access to light. However, height incurs costs from past investment in stems and support structures, from continuing maintenance costs for the stems and vasculature, and from disadvantages in the transport of water to height. Tree height at a fixed diameter (i.e. slenderness) was positively correlated with adult stature and light demand (Thomas and Bazzaz 1999, Poorter et al. 2003, 2005). The adult size of a species was expected to have a strong impact on acclimation potential, with the tallest species having the highest acclimation potential. That is, acclimation potential in the tree species did increase with increasing adult stature (cf. Thomas and Bazzaz 1999, Poorter et al. 2003). However, some leaf traits were found to be unrelated to maximum tree height, leading to the conclusion that maximum tree height is a poor indicator of shade tolerance (Gurvich et al. 2003). In this dissertation seedling growth and morphological and physiological seedling characteristics of a range of species with difference adult stature will be analysed under different light conditions.

Objectives and research questions

Lianas are an increasingly important growth form in tropical forests around the world, but are relatively unknown in southeast Asia. In this PhD research some liana communities are described and a number of structural-functional characteristics of lianas are analysed, in most cases comparative to trees, in tropical forests in Xishuangbana, SW China. Special attention is put to growth performance and ecophysiological leaf and plant characters in a framework of adaptive ecology.

The following specific questions are addressed:

1. How abundant and diverse are lianas in the mayor forest types in the area? In this thesis, we describe the species composition, community structure (diversity, structure, species similarity) and aspects of reproduction and climbing modes of the liana communities in three forest types that are located in the tropical-temperate transitional zone at Xishuangbanna, Southwest China.
2. Do lianas and trees differ in their responses to seasonal drought in the seasonal rainforest? We compared a range of leaf-level physiological attributes of a number of co-occurring liana and tree species during the wet and dry seasons in a tropical seasonal rainforest. We try to test the hypothesis that lianas are physiologically more robust than trees during the dry season, thus explaining their relatively high abundance in seasonal forests.
3. Do lianas have a stronger nutrient conserving mechanism than trees? The study compares changes in leaf size, leaf mass and foliar nutrient concentrations during leaf senescence in lianas and trees in a tropical strong phosphorus-limited montane rain forest in Xishuangbanna, south-west China. Our objectives were to compare (part of) the nutrient conservation strategies of the two plant growth forms.
4. Do lianas grow better than trees, as has often been postulated? To examine this hypothesis, a range of physiological, morphological, and biomass parameters at the leaf and whole plant level were compared in seedlings of five Bauhinia species of different growth form and with different shade tolerance.
5. How do lianas react to the major seasonal climate changes in the studied area? We investigated the effect of seasonality on physiology, morphology and growth responses in seedlings of one local liana species in three contrasting natural microhabitats: the understory, a small gap and a large gap.
6. How does species adult stature affect the plant's responses to light changes? We studied light acclimation of morphological and physiological leaf and whole-plant features of seedlings of six late-successional common woody species differing in adult

stature and shade tolerance.

The study site and the forest in Xishuangbanna

Physical geography of Xishuangbanna

Xishuangbanna (21°08′-22°33′ N, 99°56′-101°50′ E) is a mountainous region that is located in the southernmost tip of Yunnan province bordering Myanmar and Laos in the Southeast. The region has an area of 19 120 km^2. This area has a mountain–valley topography, with the mountains running north–south and with lower elevations southward. Altitude varies from 491 m above sea level (a.s.l.) at the bottom of the lowest valley in the south to 2 429.5 m (a.s.l.) at the top of the highest mountain in the north. The Mekong River runs through the region from northwest to southeast.

Climate

Lying in the East Asian Monsoon Region, Xishuangbanna is dominated by warm-wet air masses from the Indian Ocean in summer and continental air masses from the sub-tropical regions in winter. The climate is strongly seasonal with two main air masses alternating during the year: between May and October (rainy season) the South-West Monsoon delivers about 80% of the annual rainfall (Zhang 1963), whereas the dry and cold air of the Southern edges of the jet streams dominates the climate between November and April (dry season) (Figure 1). Dense radiation fog occurs in the entire dry season, with an average of 116 foggy days per year in Menglun in the center area of the region. The dry season is further divided into cool-dry (from November to February) and hot-dry (from March to April) periods. The cool-dry season is characterized by the high frequency of heavy fog during the night and in the morning on the lower hills and in the valleys (Liu et al. 2004). The hot-dry season is characterized by dry and hot weather during the afternoon and with heavy radiation fog during the morning only. Water deposition from fog averaged 0.52 and 0.41 mm d^{-1} beneath forest canopy, which account for 49% and 33% of the total water input for the cool-dry and hot-dry periods, respectively (Liu et al. 2004). Although the rainfall is seasonal, the dry season is not extreme in nature because heavy fog in dry season partially compensates for the rainfall shortage and plays an important role in easing plant water stress during the dry season (Liu et al. 2004). Due to the barrier of the Himalayas in the north, this region is sheltered from cold air from the north. Average annual temperature in Xishuangbanna is 21.7 ^{o}C at an elevation of 550 m. The hottest month is June with a mean temperature of 25.3 ^{o}C at 550 m, while the coldest month is January with an mean temperature ranging from 8.8 ^{o}C to 15.6 ^{o}C (Liu et al. 2004, Cao et al. 2006), and extremely chilling (2 ^{o}C) accidentally occurred (e.g. in 1999).

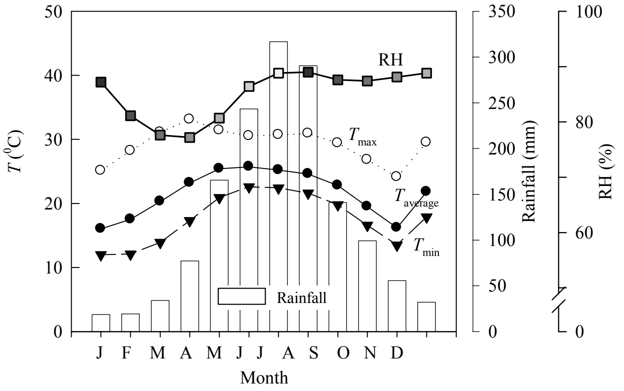

Figure 1 Seasonal changes in monthly precipitation (white bars), relative humidity (RH, %), and average (T_{average}; closed circle), maximum (T_{max}; open circles) and minimum (T_{min}; closed triangles) air temperatures from 1958 to 1998 in Xishuangbanna, SW China. (The data is from the Long-term Ecological Monitoring Station in XTBG)

Vegetation

Xishuangbanna, though far from the Equator and at a relatively high altitude, surprisingly has a rich tropical flora and typical tropical rain forests in the lowland areas (Figure 2). Because of conspicuous similarity in ecological and floristic characters, the tropical rain forest of Xishuangbanna is considered to be a type of tropical Asian rain forest. However, being at the northern geographical edge, it differs from typical lowland rain forests in equatorial areas in having some deciduous trees in the canopy layer, fewer megaphanerophytes and epiphytes and plants with microphyll leaves (Zhu et al. 2006).

Xishuangbanna is included in the Indo-Burma biodiversity hotspots and the flora of the region consists of a recorded 3336 native seed plant species, belonging to 1140 genera in 197 families, comprising 16% of China's total plant diversity (Cao and Zhang 1997, Myers et al. 2000), among which 83.5% are tropical genera and 32.8% are endemic to tropical

Asia (Zhu et al. 2006). The forests of Xishuangbanna thus harbor a biodiversity that is important both nationally and globally.

The families with highest species richness include Orchidaceae, Fabaceae, Rubiaceae, Poaceae, Euphorbiaceae, Asteraceae, Lamiaceae, Moraceae (Zhu et al. 2006). Some families have only a small number of species in Xishuangbanna, but are the dominant families in terms of stem number in the tropical forests of the region. At the generic level, *Ficus* has the highest species richness with 51 species. Based on a combination of physiological and ecological characters, floristic composition, and habitats, the vegetation of Xishuangbana is classified into the following four main vegetation types (Zhu et al. 1998, 2006):

Tropical rain forest: The tropical rain forest in Xishuangbanna has been classified into two subtypes: tropical seasonal rain forest and tropical montane rain forest (Wu 1987, Cao and Zhang 1997, Zhu et al. 2006). The former is found in the lowlands, usually below 900 m in elevation, while the later occurs locally at higher elevation. Based mainly on habitats and floristic composition, the tropical seasonal rain forest of Xishuangbanna is further classified into two formation groups including lower hill seasonal rain forest and ravine seasonal rain forest (Wu 1987, Zhu et al. 2006). Like equatorial lowland rain forest, the tropical seasonal rain forest has 3-4 indistinct tree layers, of which the top layer consists of mainly emergent trees higher than 30 m tall.

Tropical seasonal moist forest: Tropical seasonal moist forest occurs on the middle and upper limestone slopes with shallow soils ranging from 650 to 1300 m. The forest is evergreen, with two distinct layers. The top tree layer is 13-15 m tall.

Tropical montane evergreen broad-leaved forest: Tropical montane evergreen broad-leaved forest distributed on mountain slopes and summits above 1000 m elevation and valleys above 1300 m. It has two conspicuous tree layers, of which the top layer is 15-25 m tall with dense crown coverage and the lower layer is 3-15 m tall.

Tropical monsoon forest: Monsoon forest is a transitional forest type between seasonal rain forest and savanna. In Xishuangbanna, monsoon forest occurs on the banks of the Mekong River and at wide basins where there is evidently an annual dryness due to the strong monsoon climate. The monsoon forest is usually 20–25m tall with 1–2 deciduous tree layers. Woody lianas and epiphytes are scarce.

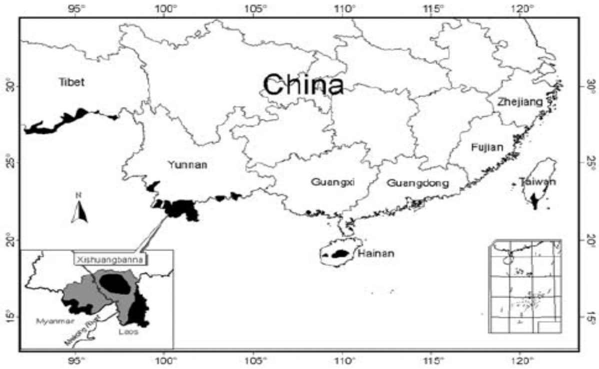

Figure 2 The location and distribution of the old growth tropical forests in Xishuangbanna in China. (The picture is from Cao et al. 2006.)

Factors influencing forest structure and species composition in Xishuangbanna

The seasonal climate coupled with the complex topography has resulted in a natural vegetation pattern consisting of both evergreen and deciduous forest patches and resulting in high species diversity (Cao et al. 2006, Zhu et al. 2006). The structure and species composition in a particular forest patch depends on three main factors: moisture, altitude, and human interaction. Although lowland areas have less rainfall, plants can often access ground water. In Xishuangbanna, fog in valley and lowland areas provides moisture in the dry season (Liu et al. 2004). Plants that are not confined to water supply throughout the year have developed approaches to avoid excessive water loss. Typical for monsoon forest in Xishuangbanna is the deciduous habit of the emergent trees that shed their leaves in the dry season (Zhu et al. 1998, 2006). In higher elevation with sandy soils, a sclerophyllus habit is common (Zhu et al. 2006). The dominant tree species have developed thick leaves with waxy coating to reduce water loss. Highland areas have lower temperatures than lowland areas.

Human interaction plays a very important role in the species and forests in Xishuangbanna (Zhu et al. 2004), which has been inhabited by different ethnic groups since over 4,000 years. Since 1960s, about half of forests have been lost due to anthropological disturbance. Among totally 12 minority groups in the local area, each ethnic group has developed its characteristic forms of land use shaping the environment they live in. The interactions with the forest include shifting cultivation, timber and fuelwood harvesting, cultivation in the forest (especially rubber plantation), collection of various non-timber forest products, and religious motivated protection of forest patches (Holy hills) and certain species as well as the introduction of exotic plants (Liu et al. 2002, Wang et al. 2004). The dominant ethnic group, Dai, is well known for preserving holy hills and has also introduced many species related to Buddhism that are now common in Xishuangbanna, such as *Dipterocarpus turbinatus* and *Ficus religiosa*. The fast-growing *Cassia siamea* has been introduced for fuelwood production in a coppice system for several hundreds years. Cultivation of the medicine herb, *Amomum villosum*, in the forest understory has changed the forest soil characteristics and structure in Xishuangbanna (Zheng et al. 2003, Liu et al. 2006). The selective cutting of timber with good wood properties for house building has led to changes in species composition in most village forest areas. Species like *Ficus* spp., *Gmelina arborea*, and *Schima wallichii* are more common after disturbances in the natural forest. For lianas, *Calamus* spp, *Acacia pennata*, *Caesalpinia cucullata*, *Trachelospermum jasminoides*, and *Gnetum montanum* are commonly used species by Dai people. Other ethnic tribes such as Hani, Yao, Lahu, Yi and Jinuo practice shifting cultivation, whereas Jinuo cultivate tea under the forest cover leading to characteristic coppice forests with huge emergent. Shifting cultivation systems practiced by these ethnic groups have led to high proportions of pioneer species such as *Macaranga* spp., *Maratus* spp., *Anthocephalus chinensis*, as well as Bamboo species.

Outline of this thesis

The thesis consists of eight chapters. Chapter 1 introduces the thesis and gives general information on liana characteristics, vegetation, and factors influencing forest structure and species composition in the studied area. It provides the basic information of lianas and ecological/physiological functions of lianas in the local area, and considers differences between lianas and trees.

Chapter 2 gives a general overview of the liana communities in three common and major forest types in the local area, differing in altitude and in rainfall: montane forest, evergreen broad-leaved forest, and seasonal rain forest. It describes the basic detailed information (diversity, abundance, structure, species similarity, aspects of reproduction and climbing modes) of lianas in the three local dominant forests.

In Chapter 3, leaf characteristics of lianas and trees during wet vs. dry seasons in the tropical seasonal rainforest are presented. The differences in leaf characteristics between lianas and trees during seasonal drought, which are expected to give lianas a competitive advantage over trees in a tropical seasonal rainforest, are addressed.

The study presented in Chapter 4 investigated changes in leaf size, leaf mass and foliar nutrient concentrations during leaf senescence in two groups of woody species (liana and tree) in a tropical strong phosphorus-limited montane rain forest in Xishuangbanna, south-west China.

In Chapter 5 the hypothesis is tested that lianas grow faster than trees. A range of physiological, morphological, and biomass parameters at the leaf and whole plant level were compared in seedlings of five Bauhinia species with different growth form and shade tolerance (two light-demanding lianas, one shade-tolerant liana, and two light-demanding trees).

In Chapter 6, photosynthetic traits and growth of seedlings of one liana species in three microhabitats are presented. The morphological and physiological responses to seasonal climatic changes and the dominant abiotic factors affecting seedlings are described and analyzed; the possible role of fog in the local area is also discussed.

Chapter 7 addresses morphological and physiological leaf and whole-plant features of seedlings of six late successional woody species with different adult stature. Acclimation of seedlings to change from low to high light is analysed. Indeed, the species largely differ in their ability to acclimate to high light.

Finally, Chapter 8 present a short summary of the thesis.

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Chapter 2

Liana communities in three tropical forest types in Xishuangbanna, SW China

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Abstract

Lianas are an important growth form in tropical forests around the world; however, they are relatively unknown in southeast Asia. We identified, measured, and determined the climbing and disperal modes for all lianas ≥ 0.2 cm in diameter in five 0.1 ha (20 x 50 m) plots in three common forest types at the tropical-temperate transitional zone in Xishuangbanna, SW China: montane forest, evergreen broad-leaved forest and seasonally wet forest. The mean density of lianas varied significantly among the three forests, with 445, 276 and 301 individuals per plot in the seasonally wet, montane, and evergreen forests, respectively. In all three forests combined, we found a total of 147 liana species, representing 48 families and 75 genera; however similarity coefficients between the forests were low. Mean species richness was 40, 26, and 21 species per plot in the seasonally wet, montane, and evergreen forest, respectively. Fisher's α differed significantly among the three forest types, with seasonally wet forest having the highest and evergreen forest the lowest values. In all three forests, most lianas were stem twiners and scramblers, with relatively few hook, tendril and root climbers. Liana species were mostly wind dispersed in the evergreen forest, but animal and gravity dispersed in the other two forests. Compared to other tropical Asian tropical forests, the diveristy and abundance of lianas is relativley high in Xishuangbanna, which may be due to the relatively warm climate, as well as high seasonal rainfall and high rates of disturbance and forest fragmentation.

Keywords: abundance, diversity, liana, mechanims of climbing, mode of dispersal, Xishuangbanna

Introduction

Lianas (woody climbers) are an abundant and diverse life-form in most tropical forests and their presence is often a key physiognomic feature differentiating tropical from temperate forests (Putz and Mooney 1991, Schnitzer and Bongers 2002). Lianas contribute substantially to the floristic, structural and functional diversity of tropical forests, where they can compete intensely with other vegetation. For example, lianas compete with trees for both above- and below-ground resources, substantially decreasing the growth rates and fecundity of adult trees, retarding regeneration of tree seedlings and saplings, and increasing the number of trees damaged and killed in treefalls (Stevens 1987, Schnitzer et al. 2000, 2005, Pérez-Salicrup 2001, Grauel and Putz 2004, Kainer et al. 2006). Lianas can also have decidedly positive effects on forests, providing valuable food resources, habitat, and connections among tree canopies that are used as pathways by arboreal animals (Emmons and Gentry 1983, Ødegaard 2000). Lianas may also play a role at the ecosystem level by contributing to the carbon budget of tropical forests, representing as much as 10% of fresh aboveground biomass (Putz 1984); however, when lianas become abundant they may displace trees and actually reduce he ability of forests to sequester carbon (Laurance et al. 2001, Phillips et al. 2002). Determining the abundance and dynamics of lianas in tropical forests is particularly timely because lianas appear to be increasing in abundance, possibly due to global climate change (Phillips et al. 2002, Wright et al. 2004).

Liana abundance in forests outside of the tropics, however, may not be increasing because cold winter temperatures at higher latitudes may be the overriding factor that limits liana abundance (Schnitzer, 2005). For example, Londré and Schnitzer (2006) found that mean abundance of lianas in 14 high-latitude deciduous temperate forests did not increase during the 45-year period from 1959–2005. These authors suggested that liana abundance and diversity is more likely to increase at the transition zone between tropical and temperate forests, where small increases in temperature may reduce the number of days below freezing. Liana communities in the tropical-temperate transition zone, however, are poorly studied, and before we can test the hypothesis that lianas are increasing in abundance in this zone, we need to first describe, in detail, liana communities that are situated there.

In this study, we describe the species composition, community structure (diversity, structure, species similarity) and aspects of reproduction and climbing modes of the liana communities in three forest types that are located in the tropical-temperate transitional zone at Xishuangbanna, Southwest China. The forests in this region differ from typical lowland rain forests in equatorial areas, in part, by having many deciduous trees in the canopy layer, fewer megaphanerophytes and epiphytes, as well as more species of microphylls (Zhu et al. 2006). However, little is known about the liana communities of this region and thus here we provide the first detailed study of lianas. We compare and contrast liana abundance, basal area, size class distributions, and species richness, dominance, and composition, among three different, but common forest types in Xishuangbanna. We also describe liana climbing modes and dispersal syndromes, and analyze whether these factors vary predictably among the forest types. Finally, we compare the liana communities in Xishuangbanna to other forests in the tropics.

Methods

Study area and site description

The study was conducted in Xishuangbanna (21°09′–22°33′ N, 99°58′–101°50′ E), which is located at the northern margin of mainland Southeast Asia and the southern end of the Hengduan Mountains (part of the Himalayas). Lying in the East Asian Monsoon Region, Xishuangbanna is dominated by warm-wet air masses from the Indian Ocean in summer and continental air masses from the sub-tropical regions in winter, which results in an alternation of rainy (May–October) and dry (November–April) seasons (Cao et al. 2006). Due to the barrier of the Himalayas in the north, this region is sheltered from northerly cold air masses. Average annual temperature in the tropical forests in Xishuangbanna is 21.4^{o}C and average annual rainfall is 1539 mm, of which about 82% occurs in the rainy season, while heavy fog in winter partially compensates for the rainfall shortage during the dry season.

Table 1 A summary of key abiotic factors describing the three study sites.

Location	Forest type	Geographical location	Altitude (m.a.s.l.)	pH value	Organic matter (%)	Soil type
Mengsong	Montane forest	21^{0}27’ N, 100^{0}25’ E	1650	4.5	4.5	Lateritic red soil
Nangongshan	Evergreen broad-leaved forest	21^{0}37’ N, 101^{0}27’ E	1300	4.9	1.4	Lateritic red soil
Baka	Seasonally wet forest	21^{0}50’ N, 101^{0}12’ E	750	3.7	2.7	Lateritic red soil

The four main tropical forest types in the area are: 1) seasonally wet forest (hereafter referred to as ‘seasonal forest’), which consists of a combination of evergreen and deciduous broad-leaved trees; 2) evergreen broad-leaved forest (‘evergreen forest’); 3) montane forest ('montane forest'); and 4) monsoon forest over limestone ('monsoon forest') (Cao et al. 2006, Zhu et al. 2006). The combination of these four forest types contributes to the relatively high tree species diversity of this region. The seasonal forest and the evergreen forests constitute the majority of the forests of this region, while the montane forest contributes significantly less (Zhu et al. 2006) (Table 1). We sampled one forest from three of these major forest types, omitting the monsoon forest because these forests contribute only a very small area of all forest types and are exceptionally difficult to work in due to their steep slopes.

Sampling procedures

We surveyed lianas between September and November 2004 in 15 20x50 m (0.1 ha) plots, five plots in each of the three forest types. In each forest, plots were separated by a minimum distance of 50 m and were at least 100 m from the forest edge. In each plot, we enumerated and measured the diameter of all free-standing and climbing liana individuals (≥ 0.2 cm). For lianas ≥ 1 cm in diameter, we measured the stems at 130 cm from the roots, measured along the stem (Gerwing et al. 2006). For smaller lianas (0.2–1 cm), we measured their diameter at 10 cm stem above ground. We defined lianas as woody climbers rooted in the ground, thus we excluded herbaceous vines, epiphytes, and hemiepiphtes. When a single liana individual had multiple vegetative offshoots connected to the main stem, we included only the largest diameter stem and excluded all multiple vegetative offshoots (methods follow those of Mascaro et al. 2004, Schnitzer et al. 2006). We also measured and enumerated all trees (DBH ≥ 5 cm) that were rooted in the plot.

We identified all lianas in the field and collected voucher samples, including flower and diaspore type, from each individual. Species were identified using the regional floras (Yunnan Flora Volumes 1–15), and these identifications were confirmed at the Xishuangbanna herbarium. Local taxonomists verified all species identifications using herbarium specimens at Xishuangbanna Tropical Botanical Garden. We classified flower type based on the size and color of flowers, as suggested by Gentry (1982, 1991b). We distinguished inconspicuous flowers, with white or green colors and smaller than 1 cm in length from conspicuous flowers, with bright colors and flower lengths generally longer than 1 cm. Diaspores are the structures that function as dispersing units, including fruits, seeds or even seeds with some part of the fruit. Based on diaspore morphology, three dispersal syndromes are commonly classified: anemochory (wind-dispersed fruits or seeds with plumose appendages or scarious wing-like appendages), zoochory (animal dispersed fruits with soft and fleshy outer layers or seeds with arils), and barochory (heavy units that fall near the materal plant). We also classified each liana species as one of five potential climbing types: (1) scramblers, (2) twiners, (3) root climbers, (4) tendril climbers, and (5) hook climbers (methods follow Putz and Chai 1987; DeWalt et al. 2000).

Data analysis

For each of the plots, we calculated liana density, species richness, Fisher's log series α (Fisher's α) and compared mean plot values among the three forests using Analysis of Variance (ANOVA). We included Fisher's α as an idex of diversity because it varies relatively little with sample size, and thus facilitiates comparisons of diversity among sites that differ in abundance (Magurran 1988). We calculated the importance value of each species in each plot as the mean of that species' relative abundance and relative basal area in each plot (Hartshorn and Hammel 1994). In addition, we calculated within–site and between-site Morisita-Horn similarity indices and plotted randomized species accumulation curves for each of the sites using EstimateS (7.5) (Colwell et al. 2004).

Results

Liana density and size-class distribution

Overall, lianas were abundant in the Xishuangbanna forests, although the density of lianas ≥ 1 cm diameter differed significantly among the three forests ($F = 32.7$, $P < 0.001$; Table 2). We recorded the highest mean density of lianas (≥ 1 cm diameter) per 0.1 ha in the seasonal forest (189.4), significantly less in the evergreen forest (89), and the fewest in the montane forest (57). Likewise, mean liana basal area and proportional basal area (based on the ratio of lianas to trees) were both highest in the seasonal forest ($F = 8.3$, $P = 0.015$ and $F = 8.2$, $P = 0.007$), while there were no significant differences between montane and evergreen forest. The mean density of small lianas (< 1 cm) was > 200 individuals per plot and the stem number did not differ significantly among the three forest types ($F = 1.2$, $P > 0.05$). More than 75% of the liana individuals were smaller than 4 cm in diameter in all forests (Table 3), while large lianas (dbh>10 cm; *sensu* Phillips et al. 2002) were sparse. The largest liana in all plots measured 42 cm in diameter (*Craspedolobium schochii)* and was found in the montane forest. More trees carried at least one liana in the seasonal than in the evergreen forest (Log-transformed, $F = 7.2$, $P = 0.028$, Table 2). Tree basal area was negatively correlated to liana basal area, but the correlations were rather weak and not significant (Log-transformed, $R^2 = 0.22$, $P > 0.05$, $N = 15$).

Table 2 Liana density, species richness, basal areas and Fisher's α of all lianas for five 0.1-ha plots in each of three forests in Xishuangbanna, SW China. The data (Means ± S.E., n=5) with different letters were significantly different between sites (ANOVA, *P*<0.05). Liana basal area is calculated as the sum of all lianas ≥ 0.2 cm diameter; Liana/tree basal area (%) was calculated by dividing liana basal area by the basal areas of trees ≥ 5 cm DBH.

Forest type	Liana species richness (0.1 ha)	Total species Number (0.5 ha)	Liana density 0.2<DBH<1 (0.1 ha)	Liana density Total≥1 cm (0.1 ha)	Liana basal area (cm^2 0.1 ha)	% of trees carried at least one liana (0.1 ha)	Liana/Tree basal area (%) (0.1 ha)	Fisher's α
Montane forest	26 (0.9) a	68	218.8 (27.5) a	57 (15.9) a	1004.0 (135.5) a	—	2.7 (0.4) a	7.1(0.3) b
Evergreen forest	21.4 (3.4) a	43	211.8 (26.5) a	89.2 (15.5) b	663.8 (54.5) a	36.1 (6.8) a	2.0 (0.3) a	5.3 (0.6) a
Seasonal forest	40.4 (3.3) b	114	255.8 (36.0) a	189.4 (13.7) c	1637.7 (127.6) b	61.9 (5.7) b	10.7 (2.7) b	10.5 (0.9) c

Table 3 Size-class distribution of lianas in each plot (0.1 ha) in three forests, Xishuangbanna, Yunnan, China. Different letters indicate statistically significant difference between the forests (ANOVA, $P < 0.05$).

DBH (cm)	Montane forest	Evergreen broad-leaved forest	Seasonally wet forest
0.2–0.5	123.3±43.0 a	98.0±48.7 b	104.4±49.9 a
0.5–1.0	100.9±34.2 b	113.8±36.0 b	151.4±22.1 a
1–2	51.9±28.5 b	59.8±15.2 b	105.2±21.8 a
2–5	18.8±16.5 b	23.0±12.1 b	65.8±8.24 a
5–10	6.6 ±4.0 b	5.0±1.9 b	17.8±3.0 a
>10	2.1±2.3 a	1.4±1.9 b	0.6±0.8 c

Species richness, diversity and dominance

In all 15 plots combined, we found a total of 147 liana species belonging to 75 genera and 48 families (Appendix A). Of these species 43, 68 and 114 species were found in the montane, evergreen and seasonal forest plots, respectively. In the montane forest, the most diverse families, in terms of the number of species, were Fabaceae (Papilionaceae) (8) and Apocynaceae (8), which combined contribute 37.2% of the total species richness. In evergreen forest, Fabaceae (8) and Rubiaceae (4) were well represented, contributing 17.6% of the total species. The seasonal forest contained 44 families and 74 genera, and the Fabaceae (11), Rubiaceae (11) and Apocynaceae (8) were the most speciose families.

Table 4 Morisita-Horn similarity values among plots, both within forests as among forests. Mean values and SD are given. Number of comparisons is 10 for within forests and 25 for among forest comparisons. Values were computed using EstimateS (Version 7.5, R.K. Colwell, http://purl.oclc.org/estimates).

	Montane forest	Evergreen broad-leaved forest	Seasonally wet forest
Montane forest	0.55 ± 0.22	0.10 ± 0.05	0.10 ± 0.07
Evergreen broad-leaved forest		0.78 ± 0.11	0.27 ± 0.11
Seasonally wet forest			0.59 ± 0.17

Species richness in the 15 plots ranged from 21.4 to 40 species. The seasonal forest plots had significantly more species than montane and evergreen forest plots ($F = 22.8$, $P < 0.0001$), while these latter two forests were not significantly different from each other (Table 2, Fig. 1). Species diversity estimated using Fisher's α was two-times higher in the seasonal forest compared to evergreen forest, while montane forest was intermediate ($F = 19.9$, $P < 0.0001$, Table 2). Because Fisher's α is relatively insensitive to sample size, the high diversity in the seasonal forest is likely to be independent of the high stem density in this forest (Mascaro et al. 2004).

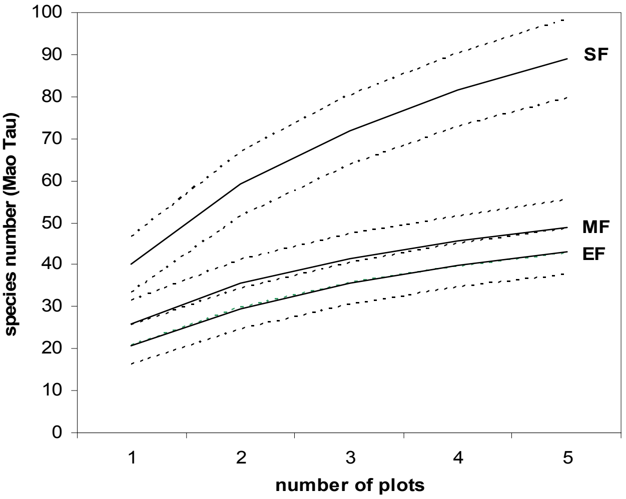

Figure 1 Species - sample curves for liana species in seasonal (SF), montane (MF), and evergreen (EF) forests in Xishuangbanna, China. Species number is the number of species expected in the pooled samples, given the empirical data (Colwell *et al.* 2004), and their 95% confidence intervals. Values are computed using EstimateS (Version 7.5, Colwell, R. K. http://purl.oclc.org/estimates).

The evergreen forest plots had highest among-plot similarities compared to the other two forest types (two T-tests, each $P < 0.0001$), suggesting that species composition was the least variable among the plots in the evergreen forest, while the seasonal and montane forests were both lower but equal in among-plot similarities (Table 4, T-test, $P > 0.05$). Similarities within forests were much higher than similarities among forests. Plots in evergreen and seasonal forest were more alike than the other forest combinations (two T-tests, each $P < 0.0001$), while the similarities between evergreen and montane and between rainforest and montane were equal (T-test, $P > 0.05$).

The top 10 species accounted for more than 75% of the total importance values of all liana species in evergreen and montane forests, while they accounted for less than 50% of the total importance values in seasonal forest (Table 5). *Celastrus monospermus* was the most dominant liana species in the seasonal forest, with an importance value of 11.9%. *Craspedolobium schochii* was the most abundant species in evergreen and montane forests, with importance values of 16.8% and 22.7%, respectively. The relative basal area of *C. schochii* was exceptionally variable in evergreen forest, ranging from 7.8% to 74.5% per plot. Only one of the top-10 species (*C. monospermus*) was shared between the montane and seasonal forests, while four species (*Dalbergia stipulacea*, *Smilax hypoglauca*, *C. monospermus*, *Bauhinia aurea)* were shared between the evergreen and seasonal forests. Only one rattan species (*Calamus nambariensis*) was found among these top-10 dominant species, exclusively in the montane forest (Appendix A).

Table 5 Ten most abundant liana species according to the density and basal area, arranged in order of decreasing relative importance value.

*Mean relative abundance (MRA) and basal area (MBA) were calculated by dividing the abundance or basal area of the local species per plot by the abundance and basal area of all the individuals in the plots, respectively, and then taking the average of the plots. RIV: relative importance value is the sum of the MRA and MBA divided by 2.

	Montane forest				Evergreen broad-leaved forest				Seasonally wet forest		
Dominant species	MRA	MBA	RIV	Dominant species	MRA	MBA	RIV	Dominant species	MRA	MBA	RIV
C. schochii	12.3(1.3)	21.3(8.6)	16.8	*C. schochii*	14.8(4.0)	30.6(15.2)	22.7	*C. monospermus*	14.1(0.9)	9.7(1.1)	11.9
M. pachycarpa	11.8(1.2)	20.2(5.5)	16.0	*M. griffithi*	11.0(2.8)	15.6(5.1)	13.3	*D. stipulacea*	4.4(0.6)	15.9(1.1)	10.1
B. angustifolia	11.4(2.0)	15.0(11.3)	13.2	*S. hypoglauca*	17.6(8.8)	5.5(1.7)	11.6	*G. parvifolium*	3.3(1.0)	6.1(0.5)	4.7
S. suberectus	7.9(1.0)	16.9(6.7)	12.4	*D. stipulacea*	9.6(7.2)	11.6(6.6)	10.6	*C. latifolium*	2.7(0.5)	6.1(0.4)	4.4
P. linearicarpum	9.2(0.5)	4.2(1.9)	6.7	*C. paniculatus*	9.8(3.1)	11.3(9.2)	10.6	*B. grandifolia*	4.1(0.6)	3.8(0.4)	3.9
C. nambariensis	9.8(2.0)	0.7(0.4)	5.3	*S. microphylla*	13.5(2.8)	1.2(0.5)	7.3	*M. hossei*	5.8(0.8)	1.6(0.6)	3.7
C. monospermus	3.7(0.8)	2.6(2.1)	3.2	*M. hossei*	4.8(1.8)	3.2(2.5)	4.0	*M. tinctoria*	4.4(0.1)	0.3(0.0)	2.3
D. pinnata	2.1(0.3)	0.5(0.3)	1.3	*C. monospermus*	2.5(1.5)	1.9(1.2)	2.1	*S. hypoglauca*	3.4(0.8)	0.8(0.1)	2.1
P. flaviflorum	1.1(0.2)	0.1(0.1)	0.6	*S. corbularia*	1.0 (0)	0.1(0.0)	0.5	*P. arborea*	2.6(0.2)	1.1(0.1)	1.8
S. aurantiaca	0.9(0.3)	0.1(0.0)	0.5	*S. suberectus*	0.5(0.5)	0.1(0.1)	0.3	*E. glaucescens*	1.3(0.2)	0.3(0.0)	0.8
Sum	70.2	81.6	75.9		85.1	81.1	83.1		46.3	45.8	46.1

Climbing mechanisms, flower and dispersal syndromes

Liana climbing mechanisms did not differ significantly among the three forest types (Log-transformed, F = 0.03, P > 0.05, Fig. 2). Twining was the predominant climbing mechanism in all forests in terms of species richness (43.1–52.4%), followed by scramblers (20–26.2%). The other three types of climbing mechanism were less common and varied in abundance among the forest types. There were more conspicuous than inconspicuous flowers in all three forest types, but differences were less pronounced in the seasonal forest (Fig. 3a). Lianas displayed a wide range of diaspore types: wind-dispersed, animal-dispersed and autochorous (Fig. 3b). The proportion of diaspore types was essentially the same in montane and seasonal forests; however, the evergreen forest differed significantly from the other two forest types due to the predominance (61.5%) of wind-dispersed species (Log-transformed, F = 0.02, P < 0.05).

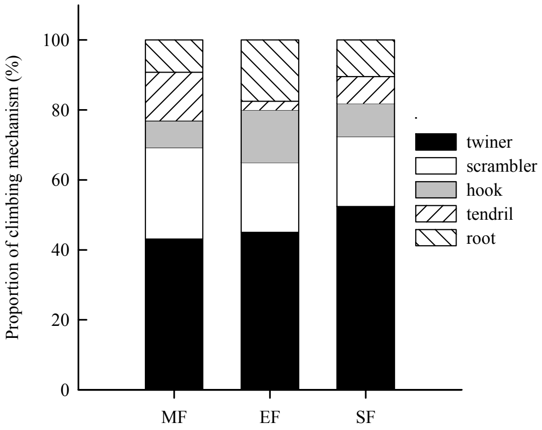

Figure 2 The proportion of each climbing mechanism of liana species in montane forest (MF), evergreen broad-leaved forest (EF) and seasonally wet forest (SF) in Xishuangbanna, China.

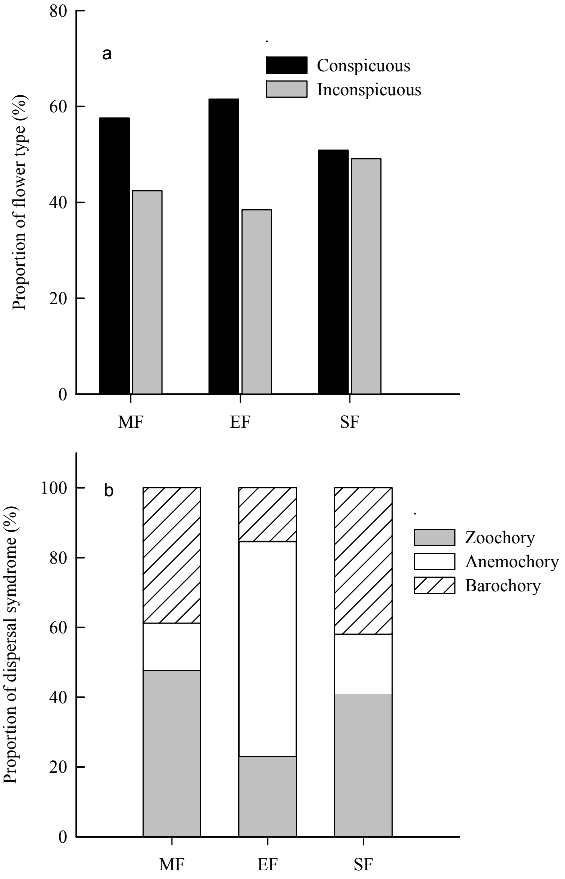

Figure 3 The proportion of the flower type (a) and dispersal syndrome (b) of liana species in the montane forest (MF), evergreen broad-leaved forest (EF) and seasonally wet forest (SF) in Xishuangbanna, China.

Discussion

Liana abundance and diversity is variable among sites throughout the tropics (Putz 1984, Gentry 1991a, Muthuramkumar and Parthasarathy 2000, Pérez-Salicrup et al. 2001, Mascaro et al. 2004, Parasarathy et al. 2004, DeWalt et al. 2006), and lianas commonly compose 10–45% of the woody individuals and species in tropical forests. In particularly liana-dense tropical forests, such as those in the Bolivian Amazon, lianas can reach an average of 2471 lianas/ha (≥ 2 cm diameter) and they can constitute as much as 44% of the woody species (Pérez-Salicrup et al. 2001).

Compared to many published studies, we found relatively high liana abundance and diversity in the three Xishuangbanna forests at the tropical-temperate transition zone. With a mean abundance of 1,118 lianas ≥ 0.2 cm diameter and 75 species/0.5 ha among each of the forests, liana abundance and diversity in Xishuangbanna was similar to, or higher than that of other tropical Asian forests. For example, at Lambir Hills in Sarawak, northwestern Borneo, mean liana abundance was 348 and 164 liana individuals (diameter ≥ 2 cm) per ha in valley and hilltop sites, respectively, with a total of 79 species/ha (Putz and Chai 1987). In the Danum Valley Conservation Area in Sabah, northeastern Borneo Campbell and Newberry (1993) found 882 individuals per ha (diameter ≥ 2 cm) in two 4 ha plots of lowland dipterocarp forest. In five forests in southern India, Parathasarathy and co-workers found on average 345 lianas (> 1.6 cm) per ha and 148 species in a total sample area of 47 ha (Muthuramkumar and Parathasarathy 2000, Parathasarathy et al. 2004). At Sepilok Forest Reserve, Malaysia, DeWalt et al. (2006) found average 1348 lianas ha^{-1} (≥0.5 cm) in three forest types. In comparison, we found a mean density of 470 lianas ≥ 2 cm for the three forests, with a mean density of 842, 275, and 294 lianas ≥ 2 cm diameter in the seasonal, montane, and evergreen forests, respectively. The liana density in Xishuangbanna is similar to that of La Selva Biological Station in Costa Rica, which has approximately 473 lianas ≥ 2 cm diameter and 1493 lianas ≥ 0.2 cm diameter (Mascaro et al. 2004).

Our finding that liana abundance was highest in the seasonal forest is consistent with the documented pattern that lianas peak in abundance with increasing seasonality (Schnitzer 2005), as the seasonality index (the sum of the absolute deviations of mean monthly rainfalls from the overall monthly mean, divided by the mean annual rainfall; Walsh and Lawler 1981), was relatively high (0.77) in the studied area. Furthermore, our findings that liana abundance and diversity were lowest in the montane forests is consistent with published data (reviewed by Schnitzer and Bongers 2002). However, because these forests (seasonal and montane) both differed in rainfall and elevation, we cannot be certain, based on our data, whether one factor is more important than another.

Liana abundance and diversity decreases with increasing latitude (Gentry 1991a, Schnitzer and Bongers 2002, Schnitzer 2005). However, whether this change is linear or a step-function is not well established. For example, Schnitzer (2005) suggested that liana abundance will drop abruptly at the tropical-temperate transition because of the inability of most lianas to cope with freezing temperatures. Alternatively, lianas may decrease linearly with increasing latitude (Gentry 1991a, Parthasarathy et al. 2004). Because liana abundance in this study is similar to, or even exceeds the abundance and diversity from a variety of tropical forest studies (Campbell and Newberry 1993, Muthuramkumar and Parthasarathy 2000, Mascaro et al. 2004, Parasarathy et al. 2004), our data support the hypothesis that liana abundance may not be a strict linear decrease with increasing latitude; rather, liana abundance and diversity may drop abruptly at higher latitudes, where the prevalence of winter freezing occurs.

Another possible explanation for the relatively high abundance of lianas in Xishuangbanna is the legacy of forest disturbance, for half of the primary forest was lost during the last 50 years (Zhu et al. 2004). In Xishuangbanna and in SW China in general, large areas of tropical forests were replaced by rubber plantations in the 1960s, leaving smaller forest remnants near local villages. Although these forest remnants remain mostly undisturbed for religious reasons (Liu et al. 2002, Zhu et al. 2004), previous disturbance and higher propagule pressure from prolific liana growth on the forest edges may have resulted in increased liana abundance in these forests (DeWalt et al. 2000, Schnitzer et al. 2000, Zhu et al. 2004). We tried to avoid these biases by selecting sites in forests with little recent disturbance and that were at least 100 m from the forest edge. Nonetheless, it is possible that human disturbance may, to some degree, explain the relative high abundance of lianas found in this study compared to other forests of this region.

Species dominance was high compared to other studies. In our study, *C. schochii* was the most dominant liana species in the montane and evergreen forests, and one of the top three liana species accounting for over 10% of relative abundance in these two forests. In a chronosequence study in central Panama, DeWalt et al. (2000) found that *Maripa panamensis* composed approximately 11% of the liana stems and was found in all stands in secondary and primary forests in Panama. Similarly, in eastern Ecuador, Burnham (2002) reported that the most dominant liana, *Machaerium cuspidatum*, represented approximately 11% of the liana stems. Mascaro et al. (2004) found extremely high dominance in a tropical wet forest at La Selva Biological Station in Costa Rica, where the 10 top species accounted for more than 70% of all species and the most dominant liana species, *Moutabea aculeata* constituted 17% of all individuals. Combined with these published reports, our finding of 12% and 15% relative abundance of *C. schochii* in the montane and evergreen forests, and 14% of *C. monospermus* in the seasonal forest suggests that strong species dominance may be a general characteristic of liana communities world-wide.

Of the five climbing mechanisms distinguished in this study, twining around the host tree was the most common, followed by scrambling. These climbing mechanisms were 3-5 times more common than tendril, root, and hook climbers, which were relatively rare (Fig 3.). Our findings are consistent with other studies, which reported that twining was found to be dominant (Jongkind and Hawthorne 2005, Kuzee and Bongers 2005), especially in older forests (DeWalt et al. 2000). Other studies, however, reported that tendril climbers were more abundant in early secondary forests compared to old growth forests (Hegarty 1988, DeWalt et al. 2000). The high ratio of stem twiners to tendril climbers in our study may indicate that the forests are in a relatively late stage of succession.

Several important functional features of tropical communities are correlated with precipitation. Gentry suggested that liana species were mostly wind-dispersed, although the species number decreased in the wetter localities (Gentry 1982, 1991b). In our study, wind-dispersal was prevalent only in the evergreen forest. A similar situation prevails in semi-evergreen and dry evergreen forests in India (Muthuramkumar and Parthasarathy 2000, Parthasarathy et al. 2004) and in a seasonally dry tropical forest in Mexican (Solorzano et al. 2002). The prevalence of succulent diaspores in montane and seasonal forests in Xishuangbanna indicates the diversity of frugivorous birds and mammals and, in turn, the possible faunal dependence of many liana species for animal dispersal. The prevalence of zoochory suggests that a holistic, whole-forest approach to conservation strategies is necessary to maintain forest diversity, because plants such as lianas are dependent on animal fauna for dispersal and thus may supply animal communities with a valuable resource. Overall, our findings demonstrate that lianas can be abundant and diverse even in the tropical-subtropical transition zone, and thus the importance of lianas for forest diversity, dynamics, and functioning likely extends into this zone as well.

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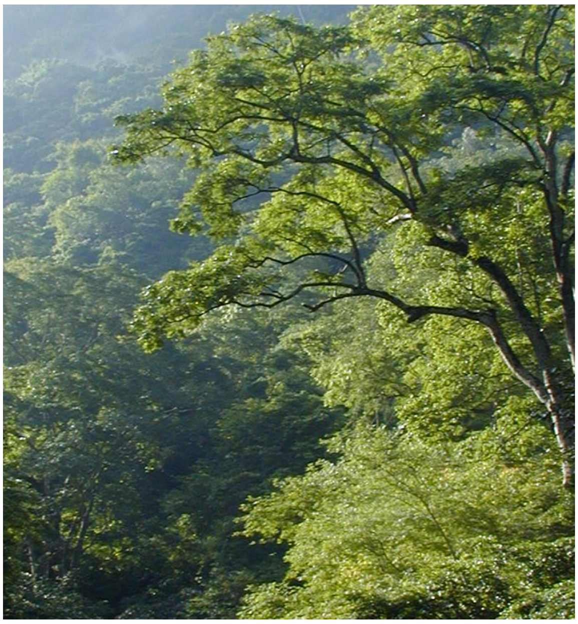
Appendix:
Complete list of climbing and free-standing lianas identified in the 15 0.1 ha plots in three forests in Xishuangbanna. 'M, E, SF' in the parenthesis represent that the liana species distributed in montane, evergreen broad-leaved and seasonally wet rainforest, respectively.

Annonaceae: *Artabotrya hongkongensis* Hance [E, M], *Fissistigma acuminatissimum* Merr. [M], *Fissistigma latifolium* (Dun.) Merr. [SF] *Fissistigma polyanthoides* (A. DC.) Merr. [SF], *Fissistigma polyanthum* (Hook.f.et Thoms.) Merr. [M]; **Apocynaceae**: *Aralia armata* (Wall.) Seem. [SF], *Tupidanthus calyptratus* Hook.f. et Thoms [M]; *Aganosma harmandiana* Pierre [E, SF, M], *Alyxia menglongensis* Tsiang et P.T. Li [SF], *Alyxia simensis* Craib [M], *Amalocalyx yunnanensis* Tsiang [E, SF], *Beaumontia grandiflora* Wall [SF], *Bousigonia angustifolia* Pierre [E, SF, M], *Ecdysanthera rosea* Hook. Et Arn. [SF], *Epigynum auritum*(Scheid.) Tsiang et P.T.Li. [M], *Melodinus henryi* Craib [SF], *Melodinus tenuicaudatus* Tsiang et P.T.Li [M], *Parabarium linearicarpum* (Pierre) Pichon [E, M], *Trachelospermum jasminoides* (Lindl.) Lem. [M], *Pottsia laxiflora* (Bl.) O. Kuntze [SF, M]; **Araceae:** *Pothos chinensis* (Raf.) Merr. [M], *Rhaphidophora hongkongensis* schoff [M], *Rhaphidophora luchunensis* H. Li. [SF]; **Aristolochiaceae:** *Aristolochia tagala* Champ [E]; **Asclepiadaceae:** *Gymnema sylvestre* (Retz.) Schult. [SF], *Marsdenia balansae* Cost [SF], *Marsdenia tinctoria* R. Br. [SF]; **Bambusoideae:** *Ampelocalmus menglaensis* Hsuehe F.Du [M], *Dinochloa multiramora* Hsueh etHui. [M], *Gigantochloa nigrocoliata* (Buse) Kurz [SF]; **Caesalpiniacea:** *Bauhinia aurea* Levl. [E, M], *Bauhinia claviflora* L.Chen [M], *Bauhinia griffithiana* (Benth.) Prain [M], *Caesalpinia tsoongii* Merr [M]; **Capparidaceae:** *Stixis suaveolens* (Roxb.) Pierre [W, FM]; **Caprifoliaceae:** *Viburnum foetidum* Wall. Varectangulatum (Graebm. Rehd.) [SF]; **Cardiopteridaceae:** *Peripterygium quinquelobum* Hassk [SF]; **Celastraceae:** *Celastrus angulatus* Maxim. [M], *Celastrus monospermus* Roxb. [SF, M], *Euonymus acanthocarpus* Franch [M]; *Celastrus paniculatus* Willd [SF]; **Combretacea:** *Combretum latifolium* Bl. [SF], *Quisqualis caudata* Craib [SF]; **Compositae:** *Vernonia cumingiana* Benth. [M], *Vernonia solanifolia* Benth [SF]; **Papilionaceae:** *Illigera rhodantha* Hance [SF, M]; **Connaraceae:** *Connarus paniculatus* Roxb. [SF, M], *Rourea minor* (Gaertn.) Leenh [SF]; **Convolvulaceae:** *Erycibe glaucescens* Wall. Ex Choisy [E, SF], *Argyreia nervosa* (Burm. f.) Bojer [M]; **Dilleniaceae:** *Tetracera asiatica* (Lour.) Hoogl. [SF]; **Dioscoreaceae:** *Dioscorea alata* Linn. [SF], *Dioscorea hispida* Dennst. [SF, M], *Dioscrorea glabra* Roxb. [E, SF]; **Euphorbiaceae:** *Phyllanthus reticulatus* Poir. [SF]; **Gnetaceae:** *Gnatum parvifolium* (Warb.) C.Y. Cheng ex Chun [E, SF], *Gnatum pendulum* C.Y. Cheng [M]; **Hernadiaceae:** *Illigera parviflora* Dunn [SF]; **Hippocrateacaea:** *Pristimera arborea* (Roxb.) A.C.Sm.[E], *Salacia aurantiaca* C.y.Wu et

S.Y. Bao.[E, SF, M]; **Icacinaceae:** *iodes vitiginea* (Hance) Hemsl [SF, M]; **Leguminosae:** *Uraria crinita* (linn.) Desv.ex DC prodr [E]; **Lygodiaceae:** *Akebia quinata* (Thunb.) Decne [E]; *Lygodium conforme* C. Chr. [E, SF]; **Malpighiaceae:** *Hiptage benghalensis* (Linn.) Kurz [SF, M]; **Menispermaceae:** *Cyclea racemosa* Oliv. [M], *Diploclisia glaucescens* (Bl.) Diels [SF], *Pericampylus glauca* (Lam.) Merr. [SF], *Stephania hernandifolia* (Willd.) Walp [E, M]; **Mimosaceae:** *Acacia megaladena* Desv., *Acacia pennata* (Linn.) Willd. ex Del. [E, SF]; *Entada phaceoloides* (Linn.) Merr [SF]; **Moraceae:** *Cudrania fruticosa* (Roxb.)Wigth ex Kurz [SF], *Ficussarmentosa* var. duclouxii (Lerl. Et Vant.) Corner [SF], *Ficus sarmentosa* var. duclouxii (Lerl. Et Vant.) Corner [SF], *Ficus sarmentosa* var.Lacrymens (Levl.) Corner [M]; **Myrsinaceae:** *Embelia oblongifolia* Hemsl. [SF], *Embelia parviflora* Wall [SF], *Embelia scandens* (Lour.) Merr. *Embelia subcoriacea* (C.B. Clarke) Mez [SF], *Embelia* Var. ribes Burm.f. [E, SF, M]; **Ruhamnaceae:** *Ventilago calyculata* Tul. [SF], *Zizyphus apetala* Hook.f. [SF], *Zizyphus oenoplia* (Linn.) Mill. [E, SF]; **Oleaceae:** *Jasminum coarctatum* Roxb. [SF] *Jasminu polyanthum* Fr. [M], *Jasminum robustifolium* Kobuski. [E, SF, M]; **Palmae:** *Calamus nambariensis* Becc. var. Xishuangbannaensis S.J.pei et S.Y.Chen [M], *Caryota monostachys* Becc.[SF], *Caryota ochlandra* Hance [SF]; **Papilionaceae:** *Craspedolobium schochii* Harms [E, W F, M], *Dalbergia pinnata* (Lour.) Prain [E, SF, M], *Dalbergia rimosa* Poxb. [E, SF], *Dalbergia stipulacea* Roxb [E, SF, M], *Millettia dielsiana* Harms [SF, M], *Millettia lantsangensis* Z.Wei [M], *Millettia oosperma* Dunn [SF], *Millettia pachycarpa* Benth.[SF, M], *Mucuna macrobotrya* Hance [SF], *Pueraria collett*i Prain [E, SF], *Pueraria stricta* Kurz [E, SF], *Spatholobus suberectus* Dunn [E, SF], *Whitfordendron filipes* (Dunn) Dunn [M]; **Passifloraceae:** *Adenia parviflora* (Blanco) Cusset [E, SF], *Passiflora altebilobata* Hemsl. [SF], *Passiflora siamica* Craib [SF]; **Piperaceae:** *Piper betle* Linn. [SF, M], *Piper magen* B.C. Cheng [SF], *Piper flaviflorum* C.DC. [SF, M], *Gynostemma pubescens* (Gagnep.) C.Y.Wu ex C.Y.Wu et S.K.Chen [M], *Neoalsomitra integrifoliola* (Cogn.) Hutch [E, SF]; **Polygalaceae:** *Securidaca inappendiculata* Hassk [SF]; **Ranunculaceae:** *Clematis menglaensis* M.C. Chang [E, SF]; **Rosaceae:** *Rubus alceaefolius* Poir. [E, SF], *Rubus rufus* Focke Var.palmatifidus Card [M]; **Rubiacea:** *Hedyotis hedyotidea* DC, *Mussaenda erosa* Champ [E, SF], *Mussaenda hossei* Craib [E, SF], *Mussaenda pubescens* Ait. f. [E, SF, M], *Randia bispinosa* (Griff.) Craib [SF], *Randia sinensis* (Lour.) Merr. [SF], *Uncaria hirsuta* Haril. [SF], *Uncaria laevigata* Wall. [SF], *Uncaria lancifolia* Hutch. [SF], *Uncaria macrophylla* Wall. [E, SF]; **Rutaceae:** *Paramignya retispina* Craib[M], *Toddalia asiatica* (Linn.) Lam. [E], *Zanthoxylum cuspidatum* Champ. [SF]; **Schizandraceae:** *Kadsura anamosma* Ker [M], *Kadsura coccinea* (Lem.) A.C. [M], *Schizandra henry*i C.B. Clarke [SF], *Schizandra henryi* C.B. Clarke var.yunnanensis A.C.Sm [SF, M], *Schizandra plena* A.C.Sm. [SF]; **Smilacaceae:** *Smilax cocculoides* Warb [SF, M], *Smilax corbularia* Kunth [E, M], *Smilax* *hypoglauca* Benth.[E, SF, M], *Smilax indica* Vitm.[SF], *Smilax microphylla* C.H. Wright [E]; **Sterculiaceae:** *Byttneria grandifolia* DC. [SF]; **Vitaceae:** *Ampelocalmus delavayana* Planch. ex Fr.[M, SF], *Cayratia mekongensis* C.Y.Wu ex W.T. Wang [M], *Cayratia tenuifolia* (Wang et Arm.) Gagnap [SF], *Cissus jarana* DC. [E, SF], *Cissus kerrii* Craib [E, SF], *Cissus subtetragona* DC. [SF], *Tetrastigma obovatum* (Wall.) planch. [M], *Tetrastigma planicaulum* (Hook.f.) Gagnep. [M].

Chapter 3

Photosynthetic differences during seasonal drought give lianas a competitive advantage over trees in a tropical seasonal rainforest



Cai ZQ, Schnitzer SA, Bongers F

Abstract

Lianas are an important component of tropical forests. The abundance of lianas throughout the tropics increases with decreasing rainfall and increasing seasonality, a pattern that differs from nearly all other plant types. In this study, we test the hypothesis that lianas are physiologically more robust than trees during the dry season, thus explaining their relatively high abundance in seasonal forests. To test this hypothesis, we compared a range of leaf-level physiological attributes of 18 co-occurring liana and 16 tree species during the wet and dry seasons in a tropical seasonal rainforest in Xishuangbanna, SW China. We measured the following physiological attributes: net photosynthetic rate (A), dark respiration (Rd), chlorophyll content (Chl$_{\mathrm{mass}}$), carotenoid to chlorophyll ratio (Car/Chl), nitrogen content (N_{mass}), phosphorus content (P_{mass}), photosynthetic N, P-use efficiency (PNUE, PPUE), and δ^{13}C. During the wet season, lianas had significantly higher N_{mass} and δ^{13}C values, and lower LMA than trees, indicating that lianas have higher water-use efficiency (WUE) and lower structural investments. However, liana and tree species did not differ significantly in the other leaf traits (A_{area}, Rd_{area}, Chl$_{\mathrm{mass}}$, Car/Chl, P_{mass}, PNUE and PPUE). Between wet and dry season, the average seasonal variation in A_{area} and N_{mass} was far lower in lianas than in trees, suggesting that lianas fix more carbon and suffer less from water stress during the dry season compared to the wet season. Average A_{area} decreased by 30.1% in tree species, compared with only 12.8 % in liana species. N_{mass}, P_{mass} and PNUE changed little for lianas, while these factors decreased strongly for tree species. The δ^{13}C, LMA, Car/Chl, and PPUE values for both lianas and trees did not vary significantly with the season. Our results support the hypothesis that the ability of lianas to fix carbon during seasonal drought may contribute to the competitive advantage of lianas over trees in the seasonal tropical forests. Lianas also had lower structural costs (LMA) and higher rates of resource use (WUE in both seasons, A and PNUE in the dry season) than did trees. Taken together, our results thus support the dry season growth advantage hypothesis for lianas.

Key words: photosynthesis, nitrogen-use efficiency, water-use efficiency, seasonal changes

Introduction

The seasonal change in rainfall is arguably the most important factor responsible for the distribution of plant species throughout the tropics. While some tropical rain forests (sensu Holdridge 1971) have little change in the amount of mean monthly precipitation during the year, rainfall in the majority of tropical forest is seasonal, with greatly reduced precipitation during one or two dry seasons per year (Walsh and Newbery 1999). Plant density, diversity, and the distribution of species and functional groups vary strongly with the length of the dry season in tropical forests (Swaine 1996, Bongers et al. 1999). During the dry season, plants are exposed to considerable drought stress, indicated by low leaf water potentials and wilting (Veenendaal et al. 1995, Engelbrecht and Kursar 2003), and drought has been associated with increased mortality and decreased growth in seedling and adult tropical plants (Veenendaal et al. 1995, Condit et al. 1995, Engelbrecht et al. 2005). Many plant species in tropical seasonal forests have special adaptations to deal with periods of extended drought, such as a decline in net assimilation rate and stomatal conductance, or a drop of all leaves (Abrams and Mostoller 1995, Holbrook et al. 1995, Borchert 1998, Eamus et al. 2001).

Most organisms decrease in abundance with decreasing mean annual precipitation and increasing seasonality (Gentry 1982). One plant group that is an exception to this general rule, however, is the lianas (woody vines), which increase in abundance with increasing seasonality (Schnitzer 2005). Lianas are a key component of tropical forests and can influence a number of important forest processes, such as competition among species for both above- and below-ground resources, substantially decreasing the growth rates and fecundity of adult trees, and retarding regeneration of tree species (Putz and Mooney 1991, Schnitzer and Bongers 2002, Schnitzer et al. 2005). Schnitzer (2005) proposed that lianas exhibit their distinct geographic pattern because of their unique ability to grow well during seasonal drought, while their competitors, particularly trees, are mostly dormant. This dry season growth advantage may allow lianas to increase in abundance in seasonal forests, whereas this competitive advantage is absent in aseasonal forests (Schnitzer 2005). Lianas may be increasing in abundance in neotropical forests (Phillips et al. 2002, Wright et al. 2004), possibly as a result of forest fragmentation and of climate change. Understanding the mechanisms responsible for the abundance of lianas, compared to trees, is needed to understand their relative distributions and predict possible changes therein.

There is evidence to support the dry season growth advantage hypothesis. For example, in the seasonally deciduous forest of BCI in Panama, Schnitzer (2005) measured the height growth of liana and tree species throughout consecutive dry and wet seasons and reported that lianas grow approximately 7-times more than trees during the dry season, but only 2-times more than trees during the wet season, suggesting that lianas suffer relatively little water stress during seasonal drought. This suggestion is consistent with observations that many liana species retain, and even produce, new leaves during severe seasonal droughts, whereas many trees do not (Putz and Windsor 1987, Opler et al. 1991, Kalácska et al. 2005). Several characteristics common to lianas may enable them to compete particularly well during seasonal droughts, including: deep and well developed root systems (Tyree and Ewers 1996, Restom and Nepstad 2004), good stomatal control and high water-use efficiency (Andrade et al. 2005), low leaf construction costs per unit photosynthetic area (Castellanos 1991), rapid vegetative growth rates (Schnitzer *et al*. 2004, 2005, Schnitzer 2005), and high potential for acclimation to changes in light intensity (Avalos and Mulkey 1999, Salzer et al. 2006) and elevated atmospheric CO_2 concentrations (Granados and Korner 2002, Zotz et al. 2006). Currently, evidence supporting the dry season growth advantage hypothesis is mostly anecdotal and, to date, there have been no systematic tests of this hypothesis.

In this study, we use detailed physiological measurements of lianas and trees to test the dry season growth advantage hypothesis. We compare seasonal variability in leaf attributes and physiology among co-occurring liana and tree species throughout wet and dry seasons in a tropical seasonal rainforest in Xishuangbanna, SW China, to determine whether lianas are less stressed and can fix more carbon, and thus grow more, during seasonal droughts than can trees. Specifically, we address two interrelated questions: 1) To what extent do leaf attributes vary between co-occurring lianas and trees during wet and dry seasons? 2) Do differences in leaf physiological characteristics give lianas an advantage for growth over trees during the dry season? We predicted that lianas should perform better than trees during the dry season by having higher carbon fixation and resources (nutrition and water) use efficiency. During the wet season, however, lianas and trees should be more similar to each other in each of these attributes.

Materials and methods

Study site

The study was conducted in a tropical seasonal rainforest in Xishuangbanna (21°09′-22°33′ N, 99°58′-101°50′ E), SW China. This region has a rich tropical flora in the lowland area, even though it is far from the Equator (Zhu et al. 2006). The natural forest vegetation in the Xishungbanna area consists of mainly tropical seasonal forest, evergreen broad-leaved forest, montane forest and limestone monsoon forest. Combined, these difference habitat types contribute to the high biodiversity of the region (Zhu et al. 2006). The tropical forest of Xishuangbanna is considered to be the northern edge of tropical SE Asia and it differs from typical lowland rain forests in equatorial areas in having fewer epiphytes and megaphanerophytes. However, there is a relatively high abundance and diversity of lianas in this region, especially in the seasonal rainforest (Cai et al. submitted), which is the most common and dominant forest type of the region.

Lying in the East Asian Monsoon Region, Xishuangbanna is dominated by warm-wet air masses from the Indian Ocean in summer and continental air masses from the sub-tropical regions in winter, resulting in a highly seasonal environment. The seasonal forest that we worked in receives approximately 1550 mm of rainfall annually, of which 85% occurs in the six-month rainy season (May-October). During the study period rainfall was clearly seasonal, with mean monthly rainfall varying from 3 mm in February to 297 mm in August 2004. Mean monthly temperature in this area is 21.4 ºC and ranges from around 14.5 – 25.7 ºC (Fig. 1a). Surface soil (0 – 20 cm) was drier in the dry season compared to the wet season, while the deep soil water content (100 cm) was similar (Fig. 1 b).

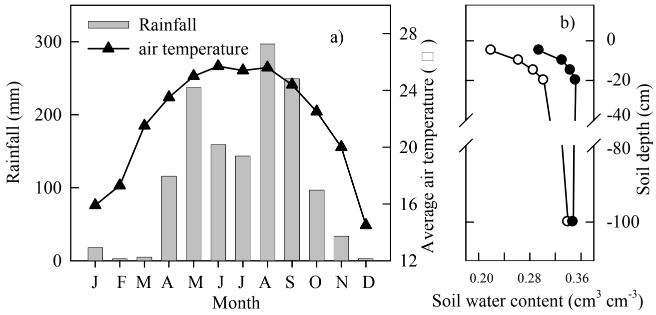


Figure 1 Seasonal changes in monthly rainfall and average air temperature (a) and volumetric water content (b) in 2004 (○, dry season in March, ●, wet season in September). Weather data from the nearby Meteorological Station of Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences.

Study species and measurements

We measured 18 liana species and 16 tree species, all evergreen (Table 1). The trees were approximately 20 m tall. Leaves of liana species were collected on the canopy of trees. To determine photosynthetic parameters, including gas exchange and dark respiration, we collected branches from the upper canopy using a tree pruner attached to a long handle. All branches were collected between 9:30 and 11:00 am, when maximum photosynthetic rates occurred. Within 10 minutes of collection, we cut the branches under water, immersed the stems in deionized water to maintain the xylem water column, and measured photosynthesis. Photosynthetic parameters were measured on the youngest, fully expanded sun canopy leaves. We were able to distinguish sun leaves from subcanopy leaves because sun leaves are thicker and lighter in color. We measured the rate of CO_2 assimilation per unit area, A_{area}, under a light-saturating irradiance (Photon flux density > 1500 μmol m^{-2} s^{-1}, provided by an internal red/blue LED light source, LI6400-02B) under ambient CO_2 concentrations with a portable photosynthetic system (LiCor Li-6400, Lincoln, NE, USA). We recorded dark respiration, Rd, in the leaf chamber after a few minutes, when stable readings were obtained. During the wet season (in September), we measured fully expanded leaves that had recently matured. During the dry season (in March and April), we selected the healthiest leaves available. We measured 4-6 leaves from individuals with comparable diameters at breast height (dbh) per species.

Following field measurements, we immediately placed each leaf in a sealed plastic bag containing damp paper towel. In the lab, we extracted the chlorophyll and total carotenoid contents from the leaves with 80% (v/v) acetone in the dark and measured pigments (Lichtenthaler and Wellburn 1983) with a spectrophotometer (UV-B 2501, Shimadzu, Japan). We measured the area of each leaf with a leaf area meter (Li-3000A, Li-Cor, NE, USA). Leaf thickness was measured from the sections near the midrib using a light microscope that was equipped with an ocular micrometer, leaf thickness was only measured in the wet season.

To determine leaf dry mass, we oven-dried the leaves for a minimum of 48 h at 70 ºC and then weighed the leaves and calculated the leaf mass ratio (LMA, cm^2 g^{-1}). Leaf density (D, g cm^{-3}) was calculated by dividing LMA by leaf thickness. For each plant, we ground three to five leaves to a fine powder for elemental analyses in the Biogeochemical Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences. The total N concentration (N_{mass}) was measured by semi-micro

Kjeldahl, using a wet digestion procedure. Phosphorus concentration was determined from atomic absorption spectrum-photometry (AAS, Type 932GBC, Scientific Equipment Pty Ltd, Australia). Instantaneous photosynthetic nitrogen- and phosphorus-use efficiency (PNUE, µmolC mol^{-1}N s^{-1}, PPUE, mmolC mol^{-1}P s^{-1}) was calculated as A_{mass} per leaf N_{mass} and P_{mass}, respectively.

We measured the δ^{13}C (in parts per thousand) of all species on 2 mg ground subsamples of leaves using a Thermo Finnigan MAT stable isotope mass spectrometer (Bremen, German) at the Stable Isotope Laboratory in Institute of Botany, the Chinese Academy of Sciences. δ^{13}C provides an integrated estimate of the ratio of photosynthesis to conductance, and therefore can be used as an index of intrinsic water-use efficiency (Farquhar and Richards 1984).

Statistical analysis

We compared the means of the various leaf traits and species groups (growth forms, liana and tree) using *t*-test for two-group comparisons, or by ANOVA followed by multiple comparison tests where more than two groups were compared. We $\log_{10}$-transformed all leaf traits before analyses, to increase normality and homogeneity of variance when necessary to satisfy the assumption of ANOVA. Correlations amongst leaf traits were analyzed with a Pearson's correlation, all reported correlations were significant at a *P* level of 0.05. All statistical analyses were carried out using SPSS version 11.0 (SPSS, Chicago, IL).

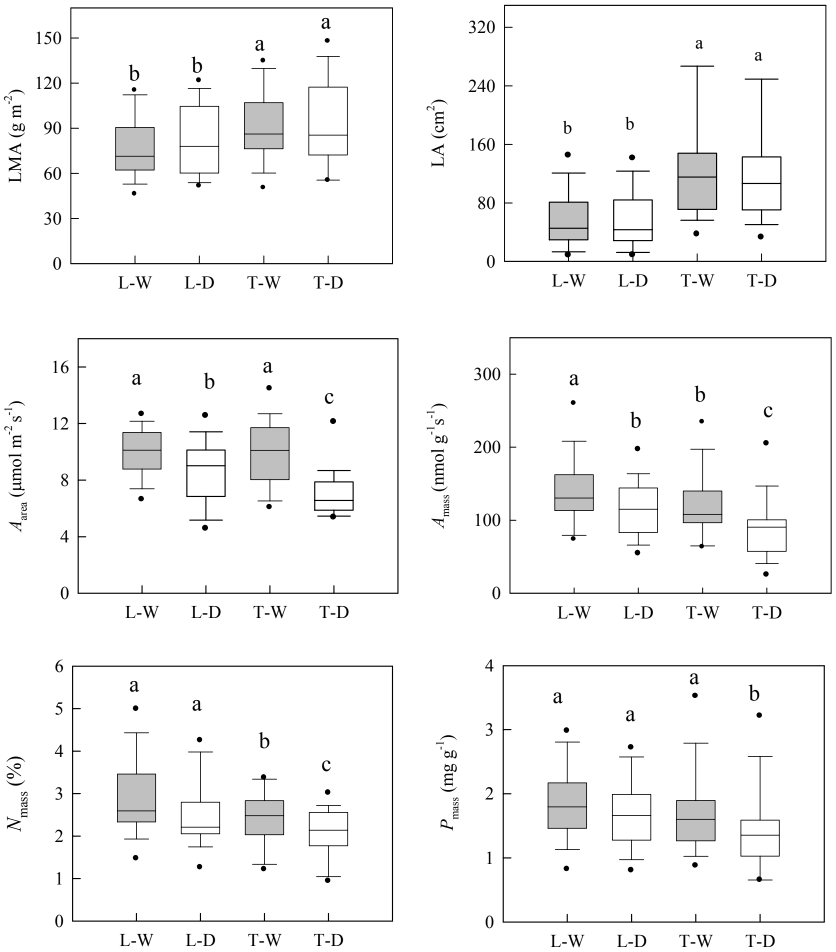
Results

Leaf traits in the wet season

During the wet season, species mean LMA varied from 46 to 134.6 g m^{-2}, with the smallest value for the liana *Byttneria aspera* and the largest one for the tree *Combretum latifolium*. A_{area} ranged from 6.05 to 17.5 µmol m^{-2} s^{-1} and A_{mass} from 65 to 259.6 nmol g^{-1} s^{-1}, with the trees *Lepianthes senegalensis* having the lowest and *Ficus cyrtophylla* having the highest value (Table 1). The tree *Syzygium latilimbum* had the lowest N_{mass} (1.21 mg g^{-1}) and the liana *Iodes covalis* had the highest (4.99 mg g^{-1}). Variation in Car/Chl was small, while the differences in values of PNUE were quite large, ranging from 26.2 to 116.9 µmolC mol^{-1} N

s^{-1}. The $\delta^{13}C$ values ranged from -28.65‰ to -34.15‰. The N:P ratio in mature leaves of lianas and trees ranged from 7.0 to 27.4, the average value (15.3) indicated that neither N or P was limiting at the community-level in this forest (Sterner and Elser, 2002).

In the wet season, lianas and trees had a similar mean *A* and R*d* based on area, P_{mass}, N:P ratios, PNUE, PPUE, Chl_{mass}, Car/Chl and *A*/Chl ratios (*t*-tests, all comparisons, $P > 0.05$), while lianas had higher $\delta^{13}C$ ($P = 0.036$), leaf density ($P = 0.029$), A_{mass} ($P = 0.022$), N_{mass} ($P = 0.044$), lower LMA ($P = 0.023$) and smaller leaf area ($P < 0.001$) compared to trees (Table 1, Fig. 2).



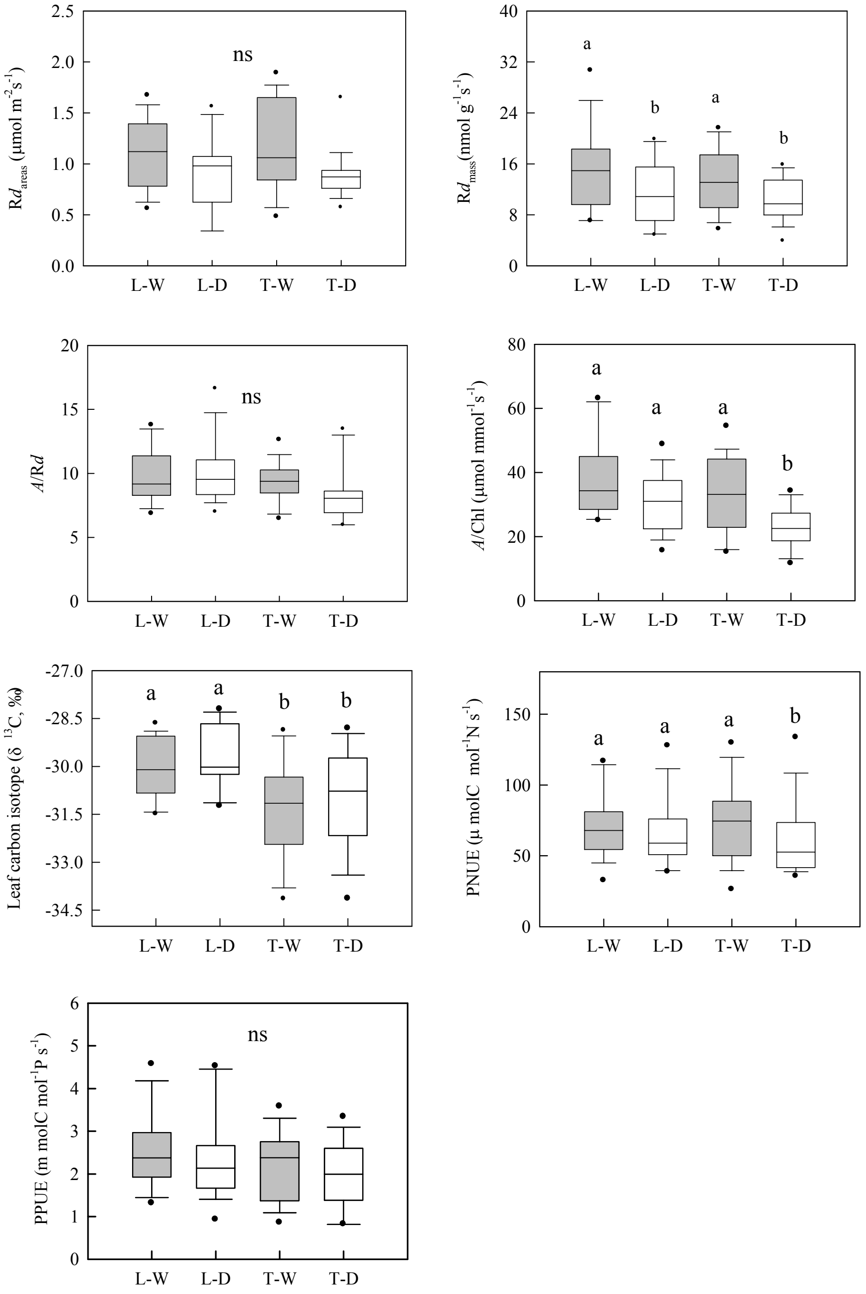

Rd_areas (µmol m-2 s-1)
2.5
2.0
1.5
1.0
0.5
0.0
ns
L-W
L-D
T-W
T-D
Rd_mass (nmol g-1 s-1)
40
32
24
16
8
0
a
b
a
b
L-W
L-D
T-W
T-D
A/Rd
20
15
10
5
0
ns
L-W
L-D
T-W
T-D
A/Chl (µmol mmol-1 s-1)
80
60
40
20
0
a
a
a
b
L-W
L-D
T-W
T-D
Leaf carbon isotope (δ 13C, ‰)
-27.0
-28.5
-30.0
-31.5
-33.0
-34.5
a
a
b
b
L-W
L-D
T-W
T-D
PNUE (µ molC mol-1N s-1)
150
100
50
0
a
a
a
b
L-W
L-D
T-W
T-D
PPUE (m molC mol-1P s-1)
6
5
4
3
2
1
0
ns
L-W
L-D
T-W
T-D

Figure 2 Box plots of leaf attributes of woody species in the seasonally rainforest. L and T indicate liana and tree species, and –W and –D represent wet and dry season, respectively. Boxes indicate median, 25th and 75th percentile values, with error bars showed 10th and 90th percentile values and solid circles indicating outliers. For each leaf variable groups with the different letter were significantly different ($P \leq 0.05$). ns, no significant ($P > 0.05$). Traits abbreviations are defined in Table 1.

Seasonal variation in leaf traits

For both lianas and trees, leaf area, $\mathrm{Chl}_{\mathrm{mass}}$, Car/Chl ratio, $\delta^{13}\mathrm{C}$ values, PPUE, and LMA remained relatively unchanged between the wet and the dry season (*t*-tests, all comparisons, $P > 0.05$). However, from wet to dry season N_{mass} ($P = 0.006$), P_{mass} ($P = 0.049$), and PNUE ($P = 0.015$) decreased significantly for tree species, while they did not change greatly for lianas (all comparisons, $P > 0.05$, Fig. 2). The similar A_{area} of liana and tree species in the wet season was not maintained throughout the dry season. Although there was a large variation in A_{area} in the dry season (4.56 to 12.53 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$), the mean A_{area} of the liana species maintained a relatively high level (8.7 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$, 87.2% of that of wet season). The mean dry season A_{area} of tree species (6.1 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$), on the other hand, declined to 60.9% of that of the wet season, and was 20.1% lower than that of liana species in the dry season. These findings suggest that lianas are able to maintain a relatively high carbon gain during the dry season, while carbon gain of trees decreased significantly.

Relationhsips between LMA and A_{mass}, WUE and PNUE

LMA was strongly negatively correlated with A_{mass} for lianas and trees (in the wet season, lianas: $A_{\mathrm{mass}} = -1.65\ \mathrm{LMA} + 264.7$, $r^2 = 0.59$, $P < 0.001$, Trees: $A_{\mathrm{mass}} = -0.93\ \mathrm{LMA} + 205.2$, $r^2 = 0.24$, $P < 0.05$, in the dry season, lianas: $A_{\mathrm{mass}} = -0.98\ \mathrm{LMA} + 192.2$, $r^2 = 0.37$, $P < 0.05$), except for trees in the dry season ($A_{\mathrm{mass}} = -0.27\ \mathrm{LMA} + 111.2$, $r^2 = 0.24$, $P = 0.06$) (Fig. 3).

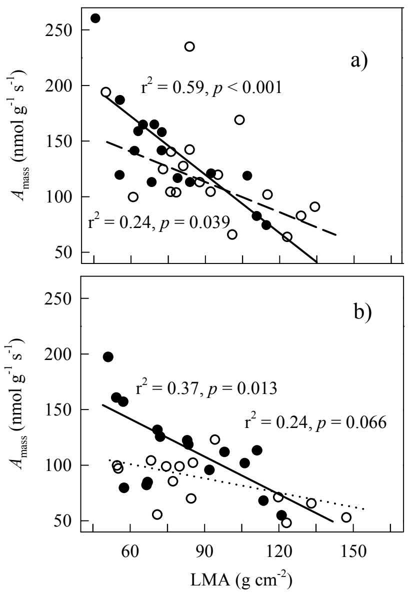


Figure 3 Relationships between LMA and photosynthetic rates (A_{mass}) of lianas (black circles, unbroken lines) and trees (open circles, broken lines) in the wet (a) and dry (b) seasons.

Significant negative relationship between WUE (indicated by δ^{13}C values) and PNUE was found in trees ($r^2 = 0.16$, $P = 0.024$, n = 32) in two seasons, but not in lianas ($r^2 = 0.01$, $P > 0.05$, n = 34) (Fig. 4).

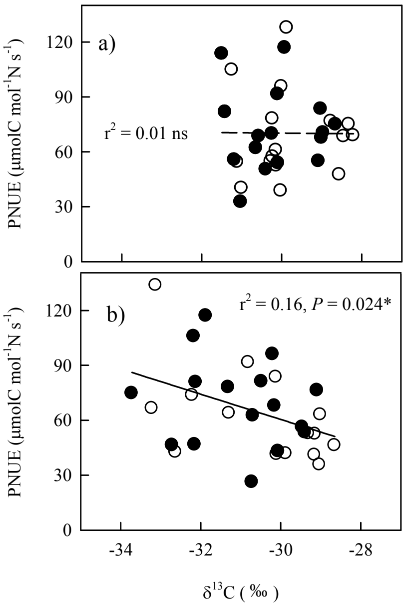


Figure 4 Relationships between carbon isotope ratio (δ^{13}C) and photosynthetic N-use efficiency (PNUE) of lianas (a) and trees (b) in the wet season (black circles) and dry seasons (open circles).

Discussion

Testing the dry season growth advantage hypothesis

Our findings support the hypothesis that the ability of lianas to grow during seasonal droughts gives them a competitive advantage in seasonal forests, which competing trees may lack. This competitive advantage may explain the global pattern of relatively high liana abundance in seasonal dry forests and low abundance in aseasonal wet forests (Schnitzer 2005). While A_{area} and N_{mass} for lianas and trees in this study fell within a wide range of values that were consistent with other studies (Reich et al. 1997, Wright et al. 2004), lianas exhibited less seasonal variation in A_{area} and had relatively high photosynthetic activity during seasonal drought compared to trees (Table 1, Fig. 2), suggesting that they are less sensitive to drought than are trees. The relatively high photosynthetic capacity of lianas over the dry season enabled them to fix more carbon over this period, and thus have a larger pool of available carbon to allocate to growth and reproduction. Indeed, in the seasonal moist forest of Barro Colorado Island (BCI), Panama, lianas grew proportionally more than trees during the dry season compared to the wet season (Schnitzer 2005). Further support comes from Zotz and Winter (1996), who reported that the tropical liana *Uncaria tomentosa* on BCI maintained a similar photosynthetic rate during the wet and dry seasons, suggesting that this liana did not suffer from seasonal drought (see also Schnitzer 2005 and citations therein). We found that lianas appear to better reduce water stress through a high WUE in our study, as indicated by their significantly higher δ^{13}C values than trees in both seasons (Fig. 2). This is in contrast with Holtum and Winter (2005) who found that the δ^{13}C values of sun-exposed leaves were similar between lianas and adjacent trees (only 5 liana species however) with remarkably uniform values (varying by less than 1‰). A higher leaf level WUE is expected to be the result of lower water availability at leaf level. This contrasts with the greater hydraulic capacity of vessels and deeper roots (Tyree and Ewers 1996, Andrade et al. 2005) expected to enable lianas to develop higher stomatal conductance and therefore sustain higher transpiration rates (Restom and Nepstad 2001). Maybe here the relatively high leaf area per stem area of lianas (Putz 1983, Gerwing and Farias 2000) counterbalances the higher water supply, as suggested by Santiago and Wright (2006).

The high values of WUE in lianas, in conjunction with high PNUE during the dry season, suggest that lianas can assimilate carbon at a relatively lower nitrogen and water investment than trees, thus allowing lianas to compete effectively with trees during seasonal droughts. The relatively high assimilation rate of lianas in the dry season may be a particularly important factor for liana growth and competitive ability, supporting the dry season growth advantage hypothesis for lianas.

Rates of resource capture and cost of resource capture: are lianas better than trees?

Patterns of photosynthetic differences between lianas and trees are not uniform. Santiago and Wright (2006), for instance, found that lianas have lower A_{area} levels than trees. Others found that these groups did not differ (Castellanos 1991, Zotz and Winter 1996), although lianas have larger vessels and hydraulic conductivity compared to trees. These last results were confirmed in our study: lianas had a similar A, R_d based on leaf area, and PNUE and PPUE to trees in the wet season. Lianas had higher N_{mass} and lower LMA than trees (Table 1), which is consistent with the result from previous studies (Kazda and Salzer 2000, Salzer et al. 2006), indicating lianas' dependency on high soil nutrient availability (Balfour and

Bond 1993). The differences in these leaf traits between lianas and trees are likely to have important implications for nutrient cycling in tropical forests if lianas increase substantially in abundance (Phillips et al. 2002, Wright et al. 2004), as high N_{mass} and low LMA is indicative of a higher leaf turnover and a higher decomposition rate (Diaz et al. 2004). The similar A/Chl and Car/Chl ratios for lianas and trees indicate that in the high-light canopy conditions, lianas and trees invest a similar level of their resources towards carbon assimilation and light harvesting, and had a similar ability to dissipate excessive light energy because xanthophylls, which are involved in light energy dissipation, is one of the components of carotenoids (Demmig-Adams and Adams 1992). In the dry season, the high δ^{13}C and PNUE in lianas (Fig. 2) indicate lianas had high water and nitrogen use efficiency, suggesting that lianas are able to capture resources more efficiently than trees.

Typically, plants with a high LMA have been found to contain more lignin (Poorter and Villar 1998), and their leaves were thus energetically expensive. The relatively low LMA of liana species may indicate that these species use less construction expenses to attain the same capacity for carbon assimilation. A_{mass} was strongly negatively related to LMA for both lianas and trees (except for trees in the dry season) (Fig. 3), suggesting that at higher LMA more biomass is allocated to structural components of the leaf rather than to metabolic components (Field and Mooney 1986). This change with LMA is stronger for lianas than trees. Another indicator of the carbon costs of resource gain is the relationship between A_{mass} and Rd_{mass}, giving a measurement of the metabolic efficiency of leaves. Across all ranges of Rd_{mass}, the A_{mass} values of liana species were similar to those of tree species. Therefore, the respiratory trade-off to net photosynthetic rates is similar between lianas and trees. The difference between lianas and trees thus lies in the leaf structural investment (LMA): lianas have lower LMA and higher carbon gain per unit leaf area.

Trade-off between water- and nitrogen- use efficiency and its ecological significance

Water and N are two of the most important resources for plant. Prolonged drought severely restricts the mobility of N through dehydrated soil and thus a co-occurrence of water deficits and N limitations is common in seasonal forests. However, an increase in the efficiency in the use of one resource sometimes leads to a reduction in the efficiency with which another is utilized (Hirose and Bazzaz 1998). Plants typically exhibit a trade-off between WUE and PNUE (Field and Mooney 1986). At low water availability in the leaves their stomata close leading to lower water loss through transpiration and thus higher WUE.

However, as a result of lower CO_2 levels photosynthesis decreases as well while N concentration remains constant, hence a lower PNUE. In our study this WUE- PNUE relationship was rather variable, and a cross species trade-off was only significant for trees, not for lianas (Fig. 4). The trade-off, however, may be obscured if high WUE was obtained without reduced stomatal conductance (g_s, Hikosaka et al. 1998, Van den Boogaard and Villar 1998, McDowell 2002). Although we did not collect data on g_s in this study, other studies have reported that, for lianas, g_s remains relatively high throughout periods of seasonal drought (Castellanos 1991, Zotz and Winter 1996). Recently, Andrade and co-workers demonstrated that lianas remained hydraulically active even during severe seasonal droughts (Andrade et al. 2005). That lianas are able to maintain g_s throughout drought may relate to their extremely efficient root and vascular systems resulting in their ability to tap water and nutrients deeper belowground than trees (Tyree and Ewers 1996, Restom and Nepstad 2004, Andrade et al. 2005). In addition, lianas had higher leaf density than did trees (Table 1), which generally results in a higher leaf elastic modulus, allowing lower leaf water potentials and thus tolerate water limitation (Niinemets 2001). Trees achieved higher PNUE at the expense of decreasing WUE, whereas lianas could simultaneously maintain relative higher WUE and PNUE (Fig. 2, 4). This interspecific difference in the trade-off of plasticity between PNUE and WUE may partially explain the regional distribution of these two species in relation to moisture and nutrient availability (Reich et al. 2003).

In conclusion, our results provide some eco-physiological evidences as to why lianas are abundant in the seasonally rainforest. From the physiological characteristics of leaf-level, lianas tended to have more carbon fixation and higher resource use efficiency (water and nitrogen) in the dry season with lower structure costs compared to trees, thus confirming the hypothesis that differences in photosynthetic attributes may contribute to the competitive advantage of lianas over trees.

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Table 1 Species means for leaf traits of woody species measured in the wet season. LA, leaf area (cm^2), LMA, leaf mass ratio (g cm^{-2}), *D*, leaf density (g cm^{-3}), A_{area}, area-based CO$_2$ assimilation (μmolmol m^{-2} s^{-1}), A_{mass}, mass-based CO$_2$ assimilation (nmol g^{-1} s^{-1}), Rd_{area}, area-based dark respiration (μmol m^{-2} s^{-1}), Rd_{mass}, mass-based dark respiration(nmol g^{-1} s^{-1}), N_{mass}, nitrogen per mass (%), P_{mass}, phosphorus per mass (mg g^{-1}), Chl$_{mass}$, mass-based chlorophyll (mmol kg^{-1}), Car/Chl, cartenoid to chlorophyll ratio, δ^{13}C, carbon isotope (‰), PNUE, photosynthetic N-use efficiency (μmolC mol^{-1}N s^{-1}), PPUE, photosynthetic P-use efficiency (mmolC mol^{-1}P s^{-1}). Log$_{10}$ transformations were used for comparisons of all parameters except Car/Chl. *, $P < 0.05$, ns, no significant ($P > 0.05$).

Species	LA	LMA	*D*	A_{area}	A_{mass}	Rd_{area}	Rd_{mass}	A/R$_d$	N_{mass}	P_{mass}	N:P	Chl$_{mass}$	A/Chl	Car/Chl	δ^{13}C	PNUE	PPUE
Liana species																	
Iodes covalis	144.5	79.2	0.31	9.17	115.8	1.13	14.3	8.12	4.99	2.73	18.2	3.8	30.1	0.23	-31.02	32.5	1.31
Fissistigma polyanthoides	77.5	69.8	0.54	11.45	164	1.67	23.9	6.86	4.19	2.38	17.6	3.5	46.5	0.18	-29.08	54.8	2.13
Bauhinia glauca	15	55.8	—	6.62	118.6	0.67	12	9.87	2.43	1.76	13.8	3.5	33.4	0.22	-30.57	68.3	2.09
Zizyphus attopensis	22.1	65.2	0.51	10.69	163.9	1.01	15.5	10.58	2.51	2.15	11.7	4.1	40.2	0.22	-30.1	91.3	2.37
Gnatum parvifolium	110.5	72.7	0.58	10.23	140.7	1.14	15.7	8.97	3.55	1.54	23.1	4	35.2	0.25	-31.18	55.5	2.84
Tetrastigma Planicaulum	58.5	72.8	0.28	11.45	157.2	1.34	18.4	8.54	2.65	1.97	13.4	2.6	61.6	0.23	-29.02	83.2	2.47
Byttneria aspera	81.8	46	0.22	11.95	259.6	1.41	30.6	8.48	3.12	2.18	14.3	4.1	63.1	0.22	-29.92	116.6	3.70
Uncaria macrophylla	101.4	111.1	0.63	9.08	81.7	0.78	7.0	11.64	2.13	1.31	16.2	2.7	30.8	0.28	-30.09	53.7	1.93
Bauhinia yunnanensis	8.1	61.8	0.39	8.67	140.4	0.65	10.5	13.34	3.61	2.98	12.1	5	27.9	0.2	—	54.4	1.46
Tinomiscium tokinensis	228	59.7	0.33	9.95	166.6	0.87	14.6	11.43	2.86	2.04	14.0	2.6	64.5	0.23	-31.41	81.6	2.53
Ficus subulata	71.1	68.7	0.74	7.72	112.3	0.56	8.2	13.78	2.54	1.46	17.4	4.2	27	0.23	-30.64	61.9	2.38
Uncaria rhynchophylla	42.8	115	0.3	8.46	73.5	0.82	7.1	10.31	1.47	0.82	17.9	2.9	25.6	0.24	-28.96	70.3	2.79
Ventilago calyculata	47.8	63.3	0.49	10	158	1.14	18	8.77	3.17	1.46	21.7	4.3	36.6	0.23	-30.24	69.7	3.35
Millettia dielsiana	41.1	63.6	0.54	10.45	164.3	1.65	25.9	6.33	3.37	1.23	27.4	5.6	29.1	0.21	-29.46	68.2	4.14
Fissistigma polyanthum	28.5	55.9	0.96	10.4	186.1	1.11	19.9	9.37	2.3	1.26	18.2	5.8	32.1	0.2	-31.49	113.4	4.57
Millettia oosperma	37	107.3	0.81	12.65	117.9	1.54	14.3	8.21	2.45	1.62	15.1	4.7	25	0.24	-29	67.5	2.26

Celastrus paniculatus	33	92.6	0.53	11.13	120.1	1.5	16.2	7.42	2.25	2.07	10.8	2.3	52.1	0.24	-28.65	74.8	1.80
Securidaca inappendiculata	32.3	84.2	0.32	9.44	112.2	0.78	9.3	12.11	3.13	1.83	17.1	2.8	40.2	0.25	-30.39	50.3	1.90
Tree species																	
Ficus cyrtophylla	71.5	50.2	0.46	9.69	193.1	0.89	17.7	10.89	3.34	1.88	17.8	4.3	45.2	0.24	-30.48	81	3.19
Combretum latifolium	135.9	134.6	0.29	12.12	90.1	1.76	13.1	6.89	1.65	1.04	15.9	3.7	24.1	0.23	-29.09	76.2	2.68
Ficus hirta	149.2	84	—	11.88	141.4	1.18	14	10.06	3.17	3.52	9.0	3.1	45.4	0.24	-30.69	62.4	1.25
Baccaurea ramiflora	116	88.1	—	9.87	112.1	1.06	12	9.31	1.95	1.42	13.7	2.9	38.3	0.22	-32.12	80.7	2.45
Carallia lanceaefolia	69.2	101.2	0.49	6.58	65	0.58	5.7	11.34	2.12	1.5	14.1	2.4	27.5	0.25	-32.06	43	1.34
Ficus auriculata	516.9	76.3	0.51	7.89	103.4	0.72	9.4	10.96	1.37	1.96	7.0	2.4	43.1	0.2	-32.17	105.8	1.64
Lepianthes senegalensis	107.3	61.2	0.41	6.05	98.8	0.48	7.8	12.6	2.97	1.28	23.1	5.5	17.9	0.23	-34.15	46.6	2.39
Barringtonia macrostachya	238.9	129	0.33	10.56	81.9	1.06	8.2	9.96	2.48	1.75	14.2	5.4	15.1	0.24	-32.71	46.3	1.45
Shorea chinensis	92.7	73.3	0.46	9.07	123.7	0.96	13.1	9.45	2.32	1.62	14.3	4.8	25.6	0.24	-33.72	74.6	2.37
Ficus callosa	191.5	104.1	0.44	17.5	168.1	1.89	18.2	9.26	2.45	1.88	13.1	3.7	45.5	0.25	-30.2	95.9	2.78
Castanopsis indica	136.9	95.5	0.53	11.34	118.8	1.65	17.3	6.87	2.14	1.21	17.6	3.6	33.1	0.21	-31.31	77.9	3.04
Mayodendron igneum	36.8	78.6	0.53	8.08	102.8	0.82	10.4	9.85	2.7	1.59	17.0	4.7	21.7	0.24	-29.39	53.3	2.00
Litsea panamonja	115.2	92.5	0.32	9.58	103.6	1.06	11.5	9.04	2.58	2.71	9.5	1.9	54.4	0.23	-30.46	56.1	1.19
Leea crispa	98.1	123.3	0.6	7.76	62.9	0.85	6.9	9.13	3.36	2.28	14.8	3.9	16.1	0.23	-30.72	26.2	0.86
Ficus superba	115.2	81.5	0.57	10.32	126.7	1.07	13.1	9.64	2.62	1.62	16.2	3.8	33.5	0.22	-31.15	67.8	2.43
Syzygium latilimbum	147.4	115.5	0.31	11.65	100.9	1.65	14.3	7.06	1.21	0.87	13.8	2.4	41.8	0.24	-28.87	116.9	3.58
	LA	LMA	D	A_{area}	A_{mass}	Rd_{area}	Rd_{mass}	A/Rd	N_{mass}	P_{mass}	N:P	Chl$_{\text{mass}}$	A/Chl	Car/Chl	δ^{13}C	PNUE	PPUE
Liana Means	**65.6**	**74.7**	**0.50**	**9.97**	**141.8**	**1.10**	**15.63**	**9.67**	**2.93**	**1.82**	**16.1**	**3.81**	**38.94**	**0.23**	**-30.07**	**70.4**	**2.6**
Tree Means	**146.2**	**93.1**	**0.45**	**10.00**	**112.1**	**1.11**	**12.04**	**9.52**	**2.40**	**1.76**	**14.4**	**3.66**	**33.02**	**0.23**	**-31.21**	**69.4**	**2.2**
Significant level	***	*	*	ns	*	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns	ns

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Chapter 4

Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China

Cai ZQ, Bongers F. *Journal of Tropical Ecology*, 2007, 23: 115-118.

Tropical montane rain forest is widely considered to be a highly threatened hotspot of global diversity (Brummitt and Nic Lughadha 2003), and one of the least understood humid tropical forest ecosystems in terms of nutrient cycling (Bruijnzeel and Proctor 1995). There is, therefore, an urgent need to improve our understanding of nutrient cycling processes in this ecosystem, including the absorption of nutrients (mainly N and P) from senescing leaves, which may be a key component of adaptive mechanisms that conserve limiting nutrients (Killingbeck 1996). Nutrients which are not resorbed, however, will be circulated through litterfall in the longer term (Aerts 1996). The degree of nutrient resorption affects litter quality, which consequently affects decomposition rates and soil nutrient availability (Aerts and Chapin 2000). The importance of resorption in nutrient conservation has led to general hypotheses that species adapted to nutrient-poor environments have high resorption efficiencies (Richardson et al. 2005), and that low leaf nutrient concentrations are associated with high resorption efficiencies within species (Aerts 1996, Kobe et al. 2005). Nutrient resorption has also been shown not to differ greatly between growth forms (e.g. shrubs, grasses, forbs and trees) (Aerts 1996). However, its relative importance among plant functional groups is still highly controversial (Richardson et al. 2005).

Lianas, which are important and less-understood components of tropical forests (Schnitzer and Bongers 2002), support substantially more leaves per unit basal area than do trees and can account for 20-40% of the canopy foliage (Gerwing and Farias 2000, Putz 1983), although their total biomass per unit area is usually only 2-4% of the woody biomass of trees. Moreover, the abundance of lianas and the amount of liana leaf litter as a proportion of total litter production has generally increased in tropical forests in recent years (Wright et al. 2004). The study presented here investigated changes in leaf size, leaf mass and foliar nutrient concentrations during leaf senescence in two groups of woody species (liana and tree) in a tropical montane rain forest in Xishuangbanna, south-west China. Our objectives were to assess leaf area shrinkage and mass loss during senescence in woody species, and to compare the nutrient conservation strategies of the two plant growth forms.

The study site was located in the undisturbed tropical montane rain forest in Mengsong (21^0 27’ N, 100^0 25’ E), Xishuangbanna, Yunnan. The climate of Xishuangbanna is dominated by the south-west monsoon with distinct wet (May-October) and dry (November-April) seasons. Mean annual rainfall was 1379 mm, of which about 80% occurs in the wet season. The potential natural vegetation at the Mongsong site is described in detail in Zhu et al. (2004). Species sampled (listed in Table 1, nomenclature follows Li et al. 1996) were the dominants in their respective growth-form groups, and all of them are evergreen species. Mature individuals of each species with comparable diameters at breast height (dbh) were marked. During the late wet season (September 2004), corresponding to the peak vegetative growth period, fully expanded sun canopy mature leaves were collected using a tree pruner attached to a long handle. In the dry season (March 2005) during the peak of leaf drop for individual species, similar collections were made for senescing leaves. Senesced leaves were collected directly off plants rather than from leaf litter, as we were concerned that decomposition of litter and leaching of leaf nutrients would lead to underestimates of nutrient concentrations in senesced leaves. These leaves are easily identified as they are generally different colour from live leaves (often red or yellow), and can be removed by a gentle flicking of the branch or leaf. Sets of 6-8 mature leaves and 6-8 senesced leaves of each species were collected and analyzed in order to assess changes in leaf area, mass and nutrient concentrations that occurred during the senescence process. The surface areas of mature and senesced leaves were determined using a leaf area meter (LI-3000, Li-Cor, USA). The samples were brought to the laboratory in polyethylene bags and oven-dried at 70°C to a constant weight, and leaf mass ratio (LMA) was then calculated for both mature and senesced leaves of each species. Changes in leaf size and leaf mass during senescence were determined for each species as the percentage differences in mean values between the mature and senesced leaves. Nutrient concentrations (N, P) of mature and senesced leaves were determined in the Biogeological Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Green and senesced leaves were analyzed by the semi-micro-Kjeldahl method (for N) and the plasma emission spectrometry technique (for P; Benton Jones et al. 1991). Since changes in leaf structure during senescence (due to losses of mass or shrinkage in leaf area) can heavily bias estimates of resorption efficiency (van Heerwaarden et al. 2003), leaf-level nutrient resorption efficiencies were calculated on a leaf unit basis (Gusewell 2005, van Heerwaarden et al. 2003). Leaf and litter nutrient concentrations were log-transformed and resorption data were square-root-transformed prior to statistical analyses to satisfy ANOVA assumptions. The relationships between mature leaf nutrient concentrations and nutrient resorption were evaluated by Spearman rank correlation analysis.

The mature leaves of the woody species investigated in the tropical montane rain forest differed considerably in size and LMA, which showed 6-fold and 3-fold variations, respectively (Table 1). Although the average leaf area and LMA in mature leaves were slightly larger in trees than in lianas, no significant differences were found between the two groups (two *t*-tests, each $P > 0.05$). During senescence, leaf shrinkage and leaf mass losses were higher in tree species than in liana species, but there were no significant differences between the two growth forms in these respects (two *t*-tests, each $P > 0.05$). Compared to previously published values for leaf litter in about 50 tropical forests (Proctor 1984) the P concentrations of the senesced leaves (mean = 0.62 mg g^{-1}) of woody plants in our study we examined were generally higher, but the N concentrations (mean = 14.9 mg g^{-1}) were similar.

There were no significant differences between the liana and tree groups in terms of the N concentrations of either their mature or senesced leaves ($P > 0.05$), but the liana species produced leaf litter with higher P concentrations than the tree species (one-way ANOVA, $F = 4.3$, $P = 0.048$). N:P ratios in mature leaves of lianas and trees ranged from 12.0 to 28.4 (average value 20.2), suggesting the presence of strong community-level P limitation in this forest (since N:P ratios > 16.0 indicate P limitation according to Tessier and Raynal 2003). High phosphorus resorption efficiency (PRE) should be favoured under P-limited conditions, and according to Killingbeck (1996), P resorption mechanisms in plants can be regarded as highly efficient if the P concentrations in their senesced leaves are <0.05 mg g^{-1}. More than half the species we examined met this criterion, in accordance with the hypothesis that high PRE are likely to be promoted by P-limited conditions. The nitrogen resorption efficiency (NRE), calculated on a leaf basis, varied from 19.4% to 71.0% (mean = 48.9%), and PRE varied from 41.0% to 79.0% (mean = 58.5%) for liana and tree species. Liana species showed similar NRE to tree species ($P > 0.05$), but had significantly lower PRE ($F = 5.1$, $P = 0.033$) than the tree species. In accordance with findings of other studies of nutrient relations during leaf senescence (Aerts 1996, Wright and Westoby 2003, Zotz 2004), nutrient resorption was not correlated with the nutrient status of green leaves prior to senescence ($r = 0.19$-0.37, $P > 0.05$) in either lianas or trees. These findings indicate that the efficiency of the resorption process is not determined by plant nitrogen status, as previously concluded in an analysis of data from temperate species (Aerts 1996) and demonstrated for various tropical forest tree species (Del Arco et al. 1991, Lal et al. 2001, Wright and Westoby 2003).

NRE and PRE were significantly positively correlated in both lianas ($r = 0.78$, $P = 0.003$) and trees ($r = 0.67$, $P = 0.008$). These correlations suggest that N resorption may be controlled by biochemical processes similar to those that control P resorption, in accordance with the results of studies of woody species in tropical forests (Lal et al. 2001) and wetland graminoids (Gusewell 2005). However, other studies have found no significant correlations between the N and P resorption efficiencies of certain plants (Chapin and Kedrowski 1983, Shaver and Melillo 1984). These discrepancies may be due, at least in part, to differences in the methodologies used by the different authors. Reductions in leaf mass during senescence could cause mass-based resorption efficiency to be underestimated by about 20% because the translocation of carbon is not taken into account, while area-based measures can underestimate resorption efficiency by about 10% (van Heerwaarden et al. 2003).

In conclusion, the relative leaf shrinkage and mass loss during senescence did not differ significantly, on average, between lianas and trees. The nutrient concentrations in the mature leaves and nitrogen resorption efficiency of the liana species were similar to those of the tree species, but the phosphorus concentrations of the liana litter were higher, and their phosphorus resorption efficiencies were lower, in the strongly P-limited montane rain forest we examined. Our results therefore provide clear evidence in favour of a novel mechanism whereby lianas may influence the ecosystems in which they occur. Through the production of nutrient-rich litter, they have the potential to greatly enhance the availability of nutrients within paths where they are abundant, and thus have significant possible effects on small-scale biodiversity.

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Table 1 Leaf area (LA, cm^2 per leaf), leaf mass ratio (LMA, g m^{-2} per leaf), leaf area shrinkage (LAS=1−senesced leaf area/mature leaf area, %), leaf mass loss (LML=1−senesced leaf mass/mature leaf mass, %), nutrient concentrations (mg g^{-1}) in mature and senesced leaves, and leaf resorption efficiency (%) of 26 woody species in the tropical montane forest. Resorption efficiency=1−nutrient concentration of senesced leaves/nutrient concentration of fresh leaves per leaf (Gusewell 2005, van Heerwaarden et al. 2003). NRE, nitrogen resorption efficiency; PRE, phosphorus resorption efficiency. Each leaf area and LMA value presented is a mean of 6-8 replicates. The nutrient concentration values are means of four replicates. Significance levels: ns, non-significant ($P > 0.05$); *, $P < 0.05$.

	Mature leaves					Senesced leaves							
Tree species	LA	LMA	N	P	N:P	LA	LMA	N	P	LAS	LML	NRE	PRE
Alangium chinensis	126.5	53.5	31.5	1.79	17.6	121.0	51.9	12.0	0.66	4.3	7.2	64.6	65.9
Alseodaphne petiolaris	163.1	128.3	17.8	0.77	23.1	149.8	95.5	7.4	0.36	8.1	31.6	71.5	68.0
Calophyllum polyanthum	27.2	177.9	16.8	0.84	20.0	26.5	153.8	16.0	0.47	2.4	15.7	19.4	53.1
Cryptocarya densiflora	85.2	187.9	21.0	0.88	23.9	79.7	172.5	18.1	0.35	6.5	14.2	25.9	66.2
Cyclobalanopsis sp.	25.9	129.4	17.1	0.72	23.8	23.7	118.8	13.3	0.35	8.8	16.3	34.9	59.1
Diospyros kerrii	86.1	190.0	18.4	0.78	23.8	85.3	178.6	7.8	0.35	0.9	6.9	60.4	57.8
Elaeocarpus sylvestris	98.7	76.2	24.0	1.03	23.2	76.7	71.0	9.6	0.47	22.3	27.6	71.0	67.0
Engelhardtia roxburghiana	67.2	102.2	23.6	1.13	20.9	56.9	95.7	20.8	0.59	15.2	20.6	30.2	58.8
Euodia trichotoma	56.2	86.1	30.6	1.65	18.5	47.5	76.8	24.5	0.90	15.5	24.7	39.7	59.9
Hovenia acerba	68.8	51.7	37.2	1.94	19.2	65.5	44.5	16.2	0.68	4.8	18.1	64.4	71.1
Michelia floribunda	38.1	79.1	20.0	1.51	13.3	34.6	67.8	8.3	0.38	9.1	22.1	67.6	80.3
Schima superba	70.3	122.1	18.6	0.87	21.4	64.5	104.9	13.3	0.46	8.4	21.3	43.5	58.3
Toxicodendron succedaneum	27.9	89.6	18.1	1.19	15.2	24.4	84.4	7.0	0.39	12.7	17.9	68.3	72.9
Toxicodendron sp.	58.8	136.5	24.1	1.78	13.5	56.9	128.2	19.1	0.97	3.2	9.1	27.8	50.3

Liana species													
Akebia trifoliata	30.0	149.0	18.1	0.89	20.4	25.5	161.7	11.2	0.51	15.2	8.0	42.9	46.8
Artabotrys hongkongensis	31.8	76.1	23.6	1.23	19.2	24.8	61.5	17.7	1.15	21.9	36.9	44.7	41.0
Craspedolobium schochii	68.2	96.4	21.5	1.27	16.9	63.5	85.2	15.5	0.72	6.9	17.7	40.6	53.5
Gnetum pendulum	54.8	110.3	31.1	1.41	22.1	51.3	89.5	27.1	0.81	6.4	24.0	33.9	56.2
Melodinus henryi	35.6	107.1	22.8	1.90	12.0	31.3	93.0	12.4	0.85	12.1	23.7	58.3	66.0
Melodinus suaveolens	32.3	91.6	26.9	1.31	20.5	25.8	81.3	18.8	0.90	20.3	29.2	50.6	51.3
Millettia pachycarpa	41.5	101.5	33.6	1.19	28.3	37.2	91.3	20.4	0.77	10.2	19.1	50.8	47.8
Smilax corbularia	62.1	100.2	15.8	1.45	10.9	53.2	87.6	10.2	0.81	14.3	25.1	51.6	58.0
Smilax hypoglauca	15.2	63.2	19.6	0.86	22.8	15.0	60.1	11.6	0.52	1.3	6.1	30.2	43.7
Smilax microphylla	69.5	87.6	22.9	0.96	23.9	61.6	73.5	16.2	0.71	11.4	25.7	38.5	44.9
Spatholobus suberectus	114.7	123.5	38.2	1.68	22.7	93.2	103.5	20.4	0.52	18.7	31.9	63.7	79.0
Uncaria rhynchophylla	27.2	105.9	20.8	0.73	28.4	23.7	96.6	9.5	0.26	12.9	20.6	63.7	71.7
Mean values													
Tree species	71.4	115	22.8	1.21	19.8	65.2	103.2	13.8	0.53	8.8	18.1	49.2	63.5
(SD)	39.3	46.4	6.3	0.44	3.8	36.5	42.5	5.5	0.21	5.9	7.3	19.3	8.2
Liana species	48.6	101	24.6	1.24	20.7	42.2	90.4	15.9	0.71	12.6	22.3	47.5	55.0
(SD)	24.9	24.4	7.6	0.37	6.5	21.1	26.5	5.4	0.25	5.7	8.8	12.2	15.9
Significant levels	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*

Chapter 5

Seedling growth strategies in Bauhinia species: comparing lianas and trees

Cai ZQ, Poorter L, Cao KF, Bongers F (*submitted*)

Abstract

Lianas are expected to differ from trees in their growth strategies. As a result these two groups of woody species will have different distributions. This study determines the differences in growth patterns, biomass allocation, and leaf traits in 5 closely related liana and tree species of the genus *Bauhinia*. Seedlings of five *Bauhinia* species (two light-demanding lianas, *Bauhinia tenuiflora* and *B. claviflora*, one shade-tolerant liana, *B. aurea*, and two light-demanding trees, *B. purpurea* and *B. monandra*) were grown in a shadehouse at 25% of full sunlight. A range of physiological, morphological, and biomass parameters at the leaf and whole plant level were compared among these five species. The two light-demanding liana species had higher relative growth rate (RGR), allocated more biomass to leaf production (higher leaf mass fraction – LMF - and higher leaf area ratio - LAR) and stem mass fraction (SMF), and less biomass to the roots (root mass fraction, RMF) than the two tree species. The shade-tolerant liana had the lowest RGR of all five species, and had a higher RMF, lower SMF, and similar LMF than the two light-demanding liana species. The two light-demanding lianas had lower photosynthetic rates per unit area (A_{area}) and similar photosynthetic rates per unit mass (A_{mass}) than the trees. Across species, RGR was positively related to SLA, but not to LAR and A_{area}. We conclude that the faster growth of light-demanding lianas compared to light-demanding trees is based on morphological parameters (SLA, LMF, and LAR), and cannot be attributed to higher photosynthetic rates at the leaf level. The shade-tolerant liana exhibited a different growth strategy from the light-demanding species.

Keywords: relative growth rate, shade tolerance, liana, tree, photosynthesis, *Bauhinia*

Introduction

In tropical rain forests, resource availability (light, water, and nutrients) varies over spatial and temporal scales. Plant species may adapt to different parts of these resource gradients, and are likely to differ in their ability to capture, use and conserve limiting resources. Spatial and temporal differences in resources availability within plant communities have led to the evolution of a variety of plant strategies (Grime 1977, Schulze and Chapin 1987). Plant performance is enhanced through morphological and physiological adaptations to the abiotic environment. In tropical rain forest, light is by far the most limiting resource for plant growth and survival (Whitmore 1996). Light-demanding species that regenerate in gaps enhance growth through a high biomass investment in thin, productive leaves with high nitrogen concentrations and a high photosynthetic capacity (Kitajima 1994, Poorter 2005, Poorter and Bongers 2006). At the same time they are well-protected against excess radiation and suffer little from photoinhibition (Powles 1984). Shade-tolerant species that regenerate in the shaded understory enhance their survival through the formation of thick well-protected long-lived leaves, and a large root system for belowground carbohydrate storage (Kitajima 1996, Canham et al. 1999, Paz 2003), thus, preventing potential aboveground biomass loss due to herbivory, fire, or falling debris.

Trees and woody climbers (lianas) are the two most important life-forms in tropical forests. Compared to trees, liana abundance and diversity is higher in disturbed areas such as treefall gaps (Putz 1984, Hegarty and Caballé 1991, Schnitzer and Carson 2001). This suggests that lianas require in general high light levels for establishment and survival, comparable to those of light-demanding tree species. However, a variety of shade tolerance strategies is found within canopy liana species (Gerwing 2004) and there are also shade-tolerant liana species that can germinate and survive in the shade (Putz 1984, Sanches and Válio 2002, Nabe-Nielsen 2002). Recently, lianas and trees were not found to be different in their regeneration requirements during the seedling and sapling life-stages (Gilbert et al. 2006).

Lianas have been assumed to differ strikingly in growth strategies and biomass allocation patterns compared to tree species (Putz and Mooney 1991). Lianas rely on surrounding plants for their structural support, and therefore they can make long and slender stems to forage for light in the high-light conditions of the forest canopy (Darwin 1867, Putz and Mooney 1991). As a result, they have height growth rates than can be seven times faster than that of trees (Schnitzer 2005). Because they are not self-supporting, lianas may invest less biomass in stems and allocate more biomass to leaves (Darwin 1867, Putz 1983, Castellanos et al. 1989, Niklas 1994). The larger proportional investment in leaf mass and/or leaf area, may then result in high growth rates in terms of biomass increment. However, to date no whole-plant growth studies have been carried out to test these hypotheses. Although lianas were assumed to be adapted for rapid growth (Putz 1983, Hegarty 1991), Den Dubbelden and Verburg (1996) found that herbaceous climbing plants had lower relative growth rates than self-supporting species under controlled conditions. Lianas are also considered to be among the most deep-rooted species in tropical forests, perhaps because they have to invest so little in stem mass. There is evidence that their roots can grow belowground to a depth of several meters (Holbrook and Putz 1996, Tyree and Ewers 1996, Restom and Nepstad 2004), and that they can tap deep sources of soil water to sustain high rates of water use (Jackson et al. 1995). This would imply that lianas invest a large biomass fraction in a deep and extensive root system. As a result of a better water availability they then may use their water less efficiently, leading to a low photosynthetic water use efficiency. However, no whole-plant studies have been carried out to check these hypotheses.

Here we present a comparative growth analysis on the biomass allocation, morphology, and leaf physiology of five *Bauhinia* species. Within the genus *Bauhinia* adaptive radiation has occurred into different life forms (trees and lianas) and different shade tolerance strategies (light-demanding vs. shade-tolerant lianas). We test the hypotheses that 1) lianas have higher biomass growth rates than trees because less biomass has to be allocated to stem support and more biomass can be allocated to productive leaves. 2) shade-tolerant lianas are intermediate between light-demanding lianas and trees in terms of growth rates and biomass allocation. We predict that compared to light demanding lianas they have less productive leaves, and compared to trees they have lower allocation to stem support.

Materials and methods

Study site and species

The study was conducted in Xishuangbanna (21°09′–22°33′ N, 99°58′–101°50′ E), SW China. Average annual temperature in Xishuangbanna is 21.4ºC. Average annual rainfall is 1539 mm, 85% of which occurs in the rainy season (May to October), whereas heavy fog compensates partially for the reduced rainfall during the dry season (November to April). We selected five species of *Bauhinia* (three scrambling lianas and two trees) (Table 1). *Bauhinia claviflora* L. Chen and *B. tenuiflora* Watt ex C.B. Clarke are light-demanding liana species that are abundant in large canopy gaps. *Bauhinia aurea* Levl is an extremely shade-tolerant liana that is found in the shaded understorey. *B. purpurea* Linn. and *B. monandra* Kurz are light-demanding tree species that are more abundant in canopy gaps.

Table 1 Characteristics of the five *Bauhinia* species used in this study.

Species	Life form	Growth strategy	Species code
B. tenuiflora Watt ex C.B. Clarke	liana	fast growth, light-demanding	BT
B. claviflora L. Chen	liana	fast growth, light-demanding	BC
B. aurea Levl	liana	slow growth, shade-tolerant	BA
B. purpurea Linn.	tree	fast growth, light-demanding	BP
B. monandra Kurz	tree	fast growth, light-demanding	BM

Experimental design

Seedlings were collected from Xishuangbanna Botanical Garden and a nearby nursery during May 2004, at the start of the rainy season. Seedlings were transplanted into 20×30 cm pots containing topsoil from the nearby forest and then moved into a shadehouse. 4-6 seedlings per species were harvested 4-6 weeks after bud expansion. The remaining 5-7 seedlings per species were grown in pots in the shadehouse at 25% of full sunlight. This irradiance level is typical for a large gap in the forest, and was created using layers of neutral-density screen on a steel frame. Light availability (photosynthetic photon flux, PPF) was measured using LI-190SA quantum sensors connected to a LI-1400 data logger (Li-Cor, Lincoln, NE, USA). All plants were watered on days without rain to maintain the soil near field capacity. Lianas were supported with dry bamboo shoots. At the end of the experiment (approximately after 6 months), physiological measurements were made for 3-4 plants per species, one leaf per plant. Morphological and biomass measurements were made for 4-6 plants per species.

Photosynthesis, N concentration and carbon isotope measurements

At the end of the experiment the light-saturated assimilation was measured under ambient

CO_2 concentrations (*ca*. 400 ppm) and temperature (25–27ºC) using a portable Li-6400 photosynthesis system (Li-Cor Li-6400, Lincoln, NE, USA). Irradiance was set at 1600 μmol m^{-2} s^{-1} with the built-in red/blue LED light source (LI6400-02B). Light-response curves showed that this was sufficient to saturate photosynthesis in all species under all treatment conditions (results not shown). Measurements were made on fully expanded, healthy leaves. Chlorophyll fluorescence was measured with a portable fluorescence system (FMS-2.02, Hansatech, King's Lynn, UK) as an indicator of photoinhibition. Minimal (F_0) and maximal (F_m) fluorescence yields were measured on leaves after maintaining them in the dark for approximately 15 min. The dark-adapted photochemical efficiency of PSII (F_v/F_m) was measured before dawn (0700) and at the middle of the day (1400). Diurnal photoinhibition was estimated as follows:

$$\% \text{ diurnal photoinhibition} = 100 - 100 \times (F_v/F_{m\ 1400\ h})/(F_v/F_{m\ 0700\ h})$$

After the photosynthesis measurements, leaves were collected and analyzed for nitrogen concentration, $\delta^{13}C$ isotope ratio and biomass. $\delta\ ^{13}C$ provides a time integrated estimate of the ratio of photosynthesis to conductance and is therefore a good estimator of the intrinsic water-use efficiency (Farquhar and Richards 1984). Leaves were ground to a fine powder for elemental analyses of $\delta^{13}C$ isotope ratio and N content. The $\delta^{13}C$ ratio (in parts per thousand, ‰) for leaves from all species was measured in 2 mg sub-samples using a Thermo Finnigan MAT stable isotope mass spectrometer (Bremen, German) at the Stable Isotope Laboratory in the Institute of Botany of the Chinese Academy of Sciences. Foliar N concentration (N_{mass}, %) was measured by semi-micro Kjeldahl analysis using a wet digestion procedure. Photosynthetic nitrogen-use efficiency (PNUE, μmol CO_2 $g^{-1}N$ s^{-1}) was determined as A_{mass} divided by N_{mass}.

Biomass allocation, morphology, and plant growth

After harvest, plants were separated into leaves (including petioles), stems, and roots. Leaf areas were determined with a leaf area meter (LI-3100A, Li-Cor, Lincoln, NE, USA). Roots were washed in tap water. All tissues were dried to a constant weight at 70 ºC for 48 h. Specific leaf area (SLA, cm^2 leaf/g leaf), leaf area ratio (LAR, cm^2 leaf/ g plant), leaf mass fraction (LMF, g leaf / g plant), stem mass fraction (SMF, g stem / g plant) and root mass fraction (RMF, g root / g plant) were calculated. Relative biomass growth rate (RGR, mg g^{-1} d^{-1}) was calculated as: RGR = [ln(final plant mass)–ln(initial plant mass)]/ time.

Statistical analyses

For morphological and physiological variables, a one-way analysis of variance (ANOVA) was used to test for statistical differences among species, and the Fisher LSD-test was used for post-hoc analysis. Data were checked for normality and homogeneity of variances, and were $\log_{10}$ or square-root transformed when necessary to satisfy the assumptions of ANOVA. Pearson correlation analyses were used to correlate: (1) net photosynthetic rate (A_{mass}) and nitrogen concentration (N_{mass}), (2) photosynthetic N-use efficiency and carbon isotope ratio, and (3) To evaluate how RGR is affected by its underlying components, it was correlated with LMF, SLA, LAR, and A_{area}. Statistical analyses were done using SPSS 11.0 (SPSS, Chicago, IL).

Result

Growth, morphology and biomass allocation

The two light-demanding liana species had a higher RGR than the two light-demanding tree species, whereas the shade-tolerant liana *B. aurea*, had the lowest RGR (ANOVA, $F = 98.5$, $P < 0.001$, Fig. 1a). LAR was significantly higher in the two light-demanding lianas compared to the other three species, whilst shade-tolerant *B. aurea* had similar LAR values as the two tree species ($F = 48.9$, $P < 0.001$, Fig. 1b). The SLA differed significantly among five species (ANOVA, $F = 75.9$, $P < 0.001$). SLA of the two light-demanding lianas was extremely high (> 390 $\mathrm{cm}^2\,\mathrm{g}^{-1}$) compared to the other three species (190-230 $\mathrm{cm}^2\,\mathrm{g}^{-1}$). The shade-tolerant liana species, *B. aurea*, had similar SLA to the tree species (Fig. 1c).

Distinct differences in biomass partitioning were found among the five studied species (Fig. 1d-f). The three liana species allocated more biomass to leaves than the two tree species ($F = 6.7$, $P = 0.004$). The light-demanding liana species allocated more to stems ($F = 39.8$, $P < 0.001$) and less to roots ($F = 71.0$, $P = 0.001$) than the tree species. The shade-tolerant liana, *B. aurea*, allocated more biomass to roots and less to stem than the four light-demanding species.

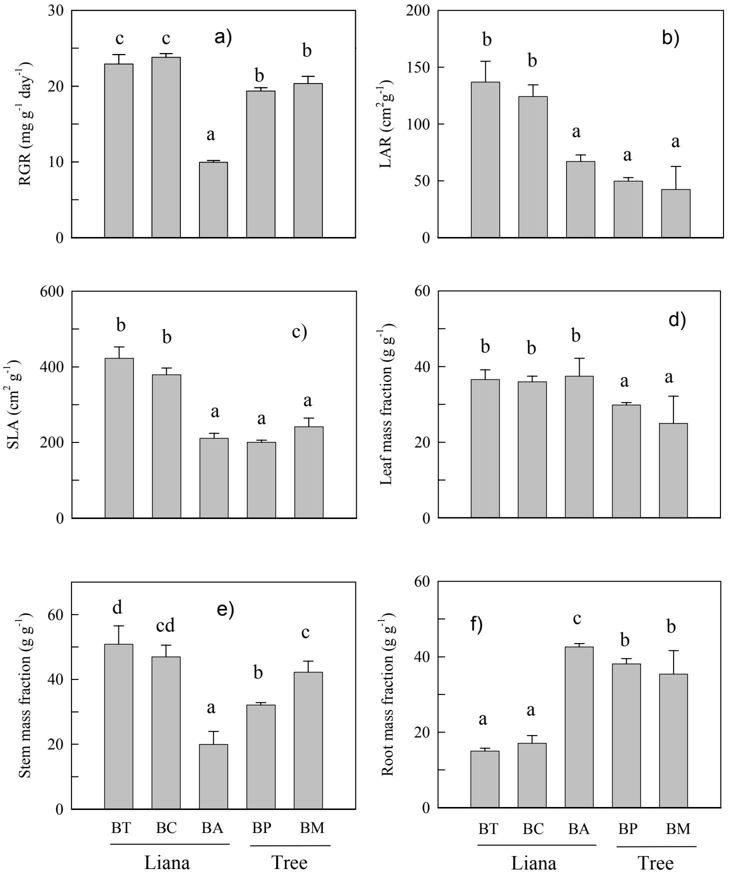

Figure 1 Growth, morphology, and biomass distribution (Mean ± SD) in seedlings of five *Bauhinia* species. Significant differences between species are indicated by different letters at $P < 0.05$. Species codes are as defined in Table 1.

RGR, relative growth rate; SLA, specific leaf area; LAR, leaf area ratio.

Leaf physiological traits

The species differed significantly in their leaf nitrogen concentration (N_{mass}) (Fig. 2, ANOVA, $F = 306.9$, $P < 0.001$), with the shade-tolerant liana having the lowest value. A_{area} in the two tree species was significantly higher than that of the two light-demanding liana species ($F = 329.2$, $P < 0.001$), whereas A_{mass} was similar between these two groups. The shade-tolerant liana species had the lowest photosynthetic rate, both per unit area (A_{area}) and per unit mass (A_{mass}). Pre-dawn $F_{\mathrm{v}}/F_{\mathrm{m}}$ values were similar for all five species (*ca*. 0.82, data not shown). Diurnal photoinhibition was most severe in the shade-tolerant *B. aurea*, but was of similar magnitude in the four light-demanding species. Carbon isotope ratios ($\delta^{13}C$) were significantly different among species ($F = 18.3$, $P = 0.001$), with no consistent difference between liana and tree species. Photosynthetic nitrogen-use efficiency (PNUE) differed amongst species ($F = 28.3$, $P < 0.001$) and was lowest for the shade-tolerant liana.

Correlations between leaf attributes and growth characteristics

There was a weakly positive relation between leaf A_{mass} and N_{mass} concentration in the studied species and a significantly negative relation between PNUE and $\delta^{13}C$ (Fig. 3).

To determine what determined interspecific variation in growth rate, RGR was related to its underlying components. RGR was significantly correlated with SLA but not with LMF, LAR or A_{area} (Fig. 4).

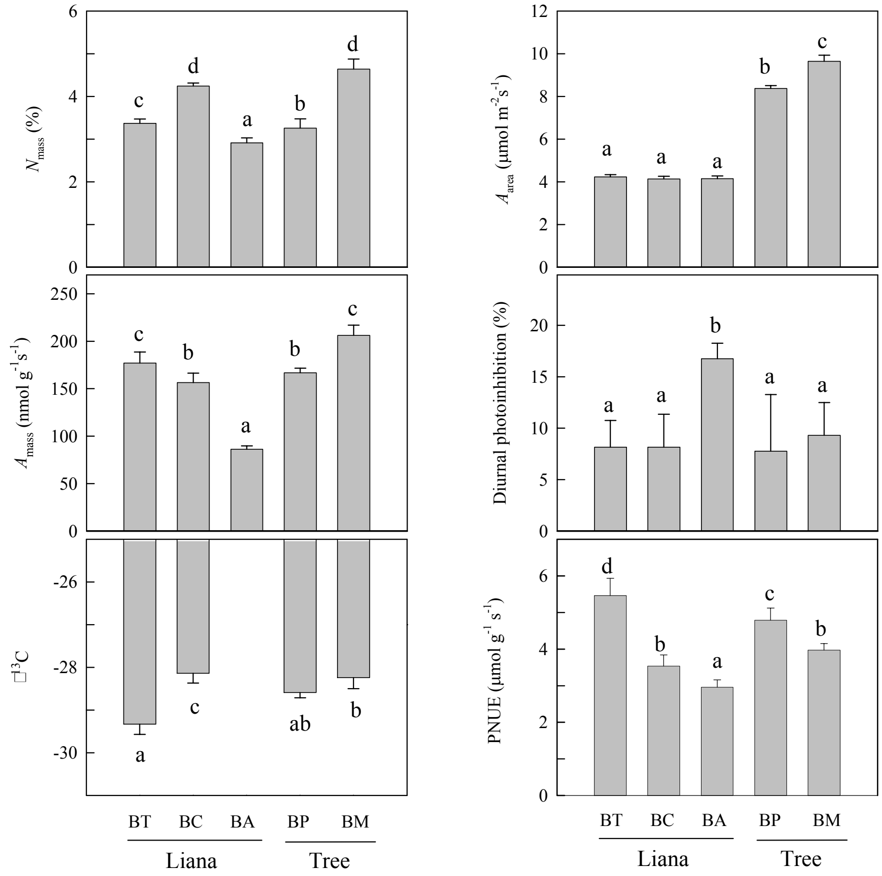

Figure 2 Leaf physiological traits (Mean ± SD) in seedlings of five *Bauhinia* species. Significant differences between species are indicated by different letters at $P < 0.05$. Species codes are as defined in Table 1.

N_{mass}, leaf nitrogen concentration; A_{area}, light-saturated photosynthetic rate based on leaf area; A_{mass}, light-saturated photosynthetic rate based on leaf mass; δ^{13}C, carbon isotope discrimination (‰); PNUE, photosynthetic N-use efficiency.

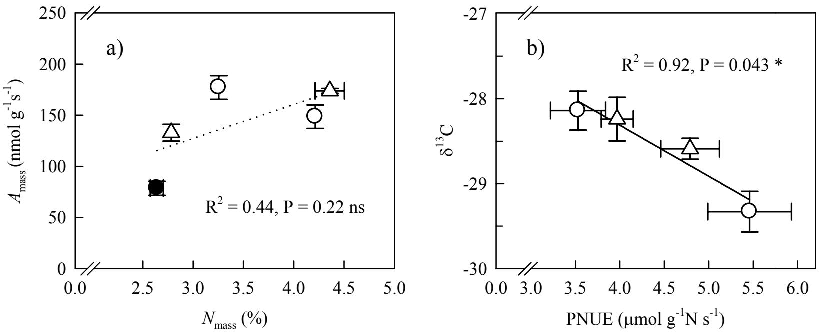

Figure 3 (a) Relationship between net photosynthetic rate per unit dry mass (A_{mass}) and leaf N concentration (N_{mass}), (b) photosynthetic nitrogen-use efficiency (PNUE) and δ^{13}C values (‰) for the studied species. (light-demanding lianas ○, shade-tolerant liana ●, and light-demanding trees △).

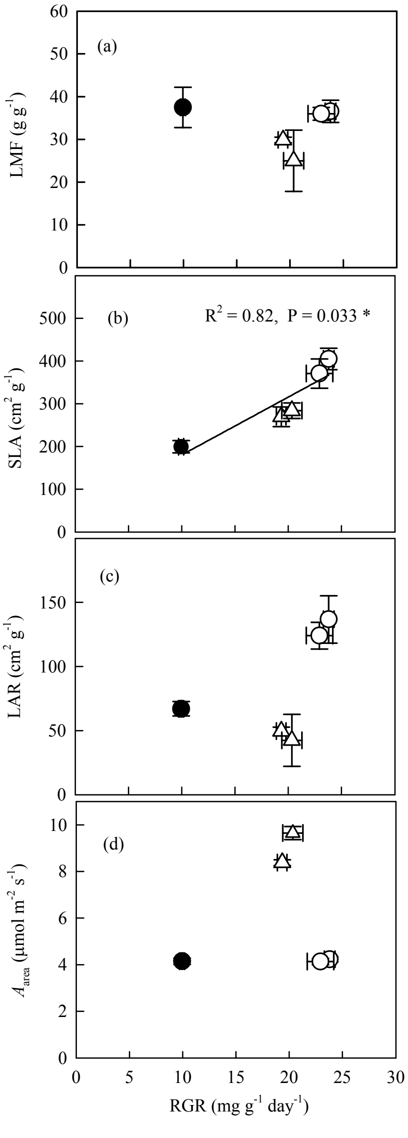

Figure 4 Relationships between relative growth rates (RGR) and (a) leaf mass fraction (LMF), (b) leaf area ratio (LAR), (c) specific leaf area (SLA), (d) net photosynthetic rates per unit area (A_{area}) for five *Bauhinia* species. (light-demanding lianas ○, shade-tolerant liana ●, and light-demanding trees △).

Discussion

Do lianas grow better than trees?

Our two light demanding lianas indeed had higher growth rates than the two light-demanding tree species (Fig 1). Lianas are usually assumed to be adapted for rapid growth (Putz 1983, Hegarty 1991) and a high RGR fits into that scheme. A higher RGR in plants is an important determinant of their distribution in productive habitats (those with a high availability of nutrients and light) through greater competitive ability (Poorter and Remkes 1990, Cornelissen et al. 1996, Poorter 2005). In contrast to this contention, however, the relative growth rate of herbaceous climbers was low compared to those of self-supporting species for seedlings grown in controlled environment chambers (Den Dubbelden and Verburg 1996). Interestingly, the equal growth rates for the liana and shrub growth form of *Toxicodendron diversilobum* were found when plants were grown in an experimental garden without competition, but the liana had high growth rates in patchy natural habitats (Gartner 1991).

The most striking differences between the light demanding lianas and trees were in biomass partitioning. The larger investment in leaf mass (LMF) and/or leaf area (LAR) resulted in high biomass growth rates of the light-demanding lianas compared to the trees (Fig. 1). This higher LMF of lianas was consistent with results of other studies in both tropical and temperate forests (Putz 1983, Teramura et al. 1991). The two light-demanding lianas had higher SMF than the two trees (Fig. 1), contrasting sharply with the general postulation that climbers allocate less biomass to support tissue than self-supporting species (Darwin 1867, Putz 1984, Bell et al. 1988). The larger investment in stem biomass of light-demanding lianas may maximize height growth (Richards 1952, see Den Dubbelden and Verburg 1996 for herbaceous climbers), enabling them to forage rapidly for a better light environment.

In looking for a functional explanation for growth differences, RGR is broken down into the product of net assimilation rate (NAR, dry mass gain per unit leaf area per day) and leaf area ratio (LAR). LAR is the product of specific leaf area (SLA) and leaf mass fraction (LMF) (Evans, 1972) and investment in leaf area improves light interception (Lambers and Poorter 1992, Poorter 2001, 2005). Our light-demanding lianas indeed have a higher LAR than the two tree species (Fig. 1) and thus are expected to have a higher light capturing ability and total photosynthetic carbon gain. However, lianas have a similar photosynthetic capacity per unit leaf biomass (A_{mass}) as trees, and the photosynthetic capacity per unit leaf area (A_{area}) is even lower (Fig. 2). The higher RGR of the light-demanding lianas thus should be attributable to their higher SLA and LMF (leading to higher LAR, Fig. 4), and not to leaf physiological traits. This is in accordance with studies comparing fast-growing and slow-growing woody species (Kitajima 1994, Cornelissen et al. 1996, Poorter 1999).

The lack of photosynthetic differences (A_{mass}) is in contrast to the prediction that lianas differ from trees in those leaf traits related to efficient use of resources. When liana-tree species pairs were examined, the two light-demanding lianas had indeed higher SLA, but physiological differences in leaves were inconsistent (Fig. 1 and 2). High SLA is a common trait in successful species and contributes to their faster growth because larger assimilatory surfaces are produced for a given amount of biomass (Veneklaas and Poorter 1998, Poorter 2005). A_{mass} represents the rate of carbon capture per unit biomass invested and thus provides a better prediction of whole-plant growth than A_{area} (Givnish 1988). The A_{mass} was similar among light-demanding lianas and trees, suggesting that these species are similarly efficient at utilizing light energy, and/or have similar amounts of carboxylating enzymes and thus similar carboxylation efficiencies (Lambers et al. 1998). In contrast to our expectation that photosynthetic rates were positively related to leaf N concentrations, we found no correlation across species (Fig. 3a), suggesting that N availability is not the limiting factor for photosynthesis. Stomatal conductance may be the limiting factor instead. With a decrease in stomatal conductance water loss decreases and thus water use efficiency increases. However, less of the total photosynthetic capacity is used due to lower CO_2 uptake, leading to a reduced photosynthetic nitrogen use efficiency (Lambers et al. 1998). This well-known trade-off between water use efficiency and nitrogen use efficiency (Field and Mooney 1986) is confirmed by our results (Fig 3b). Lianas and trees may have different positions on this trade-off axis, but our results are not consistent. This may also be due to confounding factors such as cross-species differences in leaf thickness and leaf anatomy (Vitousek et al. 1990).

A high investment in roots can contribute in balancing the demands of nutrient and light energy capture (Huston and Smith 1987). Our light-demanding lianas, however, had lower RMF than the two trees, which is in contrast with the hypothesis that lianas invest more in roots for having deep root systems and being drought tolerant in the dry season (Schnitzer 2005). Nonetheless, a low RMF not necessarily leads to a lower resorption ability for nutrients and water as root biomass per se is not directly indicative of the total absorptive area of the root system, and alterations of the root system architecture can occur without a change in total root biomass. Specific root length (total root length/root biomass) or root length per unit mass has been suggested to be a more exact method for measuring the potential ability of a plant to absorb water and nutrition resources (Eissenstat and Caldwell 1988, Hodge 2004). Although we did not collect such data, the two light-demanding lianas with fibrous root system had a larger root surface area and longer roots than the other three species with tap roots (Cai ZQ, personal observation). If lianas have better access to soil water resources than trees, then they are also expected to have inherently low photosynthetic water use efficiency. Yet, the $\delta^{13}C$ did not differ in a consistent way between lianas and trees (Fig. 2), perhaps because plants were grown at a high water availability in this pot experiment and thus did not need to be efficient in their water use, or because of the already mentioned cross-species differences in other factors.

And the shade tolerant liana?

We expected the shade tolerant liana *B. aurea* to be intermediate between the light demanding lianas and the trees. This was not the case for most parameters: RGR was lowest of all species, LAR and SLA was equal to the trees and lower to the light demanding lianas. Photosynthesis (mass basis) was indeed lower than that of the light demanding lianas. RMF was largest of all, in agreement with the large RMF widely reported for young seedlings of shade-tolerant species (Kitajima 1994, Paz 2003, Poorter 2005), which may be related to a decrease in the risk of herbivory loss for large RMF plants (Blundell and Peart 2001). SMF was lowest of all, and consistent with a shade-tolerant sit-and-wait strategy (Clark and Clark, 1992), low RGR (Veneklaas and Poorter 1998, Poorter 1999) and no active foraging, in contrast to the light demanding lianas. The relatively low LAR of *B. aurea* compared to the light demanding lianas may be related to the conservation of carbon rather than to maximization of photosynthetic surface area (Grime 1979, Kitajima 1994). The large reduction in F_v/F_m after strong midday light suggests an inefficiency at dissipating excess light, as is commonly found in shade tolerant species (Powles 1984, Houter and Pons 2005).

Conclusions

The light-demanding liana species had higher LMF and SMF, and lower RMF than the light-demanding trees. Competition for light in light-demanding lianas has favored both rapid shoot extension (ensuring that leaves are displayed above those of competitors) and production of high leaf area, which can be achieved by a high biomass allocation to leaves and by producing 'cheap' leaves (high SLA). The faster growth of the light-demanding lianas is explained by morphological traits, such as higher SLA, LAR and LMF, and is not attributed to physiological traits, such as higher photosynthetic rates and nitrogen concentrations at the leaf level. Compared to the four light demanding *Bauhinia* species, the shade tolerant *B. aurea* had a different growth strategy. Our study on 5 *Bauhinia* species shows that, even within a genus, species growth (and their underlying factors) is rather variable, and that this variation is related to life form (lianas vs trees) and to light demand.

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Chapter 6

Seasonal changes in photosynthesis and growth of *Zizyphus attopensis* seedlings in three contrasting microhabitats in a tropical seasonal rain forest

Cai ZQ, Chen YJ, Bongers F. *Tree Physiology*, 2007, (in press)

Abstract

It was hypothesized that the tropical vegetation at its most northern distribution in Asia (Xishuangbanna, SW China), would be affected by seasonal drought and chilling because its location is far from the Equator and at a relatively high altitude. To test this hypothesis, photosynthetic and growth characteristics were measured in *Zizyphus attopensis* Pierre seedlings grown in the field in three contrasting microhabitats: the understory, a small gap and a large gap. Photosynthetic capacity (light-saturated photosynthetic rate, $A_{\max}$; maximum rate of carboxylation, V_{cmax}; and electron transport, $J_{\max}$), and partitioning of leaf nitrogen into carboxylation and electron light transport (P_{c} and P_{b}, respectively) were found to differ significantly between seasons and microhabitats. Specific leaf area (SLA) did not change seasonally, but was significantly different between plants grown in each of the three microhabitats and was negatively linear related to the daily integrated photon flux density ($\mathrm{PPFD_i}$). In contrast, nitrogen content per unit area (N_{a}) changed seasonally but did not differ among microhabitats. Measurements of maximum PSII photochemical efficiency ($F_{\mathrm{v}}/F_{\mathrm{m}}$) showed that no chronic photoinhibition occurred for all microhabitats throughout the experimental period. Photosynthetic capacity was greatest in the wet season and lowest in the cool season. During the cool and dry seasons, the reduction in $A_{\max}$ was greater in seedlings grown in the large gap than in those grown in the understory and the small gap. Close logarithmic relationships were detected between $\mathrm{PPFD_i}$, leaf N_{a} and photosynthetic capacity. Stem mass ratio decreased and root mass ratio increased in the dry season. We conclude that seasonal acclimation in growth and photosynthesis of the seedlings was due to changes in biochemical features (particularly N_{a} and partitioning of total leaf nitrogen between the different photosynthetic pools) and biomass allocation, rather than to changes in leaf morphological features (such as SLA). The local light level is the main factor driving seasonal variations in growth and photosynthesis in the study area, where the presence of heavy fog during the cool and dry seasons limits irradiance, but supplies water to the soil surface layers.

Keywords: biomass allocation, leaf irradiance, nitrogen partitioning, photosynthesis, seasonality.

Introduction

Plants acclimate to changes in their light environment at several levels. At the cellular level, nitrogen (N) is re-allocated between the various photosynthetic pools (Boardman 1977, Pons and Westbeek 2004). N partitioning within leaves alters in response to changes in irradiance so as to maximize photosynthesis, with more N being allocated to Rubisco under high light conditions and more N allocated to chlorophyll in conditions of low irradiance (Hikosaka and Terashima 1995, Niinemets et al. 1998, Evans and Poorter 2001). At the leaf level, leaf area per unit biomass invested in leaves (specific leaf area, SLA) is modulated by alterations in leaf anatomy and physiology (Hanba et al. 2002). At the whole-plant level, the proportions of biomass invested in leaves, stems and roots may be altered (Givnish 1988, Popma and Bongers 1991, Paz 2003). Plants growing in low light conditions tend to develop large leaf surfaces in adaptive responses that optimize the absorption of light and photosynthetic efficiency, with low compensation and saturation points, and low light-saturated photosynthetic rates (Boardman 1977, Pearcy and Sims 1994, Cai et al. 2005). However, many shade-tolerant seedlings have higher light-saturated photosynthetic rates at low irradiances than under high light conditions, probably as a result of physiological adjustments of foliage (Mitchell and Arnott 1995). The mechanisms by which plants adapt to different light environments at the leaf and whole plant level have been investigated in many studies (Givnish 1988, Pearcy and Sims 1994, Le Roux et al. 2001, Warren and Adams 2001). However, plants growing under high light conditions also tend to be subjected to stresses resulting from other environmental factors such as extreme temperature and drought in natural conditions, and the adaptive changes of a trait to light conditions may be modified or constrained by such factors (Niinemets and Valladares 2004, Muller et al. 2005, Misson et al. 2006, Mittler 2006). Understanding the effects of multiple environmental factors on light acclimation strategies is therefore critical when assessing the significance of a particular response.

Under natural conditions, photosynthesis is biochemically regulated to maintain a balance between the rates of its component processes and the concentrations of metabolites (Geiger and Servaites 1994, Niinemets and Valladares 2004, Misson et al. 2006), and is affected by continuously changing environmental variables, such as light, water availability, and temperature (Muller et al. 2005, Mittler 2006). These spatial and temporal variations in environmental conditions require constant adjustment of the primary (light reaction) and secondary (Calvin cycle) photosynthetic processes if plants are able to succeed in a variable habitat. Plants grown in high light conditions often experience imbalances between energy absorption (and subsequent conversion through electron transport) and photosynthetic light utilization by carbon fixation because they cannot utilize all of the light absorbed for photosynthesis. At extremes of temperature and/or under drought conditions, this potentially harmful imbalance is exacerated since electron transport and the reactions of the Calvin cycle are more strongly inhibited (Demming and Adams 1992). Hence, plants have to rapidly adjust their photosynthetic apparatus in order to protect PSII components from excessive excitation and potential photoinhibitory damage. Photoinhibition resulting from prolonged exposure to light in excess of that used by the plant reduces quantum yields and would therefore be expected to reduce overall plant growth (Long et al. 1994). However, it is unclear whether this is the case in all environments, as the costs of repairing damage are not always higher than the costs of photoinhibition-avoidance mechanisms. Moreover, the performance of the whole plant depends not only acclimations at the leaf level, but also on the morphology, geometry, and dynamics of the plant canopy (Givnish 1988, Pearcy and Sims 1994, Niinemets et al. 1998). For example, understory plants have morphologies that are characterized by high SLA, high leaf area ratios and high leaf mass ratios (Popma and Bongers 1991, Osunkoya et al. 1993). Such traits confer advantages in light-limited environments as they enhance light interception, but may also be detrimental during the dry season as they lead to a limited capacity for water uptake (due to a low root mass ratio), and increases in water loss via transpiration (Givnish 1988, Pearcy and Sims 1994).

Xishuangbanna in SW China, biogeographically located in the transitional zone between tropical Southeast Asia and subtropical East Asia, has a rich tropical flora and typical tropical rain forests in the lowland area (Cao and Zhang 1997, Cao et al. 2006). The region contains over 5000 species of vascular plants, comprising 16% of China's total plant diversity, and its biodiversity is important both nationally and globally (Cao and Zhang 1997, Myer et al. 2000, Cao et al. 2006). It has been hypothesized that the vegetation there is likely to be affected by the seasonal drought and chilling because it is far from the Equator and at a relatively high altitude (Cao and Zhang 1997, Cao et al. 2006, Zhu et al. 2006). However, little is known about morphological and physiological responses to seasonal changes in this region. This study provides the first investigation of photosynthetic adaptation and growth responses in seedlings of one local species (*Zizyphus attopensis* Pierre) in three contrasting natural microhabitats: the understory, a small gap and a large gap. The main objective is to determine the morphological and physiological responses to seasonal climatic changes in *Z. attopensis* seedlings and differences in response between seedlings grown in different microhabitats, and to determine the main environmental factors affecting leaf physiology in this region.

Materials and methods

Study site and plant materials

The study was carried out in the seasonal rainforest in Xishuangbanna Tropical Botanical Garden (21°04’ N, 101°25’ E, 570 m a.s.l.), Chinese Academy of Sciences, Yunnan, SW China. The climate of Xishuangbanna is dominated by the southwest monsoon with three distinct seasons (a wet season from May to October, a cool season from November to January and a dry season from February to April; Cao et al. 2006), with heavy fog partially compensating for the shortage of rainfall during the dry and cool seasons (Liu et al. 2004). The mean annual temperature is 22.9°C and mean precipitation is 1500 mm. Due to its unique geographical location and climatic features, this area supports a tropical rainforest with a small proportion of deciduous tree species (Cao and Zhang 1997, Zhu et al. 2006). Meteorological conditions in the study areas throughout the experimental period are summarized in Figure 1.

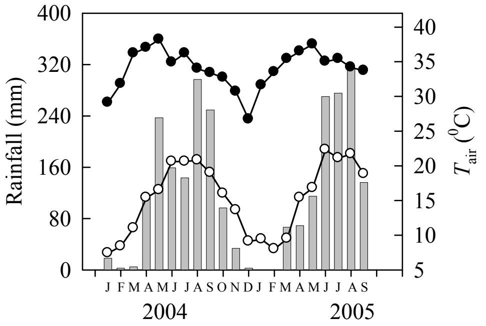

Figure 1 Seasonal changes in monthly precipitation (gray bars) and maximum (closed circles) and minimum (open circles) air temperatures in 2004 and 2005.

Zizyphus attopensis Pierre (Rhamnaceae) is a large evergreen late successional liana species. It grows on the forest floor while young but also may reach the canopy of the forest. Field observations suggest that the species is shade tolerant but requires a fair amount of light and growing space during early stages. Seeds (seed mass = 1.69 g dry weight) of this species were collected and sown *in situ* in three microhabitats: shaded understory, a small gap (2.5 m radius) and a large gap (6 m radius). The forest around the gaps was about 20 m tall, with emergent individuals exceeding this height. The canopy is dominated by a diverse assemblage of climax tree species, and has a high abundance of lianas. The seedlings of this liana species were free-standing during the period of study. To characterize light availability in the microsites, photosynthetic photon flux density (PPFD) was measured on clear days in each season using a LI-190 SB quantum sensor (Li-Cor Lincoln, NE) positioned 10 cm above the ground in the center of each microsite. All sensors were connected to two LI-1400 data loggers (Li-Cor Lincoln, NE) from dark understory to large gap. The daily course of photosynthetic photon flux density (PPFD, μmolm^{-2}s^{-1}) was recorded and the daily integrated PPFD (PPFD$_i$) was calculated.

Chlorophyll a fluorescence and gas exchange measurements

Diurnal courses of chlorophyll *a* fluorescence in leaves of four seedlings growing in each microhabitat were measured *in situ* using a portable fluorescence system (FMS-2.02, Hansatech, King's Lynn, U.K.) after 15 min dark adaptation. One leaf per plant was measured. Minimum and maximum dark-adapted fluorescence values (F_0, F_m, respectively) were obtained and F_v/F_m was used as a measurement of the maximum photochemical efficiency of PSII (Maxwell and Johnson 2000).

Gas exchange measurements were made in the morning between 9:00 and 11:00 using a portable infrared gas analyzer in open system mode (LI-6400, Li-Cor), in October 2004 (wet season), January 2005 (cool season) and March 2005 (dry season). Three plants per microsite were selected for photosynthetic measurements in each season; one leaf per plant was measured. Photosynthetic light-response curves (A-PPFD) were determined at irradiances between 1500 to 0 μmol m^{-2} s^{-1} using a built-in LED-B light source in 9-12 PPFD steps, depending on the season (for the steps see Fig. 4). During measurements, the CO_2 concentration (C_a) and vapor pressure deficit (VPD) in the cuvette were held at 400 μmol mol^{-1} and less than 1 kPa, respectively. The same samples were used to measure the response curves of photosynthesis to intercellular CO_2 concentration (C_i) (A-C_i) under light-saturated irradiance obtained from the A-PPFD curves and different CO_2 partial pressures (C_a = 20, 50, 100, 200, 400, 600, 800, 1000 μmol mol^{-1}) in the air passing over the leaf chamber. During A-PPFD and A-C_i measurements, leaf temperature was kept at the seasonal averages of 25 °C in October 2004, and at 15 °C and 20 °C in January and March 2005, respectively. Photosynthetic parameters (light-saturated photosynthetic rate, A_{max}; dark respiration rate, R_d; light saturation point, LSP; light compensation point, LCP; and apparent quantum efficiency, AQE) were calculated from the A-PPFD curves, and maximum rates of carboxylation (V_{cmax}) and electron transport (J_{max}) were estimated from A-C_i curve with Photosyn Assistant (Dundee Scientific, Dundee, Scotland). After photosynthetic measurements, leaves were harvested and weighed after drying at 70 °C for 48 h. Total leaf nitrogen was measured on dry samples by semi-micro Kjeldahl using a wet digestion procedure.

Estimation of relative allocation of nitrogen to carboxylation and bioenergetics

Based on in vitro Rubisco kinetics and the assumptions that all Rubisco was fully activated and CO_2 transfer conductance was infinite, the model proposed by Niinemets and Tenhunen (1997) was used to estimate the relative allocation of leaf N to Rubisco (P_c; g N in Rubisco g^{-1} total leaf N) and to bioenergetics (P_b; g N in cytochrome f, ferredoxin NADP reductase, and coupling factor g^{-1} total leaf N) from values of nitrogen content per unit area (N_a), V_{cmax} or J_{max}, respectively:

$P_c = V_{cmax} / (6.25\ V_{cr} N_a)$ (1)

$P_b = J_{max} / (8.06\ J_{mc}\ N_a)$ (2)

where V_{cr} is the specific activity of Rubisco (μmol CO_2 g^{-1} Rubisco s^{-1}), J_{mc} is the potential rate of photosynthetic electron transport per unit cytochrome f (mol e^- mol^{-1} cyt f s^{-1}), 6.25 (g Rubisco g^{-1} N in Rubisco) converts N content to protein content, and 8.06 (μmol cyt f g^{-1} N in bioenergetics) are used, assuming a constant 1:1:1.2 molar ratio for cyt f:ferredoxine NADP reductase:coupling factor (Niinemets and Tenhunen 1997). Temperature-dependent reference values were modified from the models for V_{cr} and J_{mc}, respectively (for details, see Appendix A in Niinemets and Tenhunen 1997). We used values of V_{cr} = 20.2, 12.26, 7.26 μmol CO_2 (g Rubisco)$^{-1}$$s^{-1}$, and J_{mc} = 156, 132.2, 111.3 mol e^- (mol cyt f)$^{-1}$ s^{-1} at 25, 20, 15 °C, respectively.

Whole-plant growth

To assess whole-plant acclimation responses, seedlings of *Z. attopensis* grown in the three microhabitats were collected using a shovel, with all their root systems intact, on four occasions (October 20, 2004; January 25, March 25 and September 15, 2005). On each occasion, four to six plants were harvested and washed free of soil particles with tap water. The plants were separated into roots, stems and leaves. Leaf area was determined with a leaf-area meter (LiCor-3000A, Li-Cor, Lincoln). All samples were dried at 70 °C to a constant mass and then weighed. Leaf mass ratio (LMR, g g^{-1}), stem mass ratio (SMR, g g^{-1}), root mass ratio (RMR, g g^{-1}), specific leaf area (SLA, cm^2 g^{-1}), and leaf area ratio (LAR, cm^2 g^{-1}) were then calculated.

Statistical analyses

For each morphological and physiological variable, data were analyzed with a two-way ANOVA, with microsite and season as main fixed factors plus a microsite × season interaction term. Pearson correlation analyses were used to correlate leaf characteristics and the daily integrated photo flux density ($PPFD_i$). All analyses were performed with SPSS 11.0 (SPSS, Chicago, IL).

Results

Seasonal changes in rainfall, air temperature and light environment

The highest monthly rainfall occurred in the wet season (from May to October) with the driest months being January and February in 2005 (when no rain fell, see Figure 1). Minimum air temperatures in the local area were about 8 °C in January 2004 and February 2005, and maximum air temperatures frequently exceeded 30 °C during the wet and dry seasons. On days with clear skies, PPFD$_i$ in the shaded understory did not differ greatly between seasons. Plants in the large gap were subjected to large seasonal variations in PPFD$_i$ with the highest value occurring in the wet season (10.04 mol m^{-2} day^{-1}) (Figure 2).

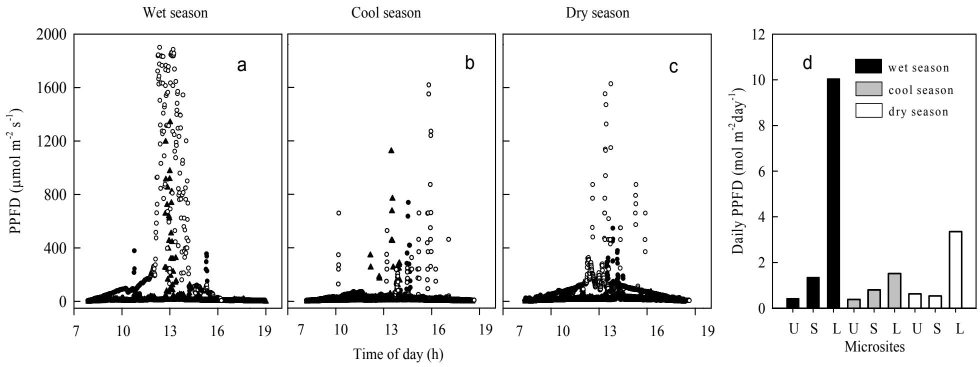

Figure 2 Diurnal courses of photosynthetic photon flux density (PPFD) (a, b, c) in understory (closed circles), a small gap (upper triangles) and a large gap (open circles) and daily-integrated leaf irradiance (PPFD$_i$) (d) on typical sunny days in different seasons and microhabitats. U, understory; S, small gap; L, large gap.

Seasonal changes in photosynthetic characteristics and leaf nitrogen partition

In both the wet and dry seasons, small reductions occurred in the maximum photochemical efficiency of PSII (F_v/F_m) at midday on clear days at all three microsites, especially in seedlings grown in the large gap (Figure 3). However, F_v/F_m values in all plants recovered to values similar to those at predawn by the late afternoon. There were no significant diurnal changes in the cool season, although the F_v/F_m values of plants grown in the large gap were lower than those in the understory and small gap sites. Gas exchange parameters (A_{max}, V_{cmax}, J_{max}, LSP, LCP, AQE, R_d) showed similar seasonal patterns, but differed in the degree of change in the three microhabitats (Table 1, Figure 4). The photosynthetic capacity (A_{max}, V_{cmax}, J_{max}) was highest in the wet season and lowest in the cool season in all microhabitats. In the understory, A_{max} decreased 2-fold in the cool season and recovered during the dry season to the level seen in the wet season. In plants growing in the large gap, A_{max} decreased 3-fold in the cool season and only partially recovered during the dry season compared to the values measured in the wet season. R_d and LSP decreased during the cool season, with greater reductions in plants growing in the large gap than in the understory. Seedlings in the large gap exhibited higher values of V_{cmax} and J_{max} than those in the small gap and understory during the wet season. The ratio of J_{max} to V_{cmax} increased in the cool season compared to the ratio in the wet season (data not shown). There were significant interactions between site and season for the gas exchange parameters.

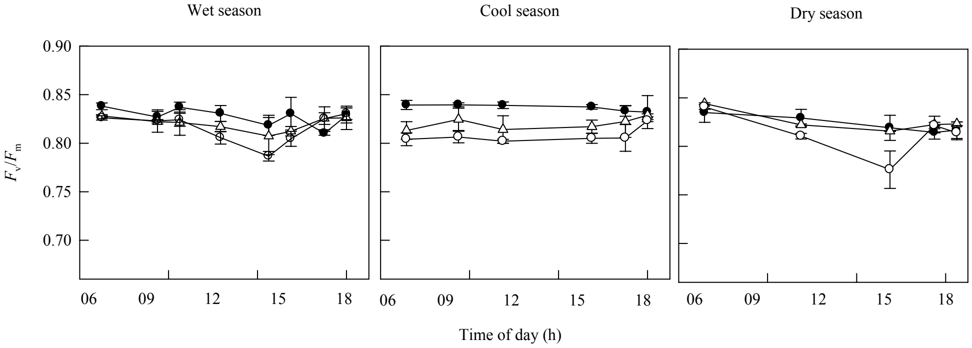

Figure 3 Diurnal changes in photochemical efficiency (F_v/F_m) of seedlings grown in the understory (closed circles), a small gap (open triangles) and a large gap (open circles). Each value is the mean ± SD of four replicate leaves.

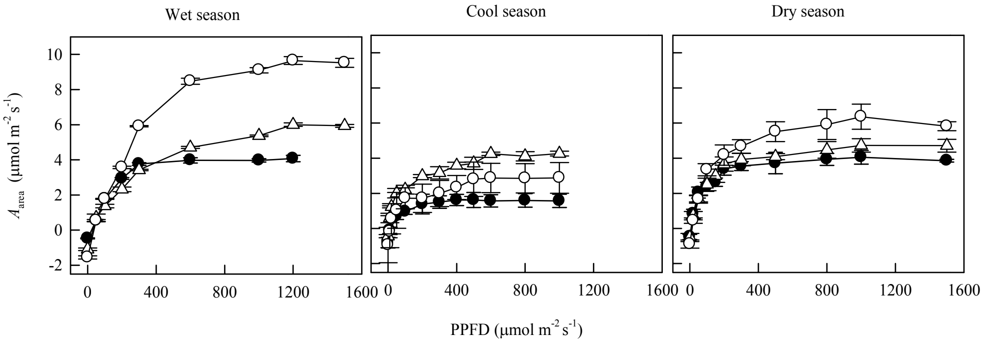

Figure 4 Seasonal changes in area-based photosynthesis (A_{area})- photosynthetic photon flux density (PPFD) responses for *Z. attopensis* seedlings grown in the understory (closed circles), a small gap (open triangles) and a large gap (open circles). Photosynthetic responses were measured at ambient temperature. Each value is the mean ± SD for three replicate leaves.

Plants from the three different microsites showed no significant seasonal differences in SLA (F = 8.79, P = 0.098), but there were significant differences in this variable between the three microsites (F = 2.23, $P < 0.01$). Leaf N content per unit area (N_a) decreased significantly in the cool season compared to the wet season in all microhabitats and increased again in the following dry season. The fraction of total nitrogen partitioned into Rubisco (P_c) was highest in the wet season and in plants in the large gap, and there were significant differences in the fraction of N partitioned into bioenergetic pools (P_b) and P_c between the three microsites and seasons (Table 2).

Table 1 Seasonal changes in photosynthetic parameters in *Zizyphus attopensis* seedlings grown at three different microsites. Significance levels of ANOVAs testing for the effects of season, microsite, and their one-way interaction are listed for each variable. Each value is the mean ± SD of three replicate leaves. U, understory; SG, small gap; LG, large gap. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. * A_{max}, light-saturated photosynthetic rate; AQE, apparent quantum efficiency; R_d, dark respiration rate; LCP, light compensation point; LSP, light saturation point; V_{cmax}, maximum carboxylation efficiency; J_{max}, maximum electron transport capability.

Photosynthetic	Wet season			Cool season			Dry season			Significance levels		
parameters *	U	SG	LG	U	SG	LG	U	SG	LG	Season(S)	Site(S)	S×S
A_{max} (μmol m^{-2} s^{-1})	4.62	6.59	11.13	2.44	4.47	4.1	4.58	5.44	7.45	***	***	***
(SD)	*0.12*	*0.08*	*0.32*	*0.44*	*0.11*	*0.60*	*0.06*	*0.07*	*0.06*			
AQE	0.023	0.030	0.027	0.0435	0.054	0.083	0.0745	0.0674	0.0804	***	**	*
(SD)	*0.0005*	*0.002*	*0.0007*	*0.0008*	*0.023*	*0.006*	*0.015*	*0.003*	*0.004*			
R_d (μmol m^{-2} s^{-1})	-0.484	-0.904	-1.17	-0.562	-0.162	-0.898	-0.441	-0.462	-0.899	***	***	**
(SD)	*0.025*	*0.129*	*0.062*	*0.10*	*0.038*	*0.16*	*0.007*	*0.012*	*0.034*			
LCP (μmol m^{-2} s^{-1})	21.13	29.93	43.5	12.11	2.51	11.88	5.81	6.70	13.1	***	***	***
(SD)	*0.71*	*2.23*	*2.90*	*3.56*	*0.015*	*5.58*	*0.68*	*0.96*	*2.19*			
LSP (μmol m^{-2} s^{-1})	223	300	456.3	68.75	75.23	42.71	66.5	91.9	105.7	***	***	***
(SD)	*2*	*15.7*	*10.3*	*9.35*	*13.90*	*6.86*	*6.23*	*17.7*	*7.37*			
V_{cmax}	50.1	67.7	97.9	15.6	18.8	19.3	32.6	42.7	50.7	*	*	***
(SD)	*7.27*	*7.51*	*8.94*	*2.90*	*3.09*	*3.20*	*4.11*	*6.89*	*3.35*			
J_{max}	87.7	96.0	138.3	49.5	67.2	70.6	79.7	89.9	120.2	*	*	**
(SD)	*6.19*	*9.85*	*10.55*	*6.26*	*6.12*	*7.90*	*7.50*	*7.29*	*5.68*			

Table 2 Seasonal changes in specific leaf area (SLA), total leaf nitrogen content per unit area (N_a), and leaf N investments in carboxylation (P_c) and bioenergetics (P_b) for seedlings grown at three different microsites. Significance levels of ANOVAs testing for the effects of season, microsite, and their one-way interaction are listed for each variable. Each value is the mean ± SD of three replicate leaves. U, understory; SG, small gap; LG, large gap. ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Variables	Wet season			Cool season			Dry season			Significance levels		
	U	SG	LG	U	SG	LG	U	SG	LG	Season(S)	Site(S)	S×S
SLA (g m^{-2})	265.9	257.8	248.4	253.8	249.1	243.5	248.3	266.8	241.8	ns	**	ns
(SD)	*10.6*	*12.6*	*12.9*	*2.8*	*2.8*	*8.2*	*11.3*	*1.8*	*11.9*			
N_a (g m^{-2})	1.26	1.50	1.75	0.85	1.07	0.96	1.31	1.26	1.56	***	ns	ns
(SD)	*0.04*	*0.11*	*0.07*	*0.08*	*0.07*	*0.10*	*0.14*	*0.12*	*0.11*			
P_c	0.311	0.352	0.437	0.303	0.344	0.386	0.321	0.408	0.420	*	*	ns
(SD)	*0.025*	*0.019*	*0.020*	*0.025*	*0.033*	*0.032*	*0.040*	*0.041*	*0.028*			
P_b	0.056	0.051	0.063	0.066	0.071	0.082	0.058	0.068	0.073	*	*	ns
(SD)	*0.004*	*0.005*	*0.005*	*0.008*	*0.006*	*0.009*	*0.005*	*0.005*	*0.003*			

Relationships between leaf morphology, nitrogen, photosynthetic capacity and local irradiance

N_a and photosynthetic capacity (A_{max}, V_{cmax}, J_{max}) were significantly positively logarithmically related with PPFD_i, while SLA decreased with PPFD_i, especially at low PPFD values (Figure 5). Photosynthetic capacity was linearly related to N_a (Figure 6), but no significant relationship was found between SLA and photosynthetic capacity (all comparisons, $P > 0.05$). Leaf N partitioning between carboxylation (P_c) and bioenergetic components (P_b) were not related to PPFD_i ($P > 0.05$, Figure 7).

Seasonal changes in biomass allocation and growth

At the whole-plant level, seedlings grown in the large gap had the highest total biomass at the end of the experimental period. Plants grown in the large gap allocated proportionally less biomass to leaves (LMR or LAR) and more to roots and stems (SMR, RMR) than those grown in the small gap. Seedlings grown in the small gap allocated less biomass to leaves and more to roots and stems compared with plants in the understory. Interestingly, in the dry season, all plants increased their RMR and decreased SMR significantly, with the exception of RMR of seedlings grown in the small gap (Figure 8).

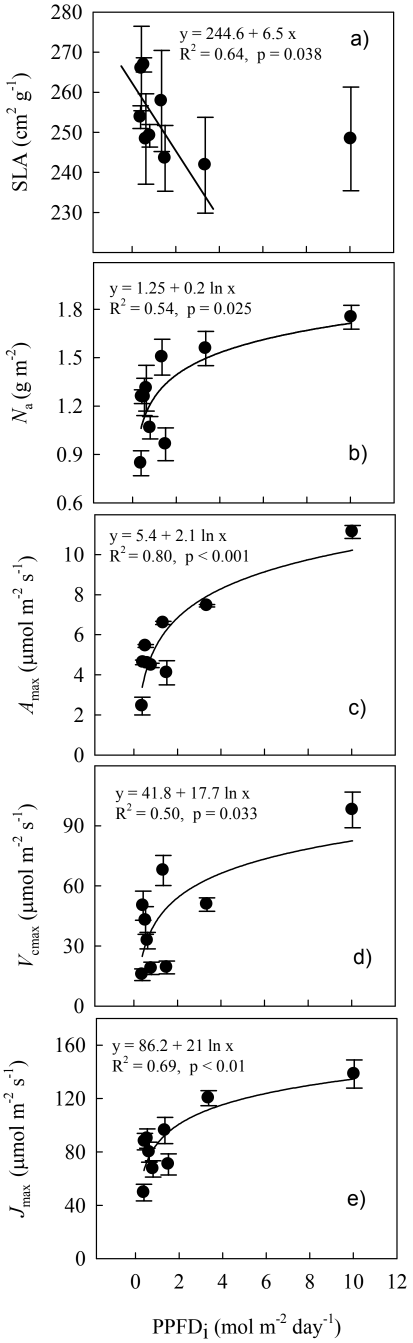

Figure 5 Relationships between integrated leaf irradiance ($PPFD_i$) and (a) specific leaf area (SLA), (b) total leaf N per unit leaf area (N_a), (c) light-saturated photosynthetic rate based on leaf area (A_{max}), (d) maximum carboxylation rate (V_{cmax}), and (e) the light-saturated electron transport rate (J_{max}).

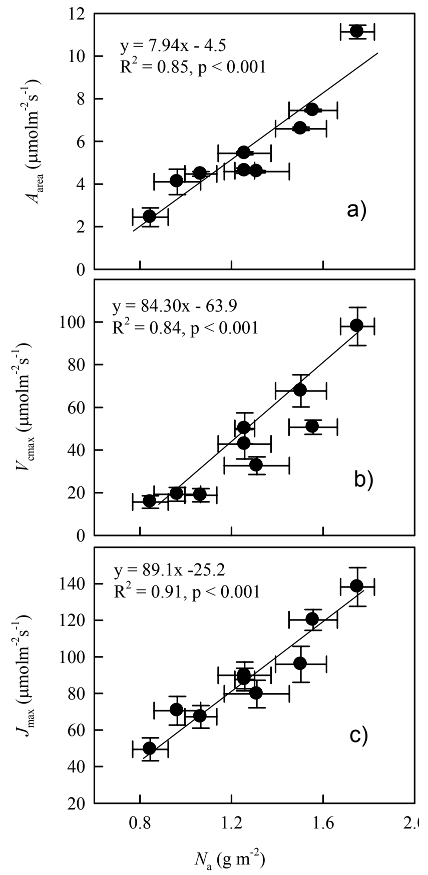

Figure 6 Relationships between total leaf N per unit leaf area (N_a) in leaves of *Z. attopensis* seedlings grown at three different microsites and (a) light-saturated photosynthetic rate based on leaf area (A_{max}), (b) maximum carboxylation rate (V_{cmax}), and (c) the light-saturated electron transport rate (J_{max}).

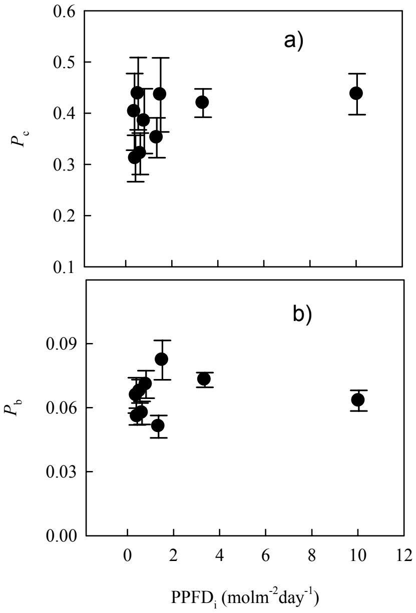

Figure 7 Relationships between integrated leaf irradiance (PPFD$_i$) and (a) the investment of leaf N in carboxylation (P_c) and (b) the investment of leaf N in bioenergetics (P_b).

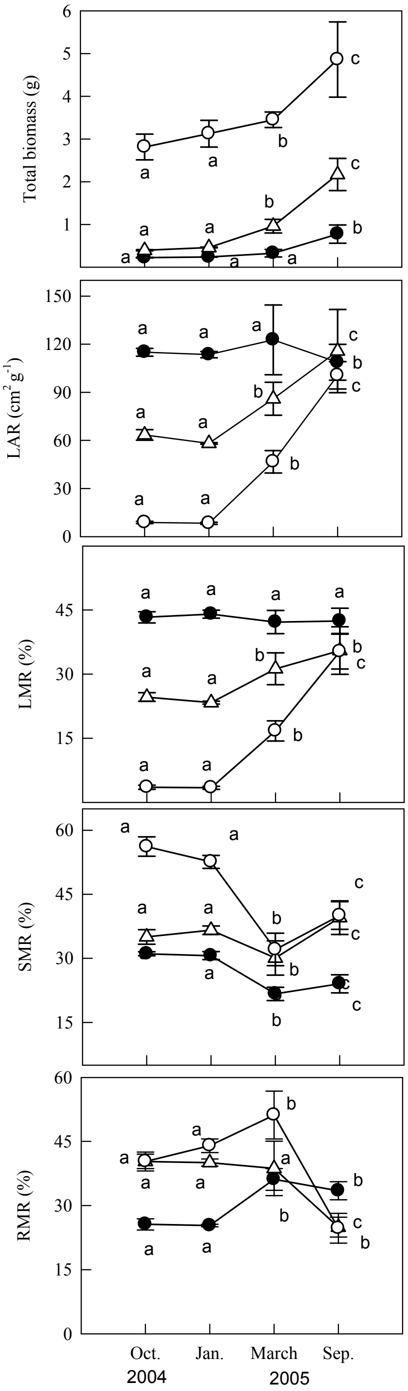

Figure 8 Seasonal changes in total biomass, leaf area ratio (LAR), and biomass allocation (leaf mass ratio, LMR; stem mass ratio, SMR; and root mass ratio, RMR) of seedlings grown in understory (closed circles), a small gap (open triangles) and a large gap (open circles). Different letters denote significant differences between seasons in the same microhabitat at $P < 0.05$. Each value is the mean±SD of four to six replicate measurements.

Discussion

Seasonal oscillations in photosynthetic variables

The larger F_v/F_m observed in understory seedlings compared to those grown in the large-gap (Figure 3) indicates that understory plants may be more efficient at trapping light energy in the pigment bed of PSII (Maxwell and Johnson 2000). The greater efficiency enhances the ability of shade-tolerant *Z. attopensis* to use light energy during the constant low light periods in the forest understory. A low dark respiration rate and light saturation point, as seen in understory seedlings (Table 2, Figure 4), may promote carbon fixation in the light-limited environment (Boardman 1977). Unsurprisingly, photosynthetic capacity was highest in all seedlings during the wet season when environmental conditions (water, temperature and light) were closest to optimal and leaves were in the peak physiological condition. The low photosynthetic capacity observed in the dry and cool seasons may be partially attributable to generally lower air temperatures and long periods of low solar irradiance, with water stress and intermittent high solar irradiance causing photoinhibition. The decrease in photosynthetic rate during the cool season was higher in seedlings growing in the large gap than in those in the understory and small gap sites (Table 1, Figure 4). This difference may be related to the greater decrease in solar irradiance at the large gap site compared to the other sites (Figure 2).

In the wet tropics, most plants grow year round in a warm climate, and are particularly vulnerable to low temperatures (Allen and Ort 2001). Cool air temperatures result in an imbalance between the light energy absorbed through photochemistry and the energy utilized through metabolism, thereby increasing the susceptibility of photosynthetic systems to photoinhibition (Greer 1990, Huner et al. 1998). Lower F_v/F_m values were observed in the cool season in plants grown in the large gap compared with those grown at the other sites, possibly indicating thermal degradation of the D_1 protein in these plants (Öquist et al. 1992). Photoinhibition at PSII is thus a possible reason for the decline in photosynthetic capacity seen in seedlings grown in large gap conditions. However, no permanent damage to PSII centers was observed, as predawn F_v/F_m values remained close to the optimal value of 0.8 in all seasons (Figure 3). The decrease in photosynthetic capacity during the cool season is unlikely to be caused by low temperatures. In northern tropical regions, such as the study site at Xishuangbanna, chilling temperatures occur only at night; daytime temperatures are mild, stimulating photosynthesis. Moreover, during the cool and dry seasons in Xishuangbanna there is heavy fog cover each day from midnight to midmorning of the following day. Fog may be beneficial to tropical seedlings by alleviating photoinhibition and photodamage, as it reduces sunlight intensity, and thus has a shade-alike function in mitigating chilling-induced photoinhibition (Egerton et al. 2000). That maybe the reason why there were no visible injuries to these native tropical forest plants, although Hong and Li (2001) had shown that low temperatures had injured chilling sensitive crops, such as coffee and cocoa, in the studied area.

During the dry season, large decreases were recorded in the maximum photosynthetic rate in leaves of seedlings grown in the large gap, whilst no significant changes were detected in shaded understory leaves (Table 1, Figure 4). This conflicts with the assumption that shade-adapted leaves are more sensitive to drought than light-adapted leaves (Abrams and Knapp 1986, Abrams and Mostoller 1995). Water deficit, another factor that limits photosynthesis, probably had little effects on seedlings grown in the understory in the present study as $A_{\max}$ and F_v/F_m did not decrease greatly in the dry season. In the dry season, the leaves are covered by water droplets from fog and the local forest soil is continuously wet (Liu et al. 2004). Fog may help ameliorate plant moisture stress by reducing transpiration or evaporation (Hutley et al. 1997) and the seedlings, possessing a high fraction of shallow roots, may use a great proportion of shallow soil water that is from fog drip (Dawson 1998). It has been reported that fog may be the only source of water for seedlings when rain is spare and deep soil water is unavailable in this forest during the dry season (Liu et al. 2005). The detection of water sources in the surface layers of soil indicates that fog may be an important contributor to the growth and survival of understory species and seedlings during the dry season in the studied area (Liu et al. 2005).

It is usually held that N content is higher in light-adapted leaves than shade-adapted leaves (Evans 1989, Ackerley 1992). However, N content has not been found to differ significantly between leaves of the same species exposed to light or shade, indicating that the higher N content of light-adapted leaves is predominantly a function of decreased SLA (Björkman and Holmgren 1963, Ackerley 1992). In this study, leaf N_a in *Z. attopensis* plants did not differ significantly between plants grown in gaps and those grown in the understory, but varied seasonally (Table 2). In the understory, greater amounts of N may be partitioned into light-harvesting systems, whereas in the gaps more N may be partitioned into Rubisco (high P_c, Table 2), resulting in similar total N_a values between sites (Evans 1989).

Close positive logarithmic relationships were observed between N_a, photosynthetic capacity ($A_{\max}$, V_{cmax} or $J_{\max}$) and leaf irradiance (PPFD$_i$) (Figure 5 and 6) in our study, whereas positive linear relationships were reported for a range of tree species (Le Roux et al. 1999 a,b, 2001, Warren and Adams 2001, Frak et al. 2002, Misson et al. 2006). Optimization of N partitioning maximizes the daily CO_2 carbon gain of individual leaves (Hikosaka and Terashima 1995). The ability to adjust allocation of total N to different pools of the photosynthetic machinery partly explains the different responses to shade and seasonal changes. It has been hypothesized that temperature adaptation involves adaptive responses to the allocation of nitrogen between electron transport and carboxylation systems that ensure that both sets of processes are colimiting at ambient conditions (Hikosaka 1997). In our study, an increased ratio of $J_{\max}$ to V_{cmax} during the cool season was observed, which is consistent with this hypothesis. However other studies investigating acclimation to growth temperature have failed to find any evidence for this hypothesis (Medlyn et al. 2002, Misson et al. 2006). P_{c} and P_{b} hardly changed with PPFD$_{\mathrm{i}}$ (Figure 7), indicating that the allocation of leaf N between Rubisco and bioenergetic systems is relatively unaffected by time integrated leaf irradiance. Similar results have also been found in tree species (e.g., in four temperate deciduous tree species, Niinemets et al. 1998; walnut, Le Loux et al. 1999a,b, Frak et al. 2002; and in *Pinus densiflora*, Han et al. 2003). These contradictory results illustrate the point that such results are dependent on experimental conditions and the species studied (Le Roux et al. 1999a, Warren and Adams 2001).

Growth

At the whole plant level, the largest biomass accumulation occurred during the wet season in all seedlings (Figure 8), indicating that most of their annual biomass is accumulated during this period. This relatively high accumulation of biomass is consistent with the high photosynthetic capacity during the wet season. Seedlings growing in the understorey had higher LMR and lower RMR and SMR than those growing in gaps, indicating that carbon allocation to the leaf at the expense of stem and root systems is one of the adaptive mechanisms in a light-limiting environment (Givnish 1988, Lambers et al. 1998, Paz 2003). LAR was found to be higher in seedlings grown in the understory than in the gaps, in accordance with results of previous studies showing that plants grown at low irradiances typically produce leaves with higher leaf areas per unit mass than plants grown at high irradiances (Givnish 1988, Popma and Bongers 1991). In the dry season, the observed increase in RMR in seedlings is a response to drought, allowing increased absorption of soil water and (thus) minimization of the water deficit (Paz 2003).

In conclusion, *Z. attopensis*, a common local liana species in Xishuangbanna tropical rain forest, has been shown to adapt to seasonal climatic changes in both understory and gap sites. Decreases in photosynthetic capacity during the cool season differed between seedlings grown in gaps and those in the understory, and were responses to low light conditions rather than to temperature. In addition, this species also showed adjustments of its photosynthetic parameters and biomass allocation during the dry season that should minimize drought stress and maintain net growth. Light appears to be the dominant factor in determining physiological changes in this species.

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Chapter 7

Photosynthetic acclimation to light changes of six tropical monsoon forest species differing in adult stature

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Abstract

We studied morphological and physiological leaf and whole-plant features of seedlings of six late-successional woody species common in the Xishuangbanna lowland rain forest in southwest China. Study species differed in adult stature and shade tolerance and included the shrubs *Lasianthus attenuatus* Jack and *Lasianthus hookeri* C.B. Clarke ex Hook. f., the sub-canopy species *Barringtonia macrostachya* (Jack) Kurz and *Linociera insignis* C.B. Clarke, the canopy tree *Pometia tomentosa* (Blume) Teijsm. & Binn., and the emergent species *Shorea chinensis* (Wang Hsie) H. Zhu. After 1 year of growth in low light (4.5% full sun), seedlings were transferred to high light (24.5% full sun) to investigate acclimation responses of existing leaves to forest gap opening and to determine whether seedling capacity for acclimation is a limiting factor in its natural regeneration. Leaves of the shrub species are shade-adapted, as indicated by their low photosynthetic capacity, efficiency in using sunflecks, low stomatal density, low Chl a/b ratio and high spongy/palisade mesophyll ratio. The shrub species utilized sunflecks efficiently because they had a short photosynthetic induction time and low induction loss. In all species, transfer of seedlings to high light resulted in a substantial initial reduction in the dark-adapted quantum yield of photosystem II (variable chlorophyll fluorescence/ maximum chlorophyll fluorescence, F_v/F_m) at midday. Predawn F_v/F_m of the taller species did not change greatly, but predawn F_v/F_m of the shrub species decreased significantly without complete recovery within 25 days of transfer to high light, indicating chronic photoinhibition and damage to the previously shade-adapted leaves. Maximum net photosynthetic rate and dark respiration of the four taller species increased considerably after transfer to high light, but not in the shrub species. Similar trends were observed for the number of newly formed leaves and relative height growth rate. We conclude that the shrubs *L. hookeri* and *L. attenuatus* have limited potential for developmental and physiological acclimation to high light, which explains their absence from forest gaps. Compared with the shrub species, the taller tree species, which are more likely to experience high light during their life span, showed a greater potential for light acclimation. Physiological differences among the four tree species were not consistent with differences in adult stature.

Keywords: chlorophyll fluorescence, leaf anatomy, light acclimation, photosynthesis, photosynthetic induction.

Introduction

In tropical rain forests, canopy gaps are important for maintaining the high diversity of plant species (Denslowet al. 1990, Hubbell et al. 1999). Shade-tolerant species comprise more than 85% of the tree species and individuals in mature tropical forests (Whitmore 1990, Lieberman et al. 1995). However, contrary to expectations, most seedlings and trees in gaps belong to shade-tolerant species that have survived tree fall, rather than being gap-dependent pioneer species (Denslow 1987, Connell 1989). Both shade-intolerant and shade-tolerant species are expected to differ in their ability to respond to changes in light environment associated with canopy gap dynamics, but this may be more important for shade-tolerant species. The ability of a plant to respond to the formation or closure of a light gap may have important repercussions on plant performance and fitness. Plant responses to increased light can occur at several organizational levels (see Chazdon 1988). At the whole-plant level, changes in growth or biomass allocation patterns may occur (e.g., Bongers and Popma 1990, Popma and Bongers 1991, Poorter et al. 2003), at the leaf level, acclimation responses may involve changes in photosynthesis and respiration (e.g., Björkman 1981, Givnish 1988, Chazdon et al. 1996) and anatomy (e.g., Bongers and Popma 1988, Cao 2000), among other parameters. Leaf structural changes may also be adaptive, e.g., a partial breakdown of antenna chlorophylls and inactivation of photosystem II (PSII) reaction centers (Öquist et al. 1992). Furthermore, when a canopy gap is created, solar radiation reaching the forest floor increases suddenly (Denslow 1987, Canham et al. 1990) and may negatively affect photosynthetic light-use efficiency of PSII, through either chronic photoinhibition or reversible down-regulation of PSII activity as a result of various protective mechanisms against excess light (Demmig-Adams and Adams 1992, Osmond 1994). Differences among species in acclimation potential and susceptibility to photoinhibition in newly formed gaps may be critical in determining the outcome of competition for resources among species (Bazzaz and Pickett 1980, Lovelock et al. 1994). Physiological changes in existing leaves and the production of new leaves with a morphology and physiology appropriate to the gap light environment are both components of the acclimation response (Bongers and Popma 1990, Newell et al. 1993, Chazdon et al. 1996, Kursar and Coley 1999, Yamashita et al. 2000). Here we report on the morphological and physiological features of leaves grown in low light and on the acclimation responses to light increases of seedlings of six shade-tolerant woody species from the Xishuangbanna lowland rain forest of southern China. Specifically, we investigated photosynthetic capacity, induction and acclimation of seedlings grown in low light and then transferred to high light. Species of different adult stature were selected to provide a range of plants differing in shade tolerance (cf. Thomas and Bazzaz 1999). To this end, we chose two shrub species that attain a maximum height of 1– 4 m, and four sub-canopy and canopy tree species with maximum heights ranging from 20 to 65 m. Shrub species in the *Lasianthus* genus are expected to be shade tolerant because they are almost never found in light gaps in the forest (Zhu 1998, 2002). The four tree species are expected to be intermediate in shade tolerance, because we assume that with the attainment of adult stature, they will increasingly show morphological and physiological characteristics of sun plants (Thomas and Bazzaz 1999, Poorter et al. 2003). We analyzed whether the shrub species have characteristics that make them better adapted to deep shade in the forest understory than the tree species. We predicted that the shrub species have a limited ability to acclimate to sudden changes in solar irradiance and that the lack of plasticity makes them obligatory shade species.

Materials and methods

Study site and plant material

The study was carried out in the Xishuangbanna Tropical Botanical Garden ($21^0$56’N, $101^0$15’E, 600 m a. s.l.), Chinese Academy of Sciences, Yunnan, SW China. The climate of Xishuangbanna is dominated by the southwest monsoon with high rainfall from May to October, so that there is a well-defined alternation of wet and dry seasons. The annual mean temperature is 22.9 °C and mean precipitation is 1,500 mm (Zhang 1963). The minimum and maximum values of temperature are about 8.7 and 34.2 °C (January and April, respectively).

The six selected woody species are two shrub and four tree species that vary in maximum stature from 1 to 65 m (Table 1). All are late-successional species common to the moist forest of the Xishuangbanna tropical area (Cao and Zhang 1997).

Table 1 List of woody species, life form and maximum canopy height. Species abbreviations are given.

Species	Abbrev.	Family	Life form	Height max. (m)
Lasianthus attenuatus Jack	LA	Rubiaceae	Understory shrub	1
Lasianthus hookeri C.B. Clark ex Hook.f.	LH	Rubiaceae	Understory shrub	4
Barringtonia macrostachya (Jack) Kurz	BM	Lecythidaceae	Sub-canopy tree	20
Linociera insignis C.B. Clarke	LI	Oleaceae	Sub-canopy tree	25
Pometia tomentosa (Bl.) Tesysm. Et Binn.	PT	Sapindaceae	Canopy tree	30
Shorea chinensis (Wang hsie) H. Zhu	SC	Dipterocarpaceae	Emergent tree	65

Plant growth

Plants of the six woody species were grown from seed. In July 2001, seeds were collected from a nearby forest and placed in a seedbed of original forest soil in a nursery growth house with about 8% full sunlight to germinate. When at least three leaves per seedling had fully developed, 15-20 seedlings of each species were transplanted individually to 12-l pots (diameter 25 cm) and placed in a poorly-lit shadehouse (4.5% of full sunlight). Shading was provided by neutral-density shade cloth. In order to minimize effects of heterogeneity within a shadehouse, the pots were rotated randomly on a weekly basis. During the course of the study, plants were treated twice with N,P,K slow-release fertilizer (Osmocote, Scotts, Marysville, OH) and were watered to maintain the soil near field capacity on days without rain. Light availability in the greenhouse was estimated by measuring photosynthetic photon flux (PPF) with two LI-190 SA quantum sensors connected to a Li-1400 datalogger (Li-Cor, Lincoln, NE, USA). One-min means of PPF were recorded over four sunny days and the daily maximum and daily mean PPF was calculated.

Experimental design

The light acclimation experiment started in July 2002 when the seedlings were 40 to 80 cm tall. Seven to 10 seedlings per species were transferred to a well-lit shadehouse (24.5% of full sunlight). The other seedlings remained in the poor-lit shadehouse, the pots were relocated to standardize a possible removal effect. Photosynthetic light response curves and plant growth were determined 20 and 30 days, respectively, after transferring plants from low to high light. The time course of chlorophyll fluorescence was measured over 25 days. All measurements were made on fully expanded and healthy leaves. The number of plants per light treatment used for morphological and physiological measurements ranged from four to eight, one leaf per plant was measured.

Photosynthetic measurements

Gas-exchange was measured in the morning between 0800 and 1130 h. Net photosynthetic rates were measured using a portable infrared gas analyzer in open system mode (Li-6400, Li-Cor), with a LED-B as the actinic light source.

Photosynthetic light response curves were developed based on measurements at eight PPF values ranging from 1,000 to 0 μmol m^{-2} s^{-1}. Before the measurements, seedlings grown in low light were allowed to acclimate to a PPF of about 400 μmol m^{-2} s^{-1} for at least 30 min. Dark respiration rate (R_d) was measured for the same leaf, after the leaves have been kept in darkness for at least 8 min. Photosynthetic light response curves were fitted to a nonrectangular hyperbola, and from these curves, the asymptotic light-saturated rate of net photosynthesis (A_{max}), quantum yield, near- light saturation point and light compensation point were determined.

The photosynthetic induction time was determined on the same leaves using for the gas exchange measurements. To ensure a leaf was not yet photosynthetically induced it was covered with black cloth for at least 3 h before measurement. After the leaf was sealed in the chamber for 15 s, a manual shutter was opened to increase the PPF to saturating levels (determined from light response curves). Net photosynthetic rate was recorded at 2- s intervals for the first 5 min, and then every 8 s until the maximum assimilation rate was achieved. The time required to reach 90% of maximum net photosynthetic rate ($T_{90\%}$) was estimated by fitting a sigmoidal curve, as described by Zipperlen and Press (1997). The induction loss was determined on the same leaf. Before measurement, a leaf was exposed to saturating light for about 40 min. Then, it was placed in the chamber in saturating light and net photosynthetic rate was monitored until a steady state was reached. The light was switched off and, after 20 min in darkness, net photosynthetic rate was measured 60 s after re-illumination. Induction state measured 60 s after an increase in irridiance (IS_{60}) was calculated as described by Chazdon and Pearcy (1986).

Chlorophyll fluorescence

To assess the magnitude and duration of photoinhibition in leaves of seedlings grown in low light following exposure to simulated gap conditions, the induction kinetics of chlorophyll fluorescence in intact leaves were measured at predawn and midday with a portable fluorescence system (FMS-2.02, Hansatech, King's Lynn, U.K.). On each seedling, a shade leaf was labeled and the initial quantum efficiency of PSII, expressed as the ratio of the measured variable chlorophyll (F_v) to the maximum chlorophyll fluorescence (F_m) ($F_v/F_m = (F_m\text{-}F_0)/F_m$, where F_0 is the dark-adapted minimal fluorescence) of the leaf, was measured 25 days following transfer to the high-light environment. Before midday measurement, a leaf clip was placed on the leaf for 15 min to allow dark acclimation. Following dark acclimation, F_0 was measured at the abaxial leaf surface. Maximum fluorescence (F_m) was recorded after a 0.8 s pulse of saturating irradiance (4,000 μmol m^{-2} s^{-1}) to close all PSII reaction centers. From this, dark-adapted initial PSII quantum efficiency (F_v/F_m) was calculated. Changes in these parameters were followed over 25 days and compared among species.

Leaf anatomy and chlorophyll analyses

Leaf anatomy was determined on seedlings grown in low light. Hand-cut transverse sections were taken from the mid-lamina region of the leaf. Leaf thickness and thickness of the palisade and mesophyll layers was measured with a compound microscope with 40× objective calibrated with an ocular micrometer. In addition, thickness of the lamina, palisade mesophyll and spongy mesophyll were measured. Spongy to palisade mesophyll thickness ratio and the total mesophyll thickness as a percentage of lamina thickness were calculated. Stomatal density and guard cell lengths were determined for the adaxial and abaxial surfaces of each leaf from prints made with nail varnish.

Chlorophyll was extracted from leaf material in cold 80% (v/v) acetone in darkness. The extract was centrifuged for 10 min at 12,000 *g* at 4°C and the chlorophyll concentration in the supernatant was determined spectrophotometrically (*UV-B 2501*, Shimadzu, Japan) following Arnon (1949).

Height growth and leaf production

Heights of all seedlings were measured just before and 1 month after transfer from low to high light. From these data, the relative growth rate of height (RGR_H) was calculated. Production of new leaves was monitored for 1 month.

Statistical analysis

Differences in induction properties and the various anatomical and morphological properties among species were tested by a one-way ANOVA. Multiple contrasts were analyzed with the Student's *t* test. Within a species, differences in net photosynthetic rate, height growth and leaf production between seedlings grown in low and those grown in high light were tested by one-way ANOVA. Statistical analysis was performed with SPSS 11.0 for Windows (SPSS, Chicago, IL).

Results

Leaf anatomy

Table 2 Anatomical and chlorophyll characteristics of leaves of six woody species grown in low light. Values are mean (±SD. Abbreviations: *n*= number of plants (one leaf per plant); FM= fresh mass, and species abbreviations are defined in Table 1. Species means followed by the same letter are not significantly different (*P*>0.05).

	Species						
Characteristic	LA	LH	BM	LI	PT	SC	n
Leaf thickness (μm)	156.7±11.4 c	189.5±14.2 b	234.6±17.7 a	181.5±11.5 b	139.5±15.3 d	178.3±8.9 b	4-6
Ratio spongy/palisade	5.37±0.45 a	4.89±0.12 b	1.62±0.21 d	2.23±0.33 c	1.79±0.38 d	1.84±0.29 cd	4-6
Rel. mesophyll thickness (%)	90.2±4.5 a	88.5±3.7 a	80.2±6.2 b	75.7±2.8 c	78.7±5.2 b	76.7±2.9 bc	4-6
Stomatal density (no.mm^{-2})	45.8±4.4 d	56.7±5.1 cd	204.8±14.5 a	111.6±8.8 c	182.0±13.2 b	71.3±6.4 cd	4-6
Guard cell length (μm)	11.3±2.3 c	14.5±3.2 b	9.5±2.6 c	17.8±2.6 a	9.8±1.9 c	9.0±0.6 c	4-6
Chl a+b (mg g^{-1} fresh weight)	2.01±0.21 bc	2.42±0.17 b	2.89±0.11 a	2.32±0.23 b	1.67±0.09 c	1.87±0.14	3-4
Chl a:b	1.68±0.23 c	1.55±0.09 c	2.16±0.14 b	2.52±0.12 a	2.45±0.16 a	2.32±0.18 a	3-4

Species differed in their expression of leaf morphological variables, and these differences were greatest for the ratio spongy/palisade, stomatal density, and Chl a/b ratio (Table 2). Seedlings of the shrubs *Lasianthus hookeri* and *L. attenuatus* had two to three times higher spongy/palisade parenchyma ratios than did seedlings of the four tree species. Stomatal density were two to four times lower in seedlings of the shrub species than in seedlings of the tree species, except for the emergent tree *Shorea chinensis*, which had values similar to those for the shrub species. Chl a/b ratios in seedlings of the shrub species were considerably lower than in seedlings of the taller tree species. Guard cell length and total chlorophyll content were variable, with seedlings of the shrub species having intermediate values.

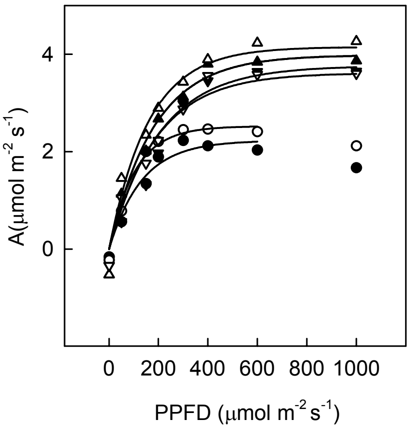

Figure 1 Photosynthetic light response curve for six woody species grown in low light. Each curve is the mean non-rectangular hyperbola obtained from four plants per species. Symbols: ● = *Lasiathus attenuatus*, ○ = *Lasianthus hookeri*, ▲= *Barringtonia macrostachya*, □= *Linociera insignis*, ▼= *Shorea chinensis*, and □= *Pometia tomentosa.*

Photosynthetic performance

Light response curves of photosynthesis of seedlings grown in low light differed differently between tree and shrub species (Figure 1). In seedlings of all species, photosynthetic capacity (A_{max}) was low, which is typical for shade plants, though A_{max} was higher for the tree species than for the shrub species (3.8 versus 2.3 µmol m^{-2} s^{-1}, Figure 1 and 2A). The light saturation point of leaves of seedlings of the tree species occurred at PPF greater than 550 µmol m^{-2} s^{-1}, whereas light saturation point occurred at about 290 µmol m^{-2} s^{-1} in leaves of seedlings of the shrub species. The light compensation point differed significantly between species (range: 22.5 to 58.5 µmol m^{-2} s^{-1}, $P<0.01$). Quantum yield did not differ significantly between species (range: 0.049 to 0.055 mol CO_2 mol^{-1} photon, $P>0.05$).

In the tree species, seedlings grown in low light had lower dark respiration rates (R_d) than seedlings transferred from low to high light (Figure 2B). In the shrub species, values for

A_{max} and R_d were similar between seedlings maintained in low light and seedlings transferred from low light to high light (Figure 2 A and B). Both A_{max} and R_d increased significantly when seedlings of the tree species were transferred from low light to high light.

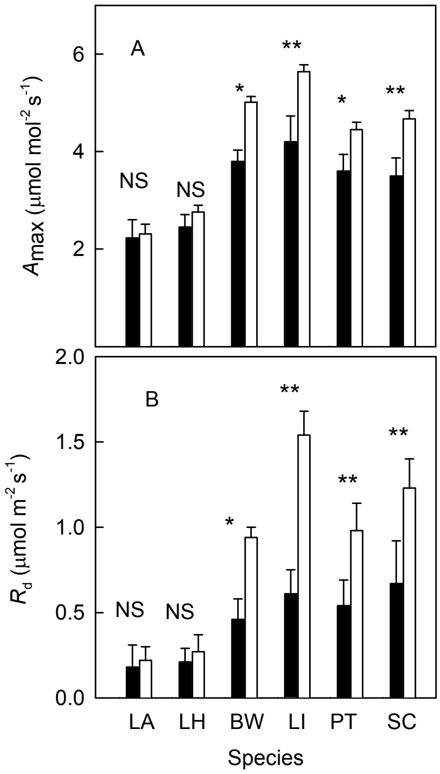

Figure 2 Maximum photosynthetic rate (A_{max}) (A) and dark respiration (R_d) (B) of pre-existing leaves of seedlings grown in low light (filled bars) and of pre-existing leaves of seedlings transferred from low to high light (open bars) for 20 days. Values are means (±SD) of four seedlings (one leaf per plant). Within a species, asterisks indicate the significance of the difference in mean values (**= $P<0.01$, *= $P<0.05$, ns= P>0.05). Species abbreviations are defined in Table 1.

When the PPF was increased from dark to saturating light, leaves of the shrub species grown in low light required about 4 min to reach 90% of their A_{max} ($T_{90\%}$) compared with 9-12 min for leaves of the tree species (Figure 3A). After fully induced leaves had been exposed to darkness for 20 min, leaves of all species maintained a relatively high induction state (IS_{60} range 60-75%), except for *Linociera insignis* (< 50%) (Figure 3B). Overall, loss of induction state was significantly greater in seedlings of the tree species than in seedlings of the shrub species.

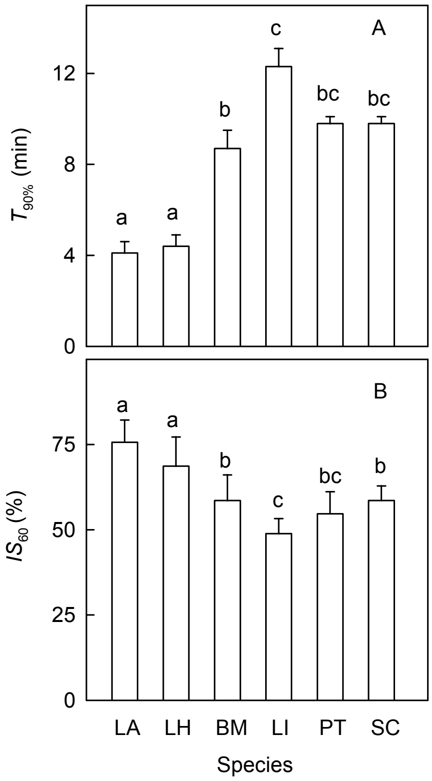

Figure 3 Photosynthetic induction responses to an increase in irradiance in seedlings of six woody species grown in low-light conditions. Mean values (±SD) of the time required to reach 90% of A_{max} (A) and the induction state after 60 s (IS_{60}) (B). Four to six plants of each species were measured. Bars with the same letter indicate means that are not significantly different (P>0.05). Multiple contrasts were analyzed by the Student's *t* test after a one-way ANOVA. Species abbreviations are defined in Table 1.

Chlorophyll fluorescence

For all species, predawn F_v/F_m ratios of seedlings maintained in low light were between 0.82 and 0.85, which is characteristic for non-stressed leaves, seedlings of all species maintained these values throughout the whole day (data not shown). Sudden exposure of seedlings of *L. hookeri* and *L. attenuatus* to high light (from 4.5% to 24.5% of full sunlight) caused photoinhibitory responses that included a substantial reduction in predawn and mid-day F_v/F_m, followed by a slow and incomplete recovery (Figure 4A and B). The reduction in F_v/F_m was more pronounced at midday than at predawn. Predawn F_v/F_m ratios were already substantially below 0.8 and the seedlings did not recover completely, indicating a 'chronic' inhibition of PSII. In contrast, predawn F_v/F_m of seedlings of the tree species did not change significantly during the 25 days after transfer to high light, although their midday F_v/F_m declined in the first few days, it then recovered almost completely (Figure 4C-F), indicating that these seedlings were only temporarily inhibited at mid-day. The increase in F_0 following exposure to high light was more pronounced at midday than at predawn in the shrub species (Figure 4G-L). The recovery in midday and predawn F_0 to the initial level was fastest in *L. insignis* (day 11), followed by *S. chinensis* (day 17), whereas more than 25 days were required for recovery in the two shrub species.

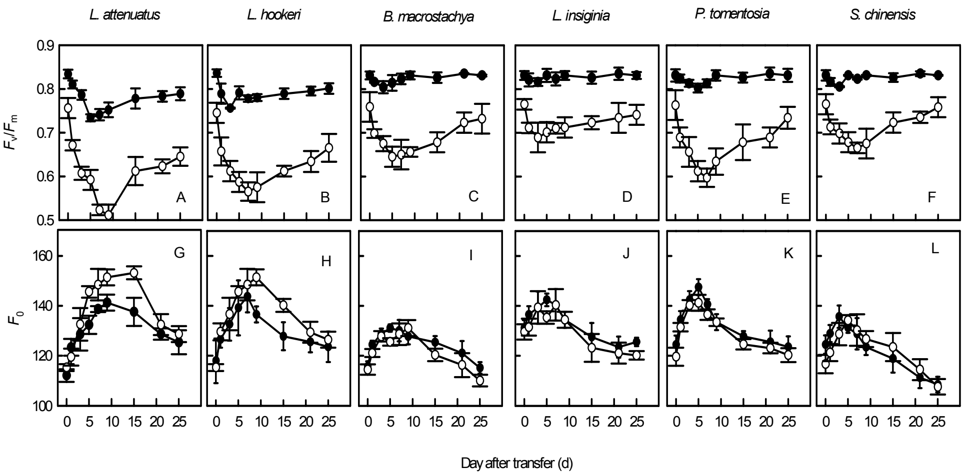

Figure 4 The time course of quantum efficiency of PSII (F_v/F_m) (A-F) and initial fluorescence of PSII (F_0) (G-L) measured directly after transferring seedlings from low light to high light condition. Measurements were made at predawn (closed circles) and at

midday (open circles) over a 25-day period. Values are means (±SD) of 4-6 seedlings (one leaf per plant).

Plant development

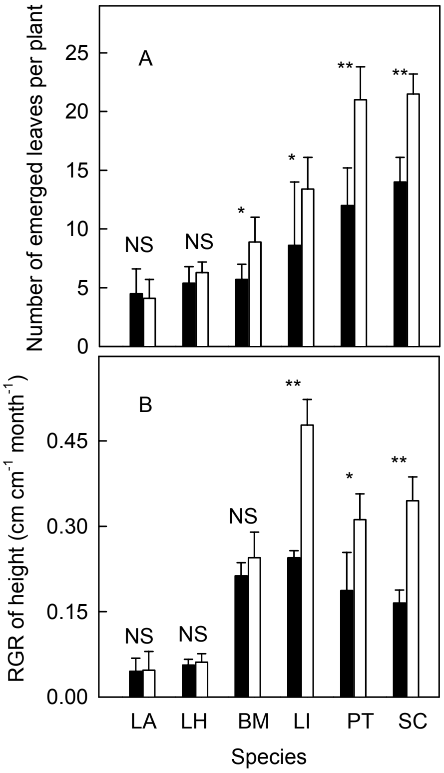

Figure 5 Leaf production (A) and relative height growth rate (RGR) (B) of seedlings grown in low light (filled bars) and of seedlings transferred from low to high light (open bars). Growth increment and leaf production was monitored for 30 days after transfer to high light. Values are means (±1 SD) of 6-8 plants. Within a species, asterisks indicate the significance of the difference in mean values (**= P<0.01, *= P<0.05, NS= P>0.05). Species abbreviations are defined in Table 1.

Among the study species, seedlings of the canopy trees *Pometia tomentosa* and *S. chinensis* produced the largest number of leaves in both low- and high-light environments (Figure 5A). Moreover, leaf production almost doubled when the seedlings were transferred from low to high light. In contrast, seedlings of the shrub species *L. hookeri* and *L. attenuatus* did not increase leaf production after transfer to high light. The relative height growth rate (RGR_H) doubled after 30 days in high light in seedlings of the three tallest tree species, *P. tomentosa*, *L. insiginia* and *S. chinensis* (Figure 5B), with seedlings of the sub-canopy tree *L. insiginia* having the highest RGR_H. In the smallest sub-canopy tree *Barringtonia macrostachya* and the two shrub species, RGR_H was similar in seedlings grown in low light or in high light.

Discussion

We found that seedlings of species with a large adult stature acclimate to transfer from low to high light. There were major differences in the ability to acclimate to high light between seedlings of shrub species and seedlings of tree species, but we did not find consistent differences in the ability to acclimate to an increase in light availability among seedlings of tree species differing in adult stature (Figures 2 and 4). Hereafter, therefore, we focus our discussion on the differences observed between seedlings of the shrub species (shrub seedlings) and seedlings of the tree species (tree seedlings).

The shrub species *L. hookeri* and *L. attenuatus* are generally best suited to low-light environments. Their leaf characteristics contribute to maximization of light capture in low light. Their leaf mesophyll tissue consists mostly of spongy cells, which facilitate the harvest of diffuse and far-red wavelengths that dominate understory light environments through increased internal light scattering (Vogelmann 1993, DeLucia et al. 1996). Their leaves also had relatively low stomatal densities and a relatively thick mesophyll layer, features generally associated with shade tolerance (Boardman 1977, Givnish 1988). Their Chl a/b ratio was relatively low, not only compared with that of the tree seedlings but also compared with shade-tolerant understory species in Brunei (Cao 2000). A low Chl a/b ratio is considered to be an adaptation to enhance absorption of the limited quantity of red light available in forest shade, and thus to maintain the energy balance between PSII and photosystem I (Boardman 1977, Björkman 1981). At the plant architecture level, *L. hookeri* and *L. attenuatus* are characterized by pendent, flexible branches and non-overlapping leaf positions, which further help capture diffuse irradiance while avoiding self-shading, and may also contribute to long-term persistence in understory habitats, where falling debris from canopy trees frequently damages plants (Van der Meer and Bongers 1996).

Although maximum photosynthetic rates of the shrub seedlings were lower than those of the tree seedlings, the time needed to reach 90% of A_{max} was much less (4 min versus 9– 12 min; Figure 3A), indicating that seedlings of these shrub species can respond quickly to sudden high-light conditions. The induction times for seedlings of the tree species are consistent with values generally found in other shade-tolerant species (e.g., Rijkers et al. 2000). We found that the induction state after 20 min of darkness remained high in the shrub seedlings (Figure 3B). These findings indicate that, in the shaded forest understory, shrub seedlings can use short periods of direct sunlight (sunflecks) more efficiently than can tree seedlings.

Seedlings of all species showed photoinhibition after sudden exposure to high light and, as expected, susceptibility differed slightly among species (Lovelock et al. 1994, Naidu and DeLucia 1997, Kitao et al. 2000). The photoinhibition responses that we observed are comparable with those found in other shade-tolerant rain forest species (Lovelock et al. 1994, Mohammed and Parker 1999, Yamashita et al. 2000). In contrast to the general pattern, however, Castro et al. (1995) failed to find long-term photoinhibition in rain forest canopy tree seedlings, except when nutrient availability was limiting. In our study, although midday F_v/F_m decreased in all species in the first several days following the transfer to high light, the tree seedlings showed almost no reduction in predawn F_v/F_m throughout the 25 days after transfer to high light, whereas predawn F_v/F_m of the shrub seedlings decreased considerably immediately upon exposure to high light. Compared with the shrub species, F_v/F_m and F_0 of seedlings of the tree species recovered more quickly and completely. Severity of photoinhibition is determined by both damage and photoprotective processes in PSII. In our study, midday F_0 and F_v/F_m of the shrub seedlings underwent two distinct phases of change after transfer to gap light conditions. In the first phase, F_v/F_m decreased with a concomitant rapid increase in F_0, representing the onset of photodamage of PSII, causing an increase in the number of closed PSII centers (Epron et al. 1992, Maxwell and Johnson 2000). In the second phase, F_0 began to decline and was accompanied by an increase in F_v/F_m. This probably indicates a gradual recovery from damage, as the process of photoprotection is established (Krause and Weis 1991). Values for F_v/F_m and F_0 indicate that leaves of seedlings of both shrub species were stressed, especially *L. attenuatus*, because predawn F_v/F_m did not fully recover during the 25 days of high-light treatment.

Although experimental observations on photosynthetic acclimation of rain forest plants to high light show a range of responses, most understory rain forest plants exhibit at least some plasticity over the range of light environments encountered in natural forest (around 1 to 20% of above-canopy light), and many are capable of considerable acclimation within this range (see Chazdon et al. 1996). We found that the photosynthetic rates and respiration rates of the tree seedlings increased significantly when seedlings were transferred to 24.5% of above-canopy light, whereas no acclimation of photosynthetic rates was observed in the shrub species (Figure 2A). In the tree species, the increased respiratory rate accompanying photosynthetic acclimation provides the energy and intermediates for constructing chloroplasts to elevate photosynthetic capacity and to enhance photoprotective mechanisms (Noguchi et al. 2001). Turnbull et al. (1993) consider that dark respiration is the parameter most sensitive to changes in light environment. Consistent with other studies (e.g., Sims and Pearcy 1991, Turnbull et al. 1993, Kursar and Coley 1999), we found that, following transfer to high light, dark respiration rates of the tree species increased 2 to 2.5 times over a period of 20 days. There was no acclimation of photosynthetic rates and no significant increase in dark respiration in the shrub seedlings (Figure 2B). These results support the hypothesis that extreme shade species lack plasticity in physiology when exposed to a change in light conditions (Boardman 1977, Björkman 1981).

The time course of acclimation at the whole-plant level depends not only on photosynthetic acclimation of existing leaves but also on the rate of production of new leaves (Newell et al. 1993, Lovelock et al. 1994). Because existing shade leaves of *L. hookeri* and *L. attenuatus* acclimated poorly to the new higher light environment, rapid production of new leaves with more advantageous morphology for high-light environments would be important for whole-plant acclimation. This, however, did not occur because new leaf production and height relative growth rate were similar between shrub seedlings grown in lowlight and in high light. The lack of acclimation by the shrub species to increasing light availability is further supported by the finding that 2 months after the experiment, *L. attenuatus* seedlings transferred to high light dropped many of their leaves and the leaves of seedlings of *L. hookeri* became yellow and started senescing. These observations indicate that the vigor of the shrub seedlings was considerably below optimum in the high-light regime.

All study species were selected on the basis of their shade tolerance. We expected the adult size of a species to have a strong impact on acclimation potential, with the tallest species having the highest acclimation potential. We found that seedlings of the smallest (shrub) species had a low acclimation potential and thus we may categorize them as obligatory shade species (cf. Boardman 1977, Chazdon et al. 1996), which is in line with the finding that *Lasianthus* is almost never found in light gaps in the forest (Zhu 1998, 2002). As predicted, seedlings of the tree species showed high photosynthetic acclimation to increased irradiance in response to simulated gap formation. Similar results have been reported for a temperate forest in North America where seedlings of canopy-dominant and understory *Acer* species exhibited different traits of adjustment to increases in irradiance (Sipe and Bazzaz 1994, 1995). A likely explanation for this difference between shrub seedlings and tree seedlings is that the shrub species usually complete their life cycle in full shade, never experiencing light availabilities greater than 1 to 5% of full sunlight unless there is a disruption of the overstory (Zhu 1998, 2002), and so would benefit little from the ability to acclimate to increased irradiance. The taller tree species, however, may eventually reach either the forest canopy or sub-canopy layer. Consequently, during their development from seedling to mature tree, individuals of the tree species will have a greater chance of exposure to high irradiances, and hence may benefit from the ability to acclimate to increased irradiance. These differences in acclimation responses may play an important role in niche specialization among woody species in wet tropical forests.

Acclimation potential in the tree species did not increase, as predicted, with increasing adult stature (cf. Thomas and Bazzaz 1999, Poorter et al. 2003). Similarly, Gurvich et al. (2003) reported that some leaf traits were unrelated to maximum tree height and concluded that maximum tree height is a poor indicator of shade tolerance.

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Chapter 8

Summary

Rubber plantation in Xishuangbanna, SW China

Lianas and trees in tropical forests in south China

summary

Lianas (woody climbers) and trees are the most important life-forms in most tropical forests. In many of these forests lianas are abundant and diverse and their presence is often a key physiognomic feature. Lianas contribute substantially to the floristic, structural and functional diversity of tropical forests, and have both positive (providing valuable food resources, habitat, and connections among tree canopies that are used as pathways by arboreal animals) and negative (reducing tree growth, fecundity and survivorship) effects on forests.

Lianas are increasingly well studied in many areas around the world, but in southeast Asia they are relatively unknown. This PhD dissertation describes liana communities in selected but well distributed tropical forests in Xhishuangbanna, southwest China. In addition the question what makes lianas functionally different from trees is addressed. A number of structural-functional characteristics of lianas are analysed, comparative to trees. Special attention is put to growth performance and ecophysiological leaf and plant characters in a framework of adaptive ecology. The last part of the dissertation addresses adaptive behavior, both within one liana species as across a number of species differing in adult stature.

Liana communities in different forests

The liana communities of three common forest types are analysed: seasonally wet. montane forest and evergreen broad-leaved forest. In each forest five 0.1 ha (20 x 50 m) plots were established. The density of lianas varied significantly among the three forests, with on average 445, 276 and 301 individuals per plot in the seasonally wet, montane, and evergreen forests, respectively. All three forests combined consisted of a total of 147 liana species, representing 48 families and 75 genera. A plot had on average 40, 26, and 21 species in the seasonally wet, montane, and evergreen forest, respectively. The forests were rather different as similarity between their liana assemblages was low. In all three forests, most lianas were stem twiners and scramblers, with relatively few hook, tendril and root climbers. Liana species were mostly wind dispersed in the evergreen forest, but animal and gravity dispersed in the other two forests.

The higher liana abundance in the seasonal forest is consistent with the documented pattern that lianas peak in abundance with increasing seasonality. Compared to other tropical Asian tropical forests, the diversity and abundance of lianas is relatively high in Xishuangbanna, which may be due to the relatively warm climate, as well as its high seasonal rainfall and its high rates of disturbance and forest fragmentation.

How different are lianas from trees?

In two studies a large number of liana and tree species were compared for selected leaf structural and physiological characteritics. Chapter 3 focusses on differences in adaptation to climate seasonality. Most organisms decrease in abundance with decreasing annual precipitation and increasing seasonality. However, lianas are an exception to this general rule: they increase in abundance with increasing seasonality (Schnitzer 2005). In this chapter the hypothesis is tested that lianas are physiologically more robust than trees during the dry season, thus contributing to an explanation of their relatively high abundance in seasonal forests. We compared a range of leaf-level physiological attributes of 18 co-occurring liana and 16 tree species during the wet and dry seasons in a tropical seasonal rainforest in Xishuangbanna. During the wet season, lianas (liana leaves) had significantly higher nitrogen concentrations (N_{mass}), $\delta^{13}C$ values, and lower leaf mass per area (LMA) than trees, indicating that lianas have higher water-use efficiency (WUE) and lower structural investments. However, liana and tree species did not differ significantly in photosynthesis (A_{area}), dark respiration ($\mathrm{R}d_{\mathrm{area}}$), chlorophyll content ($\mathrm{Chl}_{\mathrm{mass}}$), carotenoid to chlorophyll ratio (Car/Chl), phosphorus concentration (P_{mass}), N:P ratios, and photosynthetic nitrogen- and phosphorus- use effeciency (PNUE, PPUE). During the dry season, the decrease in A_{area} and N_{mass} was far lower in lianas than in trees, suggesting that lianas fix more carbon and suffer less from water stress during this season. From the wet to the dry season, average A_{area} decreased by 30.1% in tree species, compared with only 12.8 % in liana species. N_{mass}, P_{mass} and PNUE changed little for lianas, while these factors decreased strongly for tree species. The $\delta^{13}C$, LMA and Car/Chl values for both lianas and trees did not vary significantly with the season.

These results show that lianas are less negatively effected by a dry season than trees, providing eco-physiological evidences as to why lianas are abundant in the seasonally rainforest. The leaf-level physiological characteristics show that lianas tend to fix more carbon, have a higher resource capture efficiency (water and nitrogen) in the dry season, and have lower cost of resource capture, compared to trees, thus confirming the hypothesis that differences in photosynthetic attributes may contribute to the competitive advantage of lianas over trees in seasonal forests.

Chapter 4 addresses the question whether lianas are more efficient than trees in nutrient resorption during leaf senescence. This would give an additional advantage in nutrient poor environments as many tropical forests are. The chapter presents changes in leaf size, leaf mass and foliar nutrient concentrations during leaf senescence in 12 liana and 14 tree species in a tropical strongly phosporus-limited montane rain forest in Xishuangbanna. The relative leaf shrinkage and mass loss during senescence did not differ significantly between lianas and trees. Nutrient concentrations in mature leaves and nitrogen resorption efficiency of liana species were similar to those of tree species, but the phosphorus concentrations of liana litter were higher, and liana's phosphorus resorption efficiencies were lower. These results therefore provide clear evidence in favour of a novel mechanism whereby lianas may influence the ecosystems in which they occur. Through the production of nutrient-rich litter, they have the potential to greatly enhance the availability of nutrients in areas where they are abundant, and thus they may have significant effects on small-scale biodiversity.

Another important difference between lianas and trees is the larger growth rate of lianas, as has been often postulated. To examine this hypothesis more closely, a range of physiological, morphological, and biomass parameters at the leaf and whole plant level were compared in seedlings of five *Bauhinia* species of different life form and light demand: two light-demanding lianas, one shade-tolerant liana, and two light-demanding trees. Seedlings of these five species were grown in a shadehouse with 25% of full sunlight. Compared to trees, the two light-demanding lianas had lower photosynthetic rates per unit area (A_{area}) and similar photosynthetic rates per unit mass (A_{mass}). High specific leaf area (SLA) and leaf mass fraction (leaf mass/plant mass, LMF) in the two light-demanding lianas were reflected in a higher leaf area ratio (LAR). The two light-demanding liana species had higher relative growth rate (RGR), allocated more biomass to leaf production (higher LMF and LAR) and stem mass fraction (SMF), and less biomass to the roots (root mass fraction, RMF) than the two tree species. The shade-tolerant liana had the lowest RGR of all five species, and had a higher RMF, lower SMF, and similar LMF than the two light-demanding liana species. Across species, RGR was positively related to SLA, but not to LAR and A_{area}. The faster growth of light-demanding lianas compared to light-demanding trees is based on morphological parameters (SLA, LMF, and LAR), and cannot be attributed to higher photosynthetic rates at the leaf level. The shade-tolerant liana exhibited a different growth strategy from the light-demanding species. Our study shows that, even within a genus (in this case *Bauhinia*), plant growth is rather variable, and that this variation is related to life form (lianas vs trees) and to light demand (light-demanding vs shade tolerant).

Seasonal acclimation of a liana

Under natural conditions, photosynthesis is biochemically regulated to maintain a balance between the rates of its component processes and the concentrations of metabolites, and is affected by continuously changing environmental variables, such as light, water availability, and temperature. Xishuangbanna, biogeographically located in the transitional zone between tropical Southeast Asia and subtropical East Asia, has a rich tropical flora and typical tropical rain forests in the lowland area. It has been hypothesized that the vegetation there is likely to be affected by the seasonal drought and chilling because it is far from the

Equator and at a relatively high altitude. To test this hypothesis, Chapter 6 addresses the photosynthetic adaptation and growth responses in seedlings of a local liana species (*Zizyphus attopensis* Pierre) in three contrasting natural microhabitats: understory, a small gap and a large gap. Photosynthetic capacity (light-saturated photosynthetic rate, $A_{\max}$), maximum rate of carboxylation (V_{cmax}) and electron transport ($J_{\max}$), and partitioning of leaf nitrogen into carboxylation (P_c) and electron light transport (P_b) differed significantly between seasons and microhabitats. Specific leaf area (SLA) did not change seasonally, but was different between plants grown in each of the three microhabitats and was negatively linear related to the daily integrated photon flux density ($\mathrm{PPFD_i}$). In contrast, nitrogen content per unit area (N_a) changed seasonally but did not differ among microhabitats. Measurements of maximum photosystem II (PSII) photochemical efficiency showed that no chronic photoinhibition occurred for all microhabitats throughout the experimental period. Photosynthetic capacity was greatest in the wet season and lowest in the cool season. During the cool and dry seasons, the reduction in $A_{\max}$ was greater in seedlings grown in the large gap than in those grown in understory and small gap. Close logarithmic relationships were detected between $\mathrm{PPFD_i}$, leaf N_a and photosynthetic capacity. Stem mass ratio decreased and root mass ratio increased in the dry season. These results show that seasonal acclimation in growth and photosynthesis of the seedlings was due to changes in biochemical features (particularly N_a and partitioning of total leaf nitrogen between the different photosynthetic pools) and biomass allocation, rather than to changes in leaf morphological features (such as SLA). The local light level is the main factor driving seasonal variations in growth and photosynthesis in the study area due to the presence of heavy fog during the cool and dry seasons which reduces irradiance and supplies water to the soil surface layers.

Light acclimation, adult stature and shade tolerance

Finally, Chapter 7 addresses light acclimation of seedlings of six late-successional common woody species differing in adult stature and shade tolerance. Especially morphological and physiological leaf and whole-plant features are analysed. After 1 year of growth in low light (4.5% full sun), seedlings were transferred to high light (24.5% full sun) to investigate acclimation responses of existing leaves to forest gap opening and to determine whether seedling capacity for acclimation is a limiting factor in its natural regeneration. Leaves of the small shrub species are shade-adapted, as indicated by their low photosynthetic capacity, efficiency in using sunflecks, low stomatal density, low Chl a/b ratio and high spongy/palisade mesophyll ratio. The shrub species utilized sunflecks efficiently because of a short photosynthetic induction time and low induction loss. In all species, transfer of seedlings to high light resulted in a substantial initial reduction in the dark-adapted quantum yield of photosystem II (F_v /F_m) at midday. Predawn F_v /F_m of the taller species did not change greatly, but predawn F_v /F_m of the short species (shrubs) decreased significantly without complete recovery within 25 days of transfer to high light, indicating chronic photoinhibition and damage to the previously shade-adapted leaves. Maximum net photosynthetic rate and dark respiration of the four taller species increased considerably after transfer to high light, but not in the shrub species. Similar trends were observed for the number of newly formed leaves and relative height growth rate. We conclude that the short species have limited potential for developmental and physiological acclimation to high light, which explains their absence from forest gaps. Compared with shrub species, the taller tree species, which are more likely to experience high light during their life span, showed a greater potential for light acclimation. Physiological differences among the four tree species were not consistent with differences in adult stature.

Lianas versus trees: are differences adaptive?

Phenotypic changes that we see over evolutionary time, across diverse environments and among taxa, often reflect adaptive evolution. In the broad sense adaptations are phenotypic traits that have been favored by natural selection, and can be identified by being variable, heritable and responsible for variation in fitness. The evolution of growth forms since the early terrestrial radiations is a complex history of innovation, complexification, simplification, conservatism, radiation and extinction (Rowe and Speck 2003, 2005). Trees and lianas have different ecological preferences and different attributes, but we are far from being able to link this directly to evolutionary differences. In more general terms we are confronted with questions like: are certain types of growth form highly constrained and immovable in evolutionary terms? Are some plant groups more ‘flexible’ in their capacity to evolve widely differing growth forms and is this capacity related to the evolutionary age or complexity of the group? What are the ecological factors that coerce to either canalise or facilitate growth form variation and evolution? Much more work is needed to be able to answer these questions. It is clear that lianas have growth strategies different from trees, as shown for some aspects in this thesis, but lianas do not always follow expected patterns. Additionally, for some characteristics lianas are far less different from trees than expected, as has been showed by a number of recent studies (Gilbert et al. 2006, Santiago and Wright 2007, Selaya 2007, this thesis). These new results shed new light on patterns of adaptive ecology of lianas versus trees in tropical forests. Together, these results force us to re-evaluate the broad generalizations that we sometimes use. This warrants further studies on the ecological differences between lianas and trees, including variations therein among forest types in different climates.

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Lianen en bomen in tropisch bos in zuid China
Samenvatting

Lianen (houtige klimmers) en bomen zijn in de meeste tropische bossen de voornaamste levensvormen. In veel van deze bossen zijn lianen abundant en gevarieerd, en hun aanwezigheid is veelal beeldbepalend voor het bos. Lianen dragen aanzienlijk bij aan de rijkdom aan plantensoorten en de structurele en functionele diversiteit van tropische bossen, en hun effecten op bossen kunnen zowel positief (als bron van voedsel, habitat en verbindingen tussen boomkronen voor boomlevende dieren) als negatief (vermindering van boomgroei, -productiviteit en –overleving) zijn.

Lianen worden in veel gebieden in de wereld in toenemende mate bestudeerd, maar in Zuidoost-Azië zijn ze nog relatief onbekend. Dit proefschrift beschrijft lianengemeenschappen in geselecteerde maar veel voorkomende tropische bossen in Xhishuangbanna, in Zuidwest-China. Daarnaast wordt de vraag behandeld wat maakt dat lianen functioneel verschillen van bomen. Een aantal structuur- en functionele eigenschappen van lianen worden geanalyseerd en vergeleken met die van bomen. Speciale aandacht wordt besteed aan groeiprestatie en ecofysiologische eigenschappen op blad- en plantniveau in het licht van ecologische aanpassing. Het laatste deel van het proefschrift behandelt aanpassingsgedrag, zowel binnen één lianensoort, als tussen een serie soorten die verschillen in groeivorm.

Lianen gemeenschappen in verschillende bossen

Van drie algemene bostypes is de lianengemeenschap geanalyseerd: van seizoenbos, bergbos, en altijdgroen loofbos. In elk bos zijn vijf 0.1 ha (20x50m) plots opgezet. De lianendichtheid verschilde significant tussen de drie bossen, met gemiddeld 445, 276 en 301 individuen per plot in respectievelijk het seizoenbos, het bergbos en het altijdgroene loofbos. Samen kwamen er in de drie bossen 147 soorten lianen voor, uit 48 families en 75 genera. Per plot kwamen gemiddeld 40 soorten voor in het seizoenbos, 26 in het bergbos en 21 in het altijdgroene loofbos. De bossen verschilden aanzienlijk van elkaar, want de similariteit tussen de lianengemeenschappen was laag. In alle drie de bossen waren de meeste lianen stamwikkelaars en stamklimmers, met relatief weinig haak-, rank- of wortelklimmers. Lianensoorten in het altijdgroene bos kennen vooral windverspreiding van zaden, terwijl verspreiding door dieren en door zwaartekracht in de andere bossen meer voorkwam.

De hogere lianendichtheid in het seizoenbos komt overeen met het beschreven patroon van toename in lianendichtheid naarmate de seizoenen prominenter worden. In vergelijking met andere Aziatische tropische bossen is de diversiteit en abundantie van lianen relatief hoog in Xishuangbanna, hetgeen door het relatief warme klimaat zou kunnen komen, of door de hoge regenval en de grote mate van verstoring en fragmentatie van het bos.

Hoe verschillend zijn lianen van bomen?

In twee studies zijn een grote hoeveelheid lianensoorten en boomsoorten met elkaar vergeleken voor wat betreft bladstruktuur- en fysiologische eigenschappen. Hoofdstuk 3 richt zich op verschillen in aanpassing aan de seizoensveranderingen van het klimaat. De meeste organismen nemen af in abundantie met afnemende jaarlijkse neerslag en toenemende seizoensmatigheid. Lianen zijn echter een uitzondering op deze regel: hun aantal neemt juist toe met toenemende seizoensverschillen (Schnitzer 2005). In dit hoofdstuk wordt de hypothese getest dat lianen fysiologisch gezien meer robuust zijn dan bomen in het droge seizoen, en dat dat hun relatieve hoge abundantie in seizoenbos helpt te verklaren. Van 18 samen voorkomende lianensoorten en 16 boomsoorten hebben we op bladniveau een serie fysiologische kenmerken vergeleken in een tropisch seizoenbos in Xishuangbanna, in het natte en in het droge seizoen. Tijdens het natte seizoen hadden lianen significant hogere stikstof concentraties (N_{mass}), $\delta^{13}C$ waarden en lagere bladmassa per oppervlakte (LMA) dan bomen, wat duidt op een hogere watergebruiksefficientie (WUE) en lagere investeringen in structuur. Lianensoorten en boomsoorten verschilden echter niet significant in fotosynthese (A_{area}), bladademhaling ($\mathrm{R}d_{\mathrm{area}}$), hoeveelheid chlorofyl ($\mathrm{Chl}_{\mathrm{mass}}$), de verhouding van carotenoïden over chlorofyl (Car/Chl), fosforconcentratie (P_{mass}), N:P ratios, en fotosynthetische stikstof- en fosfor gebruiksefficiëntie (PNUE, PPUE). In het droge seizoen was de afname van A_{area} en N_{mass} een stuk lager in lianen dan in bomen, hetgeen suggereert dat lianen meer koolstof vastleggen en minder te lijden hebben van droogtestress tijdens dit seizoen. Ten opzichte van het natte seizoen nam de gemiddelde A_{area} in het droge seizoen met 30.1% af in bomen, vergeleken bij een afname van slechts 12.8% in lianen. N_{mass}, P_{mass} en PNUE veranderden weinig voor lianen, terwijl deze parameters in bomen sterk afnamen. De $\delta^{13}C$, LMA en Car/Chl waarden veranderden noch voor lianen, noch voor bomen significant met de seizoenen.

Deze resultaten laten zien dat lianen minder negatieve effecten ondervinden van een droog seizoen dan bomen, daarmee eco-fysiologisch bewijs biedend voor het waarom van de hoge lianenabundantie in tropisch seizoenbos. De fysiologische eigenschappen op bladniveau laten zien dat lianen in vergelijking met bomen over het algemeen meer koolstof vastleggen, hulpbronnen (water en stilstof) met een hogere efficiëntie opnemen, en lagere kosten hebben voor het opnemen van hulpbronnen, daarmee de hypothese bevestigend dat verschillen in fotosynthetische kenmerken kunnen bijdragen tot een concurrentievoordeel van lianen over bomen in het seizoenbos.

Hoofdstuk 4 behandelt de vraag of lianen efficiënter zijn dan bomen in nutriëntenresorptie uit afstervende bladeren. Dit zou extra voordeel bieden in nutriëntenarme milieus, wat veel tropische bossen zijn. Het hoofdstuk laat veranderingen zien in bladgrootte, bladmassa, en nutriëntenconcentratie van het blad tijdens bladafsterving in 12 lianensoorten en 14 boomsoorten in een nat tropisch bergbos met sterke fosforbeperking in Xishuangbanna. De relatieve bladkrimp en massaverlies tijdens bladafsterving verschilde niet significant tussen linanen en bomen. Nutriëntenconcentraties in volgroeide bladeren en de efficiëntie van nutriëntenresorptie waren vergelijkbaar met die van boomsoorten, maar de effiëntie van fosforresoptie van lianen was lager, en de fosforconcentratie in het bladafval van lianen was hoger. Deze resultaten leveren daarom duidelijk bewijs ten gunste van een nieuw mechanisme waarmee lianen het ecosysteem waarin zij voorkomen kunnen beïnvloeden. Door de productie van nutriëntenrijk bladafval hebben zij in de gebieden waarin zij veel voorkomen de mogelijkheid de beschikbaarheid aan nutriënten sterk te verbeteren, en zo kunnen zij een aanzienlijk effect hebben op locale biodiversiteit.

Een ander belangrijk verschil tussen lianen en bomen is de vaak veronderstelde grotere groeisnelheid van lianen. Om deze hypothese nader te onderzoeken zijn een serie fysiologische, morfologische en biomassa parameters op bladniveau en op plantniveau vergeleken in zaailingen van vijf *Bauhinia* soorten die verschillen in groeivorm en lichtbehoefte: twee lichteisende lianen, één schaduwtolerante liaan en twee lichteisende bomen. Zaailingen van deze vijf soorten zijn gekweekt in een schaduwkas met 25% van het volle zonlicht. Vergeleken bij bomen hadden de twee lichteisende lianen lagere fotosynthese snelheden per eenheid blad oppervlak (A_{area}) en vergelijkbare fotosynthese snelheden per massa eenheid (A_{mass}). Een groot specifiek bladoppervlak (SLA) en fractie blad massa (LMF; bladmassa/plantmassa) in de twee lichteisende lianen werden weerspiegeld in een hogere blad oppervlak ratio (LAR; bladoppervlak/plantmassa). De twee lichteisende lianensoorten hadden een hogere relatieve groeisnelheid (RGR), ze alloceerden meer biomassa voor bladproductie (hogere LMF en LAR) en voor de stam (hogere stam massa-fractie, SMF; stammassa/plantmassa), en minder biomassa naar de wortels (wortel massa fractie, RMF; wortelmassa/plantmassa) dan de twee boomsoorten. De schaduwtolerante liaan had de laagste RGR van alle vijf soorten en had een hogere RMF en een lagere SMF dan de twee lichteisende lianen maar dezelfde LMF. Gezien over alle soorten samen was RGR positief gerelateerd aan SLA, maar niet aan LAR en A_{area}. De snellere groei van de lichteisende lianen in vergelijking met de lichteisende bomen vindt zijn oorsprong in morfologische parameters (SLA, LMF en LAR), en kan niet toegeschreven worden aan hogere fotosynthese snelheid op bladniveau. De schaduwtolerante liaan vertoonde een andere groeistrategie dan de lichteisende soorten. Onze studie laat zien dat, zelfs binnen een genus (in dit geval *Bauhinia*) plantengroei tamelijk variabel is, en dat deze variatie gerelateerd is aan groeivorm (lianen vs. bomen) en aan lichtbehoefte (lichteisend vs schaduwtolerant).

Seizoensaanpassing van een liaan

Onder natuurlijke omstandigheden wordt fotosynthese biochemisch gereguleerd om een evenwicht in stand te houden tussen de snelheid van de plaatsvindende processen en de concentraties metabolieten, en wordt zij beïnvloed door continu veranderende omgevingsfacoren, zoals licht, waterbeschikbaarheid en temperatuur. Xishuangbanna, biogeografisch behorend tot de transitiezone tussen tropisch Zuidoost-Azië en subtropisch Oost-Azië, heeft een rijke tropische flora and typische tropische regenwouden in de laaglanden. Er wordt verondersteld dat de vegetatie beïnvloed wordt door een droog seizoen en door afkoeling, omdat het ver van de evenaar ligt en op relatief grote hoogte. Om deze hypothese te testen gaat hoofdstuk 6 in op de fotosynthetische aanpassing en de groeireacties in zaailingen van een lokale lianensoort (*Zizyphus attopensis* Pierre) in drie contrasterende natuurlijke microhabitats: de ondergroei, een kleine open plek in het bos, en een grote open plek in het bos. Fotosynthetische capaciteit (licht verzadigde fotosynthese snelheid, A_{max}), maximale carboxylatie snelheid (V_{cmax}), maximale electronen transport (J_{max}) en verdeling van bladstikstof in carboxylatie (P_{c}) en elektronentransport (P_{b}) verschilde significant tussen seizoenen en microhabitats. Specifiek bladoppervlak (SLA) veranderde niet met de seizoenen, maar verschilde wel tussen de microhabitats waarin de planten gekweekt waren, en was negatief lineair gerelateerd aan de dagelijkse lichthoeveelheid ($\mathrm{PPFD_i}$). Het stikstofgehalte per eenheid bladoppervlak (N_{a}) daarentegen veranderde per seizoen maar verschilde niet tussen microhabitats. Metingen van de maximale fotochemische efficiëntie van fotosysteem II (PSII) lieten zien dat er tijdens de experimentele periode in geen van de microhabitats sprake was van chronische fotoinhibitie van fotosynthese. De fotosynthetische capaciteit was het hoogst in het natte seizoen en het laagst in het koele seizoen. Tijdens het koele en het droge seizoen was de reductie in A_{max} groter voor zaailingen in de grote open plek dan voor zaailingen in de ondergroei en in de kleine open plek. Tussen PPFDi, N_{a} en de fotosynthetische capaciteit werd een nauwe logaritmische relatie gevonden.

De stam massa ratio nam af, en de wortel massa ratio nam toe in het droge seizoen. Deze resultaten laten zien dat seizoensaanpassing in groei en fotosynthese van de zaailingen was toe te schrijven aan veranderingen in biochemische kenmerken (in het bijzonder N_{a} en de partitionering van het totaal aan bladstikstof tussen verschillende fotosynthetische centra) en biomassa allocatie, in plaats van door veranderingen in morfologische eigenschappen (zoals SLA). Het lokale lichtniveau is de belangrijkste drijvende kracht achter seizoensvariaties in groei en fotosynthese in het studiegebied. Dit is een gevolg van de zware mist tijdens de koele en droge seizoenen, welke de instraling van zonlicht vermindert en het grondoppervlak van water voorziet.

Aanpassing aan licht, grootte en schaduwtolerantie

Hoofdstuk 7 tenslotte, behandelt de aanpassing aan licht van zaailingen van zes algemeen voorkomende houtige late-successiesoorten die verschillen in grootte en schaduwtolerantie. Met name de morfologische en fyiologische blad-, en planteigenschappen zijn geanalyseerd. Na één jaar groei bij lage lichtintensiteit (4.5% van vol zonlicht), zijn de zaailingen overgeplaatst naar hoge lichtintensiteit (24.5% van vol zonlicht) om de aanpassing te onderzoeken van bestaande bladeren aan het openen van het kronendak, en om te bepalen of het aanpassingsvermogen van zaailingen een beperkende factor is voor natuurlijke verjonging. De bladeren van de kleine struiksoorten zijn aangepast aan schaduw, zoals blijkt uit hun lage fotosynthetische capaciteit, hoge efficiëntie in het gebruik van korte periodes van direct lichtinval, lage stomatale dichtheid, lage Chl a/b ratio en hoge spons/palisade mesofyl ratio. De struiksoorten gebruikten korte periodes van direct lichtinval efficiënt door een korte fotosynthese inductietijd en een laag inductieverlies. In alle soorten resulteerde de verplaatsing van de zaailingen naar hoge lichtintensiteit in een aanzienlijke initiële afname van de waarde van de donker-aangepaste kwantumopbrengst van PSII (F_v/F_m) in de middag. De F_v/F_m waarde voor zonsopkomst van de grotere soorten veranderde niet zo erg, maar de F_v/F_m voor zonsopkomst van de struiksoorten nam significant af, zonder compleet herstel binnen 25 dagen na de verplaatsing naar hoge lichtintensiteit, wat duidt op chronische foto-inhibitie en schade aan de schaduw-aangepaste bladeren. De maximale fotosynthese snelheid en bladademhaling in de vier grotere soorten nam aanzienlijk toe na de verplaatsing naar hoge lichtintensiteit, maar niet in de struiksoorten. Vergelijkbare trends werden waargenomen voor de hoeveelheid nieuw ontwikkelde bladeren, en de relatieve groeisnelheid. We concluderen dat de kleinere soort een beperkt vermogen heeft voor groei- en fysiologische aanpassing aan hoge lichtintensiteit, wat hun afwezigheid in open plekken in het bos verklaart. In vergelijking met struiksoorten lieten de grote soorten, die tijdens hun leven met grotere waarschijnlijkheid aan hoge lichtintensiteit blootgesteld worden, een groter vermogen voor aanpassing aan licht zien. Fysiologische verschillen tussen de vier soorten waren niet consistent met de verschillen in hun grootte.

Lianen versus bomen: zijn de verschillen aanpassingen?

Fenotypische veranderingen die over evolutionaire tijd plaatsvinden, in gevarieerde milieus, en tussen taxa, reflecteren vaak evolutionaire aanpassing. In brede zin zijn aanpassingen fenotypische eigenschappen die bevoordeeld zijn in de natuurlijke selectie, en die gekenmerkt kunnen worden als variabel, erfelijk en verantwoordelijk voor variatie in fitness. De evolutie van groeivormen sinds de vroege verspreiding van het leven op aarde is een complexe geschiedenis van innovatie, complexificatie, simplificatie, conservatisme, verspreiding en uitsterving (Rowe & Speck 2003, 2005). Bomen en lianen hebben verschillende ecologische voorkeuren en verschillende eigenschappen, maar we zijn bij lange na niet in staat om dit direct met evolutionaire verschillen in verband te brengen. In meer algemene termen worden we confronteerd met vragen als: zijn bepaalde typen groeivormen zeer beperkt en in evolutionaire zin onveranderbaar? Zijn sommige plantengroepen flexibeler in hun vermogen om sterk verschillende groeivormen te ontwikkelen en is dit vermogen gerelateerd aan de evolutionaire ouderdom of aan de complexiteit van de groep? Wat zijn de ecologische factoren die de kanalisatie of de facilitatie afdwingen van de variatie in, en evolutie van, groeivormen? Er is nog veel onderzoek nodig om deze vragen te kunnen beantwoorden. Het is duidelijk dat lianen andere groeistrategiën hebben dan bomen, zoals delen van deze thesis laten zien, maar lianen volgen niet altijd de voorspelde patronen. Daarnaast geldt voor sommige eigenschappen dat lianen lang niet zoveel van bomen verschillen als gedacht, zoals in een serie recente studies naar voren is gekomen (Gilbert et al. 2006, Santiago and Wright 2006, Selaya 2007, deze thesis). Deze nieuwe resultaten dwingen ons om bepaalde generalisaties die wij plachten te gebruiken opnieuw te evalueren. Dit geeft grond voor verder onderzoek naar de ecologische verschillen tussen lianen en bomen, inclusief de variaties daarin binnen bostypen in verschillende klimaten.

摘要:

木质藤本和树木是大多数热带森林最重要的两种生活型植物。热带森林的木质藤本种类繁多，它不仅是热带森林结构中重要的外貌特征，而且其丰富度也被认为是热带森林与温带森林外观上最显著的区别。森林中，木质藤本对生物多样性的维持、树木的生长和发育、生态系统的过程等方面起着十分重要的作用。

在全世界范围内，很多地区有关木质藤本的研究很多，但在东南亚相对较少。在本人博士研究期间，以中国西南地区西双版纳热带森林为研究对象，描述了三种不同森林木质藤本群落的基本特征，探讨了木质藤本与树木不同功能的作用。与树木相比，分析了木质藤本的一些叶片的结构－功能相关特征。特别是在适应生态的总体框架里，关注了不同生态学习性和生活型植物的生长行为、叶片和植株的生理特征，以及其对环境因子的适应行为。主要结论如下：

1． 在西双版纳山地雨林、季风常绿阔叶林和湿性季节雨林里，木质藤本的密度差异显著，分别为445, 276 和 301 株/0.1 ha。在三个森林里，总共有147 木质藤本，蒂属于48个科，75个属。在这三个森林间，木质藤本的物种相似性较低。大多数木质藤本的攀援机制为茎缠绕和爬行，而钩刺、卷须和根附相对较少。在季风常绿阔叶林里，风传播的木质藤本相对最多，而其它两种森林里，动物和重力传播的较多。季节雨林里，木质藤本丰富度和多样性相对最高，这与随季节性增加，木质藤本丰富度增加的趋势一致。相对于亚洲其它热带森林，西双版纳木质藤本的丰富度和多样性相对较高，这可能与其温暖的气候和植被受到严重的人为干扰，以及降雨较高的季节性有关。

2． 在季节雨林里，我们选择了18种木质藤本和16种树木，在湿季和干季了分别采集冠层叶片研究了一些形态、结构和生理特征。与树木相比，在湿季木质藤本有明显高的氮含量(N_{mass}), 碳同位素值(δ^{13}C)和低的叶片质量比(LMA)，表明木质藤本有相对较高的水分利用效率和低的结构投资。然而，木质藤本和树木在最大净光合速率(A_{area})、暗呼吸、叶绿素含量、类胡萝卜素/叶绿素、磷含量(P_{mass})，N:P比, 以及光合氮和磷的利用效率(PNUE, PPUE)上没有显著差异。在干季，与树木相比，木质藤本的净光合速率和氮含量下降较少，表明其遭受较轻的水分胁迫和进行更多的碳固定。从湿季到干季，树木的A_{area}平均下降了30.1%，而木质藤本仅下降了12.8 %；对于木质藤本而言，N_{mass}, P_{mass} 和PNUE变化很小，而树木的这些参数变化很大。另外，木质藤本和树木的δ^{13}C, LMA等参数没有显著的变化。总之，相对树木，木质藤本受季节干旱的负面影响较小，从而在生理生态角度支持了木质藤本在季节森林里丰富的机制：从叶片的水平看，在干季，木质藤本趋向于有更高的碳固定、更高的资源利用效率（水分和氮） 和低的结构耗费，因而证实在季节森林里光合特性的差异有助于木质藤本的竞争力。

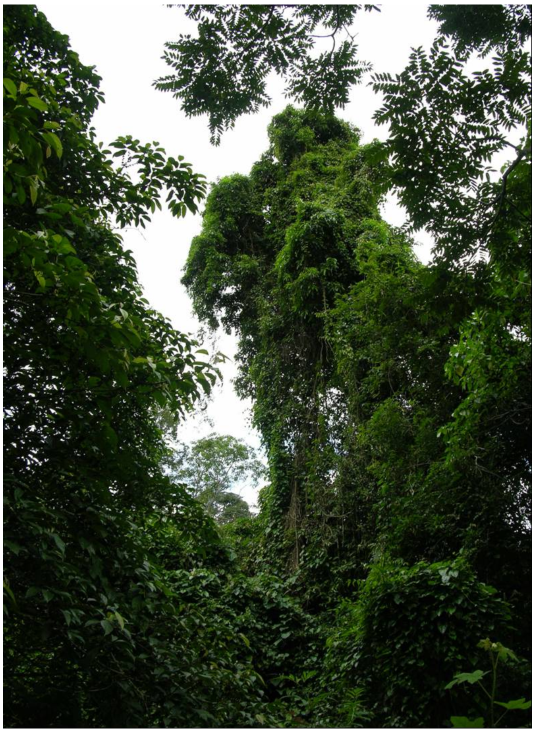
3． 在衰老过程中，叶片营养的回收是植物维持资源的重要对策之一。在土壤磷严重亏缺的山地雨林里，研究了12种木质藤本和14种树木的叶片营养的回收率的差异。在衰老后，木质藤本和树木的叶片相对面积缩小和质量的丢失没有显著差异。木质藤本成熟叶的氮含量和氮的回收率与树木相似，但木质藤本衰老叶中磷的含量较高，磷的回收率较低。这表明，在强烈受磷限制的森林里，木质藤本通过产生高含量磷的凋落物提高土壤营养的相对有效性，从而对这个生态系统的生物多样性和功能产生潜在的影响。

4． 在羊蹄甲属里选择了五种具有不同生态学习性(需光种和耐荫种)的木质藤本和树木，研究

了其生长对策的差异。五种植物的苗木种于25%的荫棚中。与树木相比，两种需光的木质藤本有相对较低的单位面积光合速率(A_{area})和相似的单位质量光合速率(A_{mass})；其相对高的比叶面积(SLA)和叶生物量比(LMF)导致了高的叶面积比(LAR)。与两种需光的树木相比，两种需光的木质藤本具有高的相对生长速率(RGR)，分配到叶片(具有高的LMF和LAR)和茎的生物量较高，而分配到根的生物量较低。与两种需光的木质藤本相比，耐荫的木质藤本具有相对低的RGR，高的RMF，低的SMF，相似的LMF。RGR与SLA具有显著的正相关，而与LAR和A_{area}的相关性不显著。与需光的树木相比，需光的木质藤本相对较高的RGR主要基于形态参数 (如，SLA, LMF和LAR)，而并不是叶片水平相对高的净光合速率。耐荫的木质藤本表现出与需光种明显不同的生长对策。

5． 在自然状况下，植物的光合生理和代谢过程受到多种不断变化环境因子的影响。西双版纳地区位于热带和亚热带的交错带，生物多样性十分丰富，一年具有显著的干湿季和雾凉季。由于远离赤道，当地的植被被认为受到季节性干旱和低温的影响。以生长在三个不同微环境里(林下，小林窗和大林窗)的当地一种木质藤本(毛果枣)为研究材料，探讨了其光合和生长特征对季节变化的适应性。在不同季节和微生境里，光合能力(最大净光合速率, A_{max}; 最大羧化能力, V_{cmax}; 电子传递效率, J_{max})和分配于羧化作用和电子传递的叶片氮(P_c, P_b)变化和差异显著。比叶面积(SLA) 的季节性变化不明显，但在不同生境间差异显著，且与总的光强($PPFD_i$)成负相关。而单位面积氮含量(N_a)季节变化显著，但微生境间不明显。日间最大光化学效率(Fv/Fm)的趋势表明在所有微生境和季节里，植株没有发生长期光抑制。光合能力在湿季最大，雾凉季最低。在干季和雾凉季，大林窗里苗木净光合速率的降低幅度最大。在$PPFD_i$、N_a和光合能力之间具有紧密的对数相关。在干季，茎的生物量分配降低，根的生物量分配增加。结果表明，不同微生境间苗木的季节性适应主要由于生化特性的变化过程(特别是N_a 和叶片总N在不同组分间的分配)和生物量的分配，而不是叶片形态特征(SLA)的变化。由于在当地干季和雾凉季的浓雾具有降低光强和补充表层土水分的功能，光环境是影响光合生理和生长的主要驱动性因子。

6． 选取林下斜基粗叶木两种小灌木和望天树等4种树木的幼苗为材料，从叶片形态解剖、光合生理以及整株的形态和生长等角度系统研究了不同成年植株大小和耐荫性的木本植物对光环境适应的差异。研究结果表明，小灌木(粗叶木)表现出适应在低光环境里的生存和生长的特点：它们的叶片在低光下的最大捕光能力和强的光斑利用能力。叶片大多数为海绵组织，通过内部光的散射加速林下散射光和远红光的收获，低的叶绿素a/b值有利于提高林下红光的吸收，同时维持光合系统I和II的能量平衡。从植株的结构来看，粗叶木有下垂的柔软枝条和非重叠的叶片，这有助于避免自遮荫和捕获散射光，并有利于避免林下常常遭受落枝的破坏。当人工模拟林窗后，灌木和树木对光强变化的适应表现出显著的差异，小灌木叶片光化学效率发生了不可逆转的影响，且其光合特性和生长表现出的可塑性极低；而树木的光化学效率表现出可逆的影响，其生理和形态的可塑性较强，但光合特性的影响和恢复速率的趋势与成长植株的大小不一致。



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Cai Zhiquan was born on 4 October 1973 in Hubei, China. He received his primary education in his home village, and secondary education at Luotian county (1979-1988). In 1988, he left his hometown and was admitted to the Huanggang High School in Huangzhou, Hubei. After graduation in 1991, he studied forest science in Hubei Minority College. In 1997-2000, he completed his graduate studies in Nanjing Forestry University and got a MSc degree in forest ecology. In 2000, he started work as a scientist in Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences. In 2002, he was supproted by Xishuangbanna Tropical Botanical Garden and attended Extensive English courses in Sichuang University in Chengdu. During a over 7-year period in Xishuangbanna, he concentrated on research work in plant ecology and ecophysiology. In 2003, he became a sandwich PhD student between Wageningen University and Xishuangbanna Tropical Botanical Garden and began his research work on lianas and trees in tropical forests in Xishuangbanna. The work was finacially supported by the National Natural Science Foundation in China (grant 30500065 to Cai) and a sandwich PhD grant from Wageningen University.

Cai Zhiquan is married and father of one daughter.


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- Quality: from soil to healthy people (2006)
- Wet vs dry forests: functional differentiation (2007)
- Church forest in Ethiopia: functional differentiation (2007)

PE&RC Annual Meetings, Seminars and Introduction Days (1 credit)

- Introduction weekend (2004)

International Symposia, Workshops and Conferences (8 credits)

- International symposium on modern ecology series (Beijing, China, 2005)
- Association for tropical biology and conservation (ATBC, 2006)
- Association for topical biology and conservation (ATBC, 2007)
- Ecological and environmental sciences (Beijing, China, 2007)

Laboratory Training and Working Visits (4 credits)

- Chlorophyll fluorescence (Xishuangbana Tropical Botanical Garden, Chinese Academy of Science, 2004)
- Seed biotechnology (Xishuangbana Tropical Botanical Garden, Chinese Academy of Sciences, 2005)
- Plant ecophysiology (Institute of Botany, Chinese Academy of Sciences, 2005)