Journal of Vegetation Science **22** (2011) 917–931

Leaf attributes and tree growth in a tropical dry forest

R. K. Chaturvedi, A. S. Raghubanshi & J. S. Singh

Keywords
Leaf attributes; Photosynthetic rate; Relative growth rate; Soil moisture content; Tropical dry forest.

Abbreviations

A_{area} = Area-based photosynthetic rate (μmol m^{-2} s^{-1}); A_{mass} = Mass-based photosynthetic rate (nmol g^{-1} s^{-1}); Chl = Chlorophyll concentration (mg g^{-1}); Gs_{area} = Area-based stomatal conductance (mol m^{-2} s^{-1}); Gs_{mass} = Mass-based stomatal conductance (mmol g^{-1} s^{-1}); LCC = Leaf carbon concentration (% dry wt.); LNC = Leaf nitrogen concentration (% dry wt.); LPC = Leaf phosphorus concentration (% dry wt.); RGR = Relative growth rate (cm^{2} · cm^{-2} · yr^{-1}); SLA = Specific leaf area (cm^{2} g^{-1}); SMC = Soil moisture content (cm^{3} cm^{-3} expressed as % volumetric SMC); TDF = Tropical dry forests; WUEi = Intrinsic water use efficiency

Nomenclature:
(Duthie 1903–1929)

Received 19 November 2010
Accepted 5 April 2011
Co-ordinating Editor: Dr. Lindsay Turnbull

Chaturvedi, R.K. (corresponding author, ravikantchaturvedi10@gmail.com); **Raghubanshi, A.S.** (raghubansh@gmail.com) & **Singh, J.S.** (singh.js1@gmail.com): Ecosystems Analysis Laboratory, Department of Botany, Banaras Hindu University, Varanasi 221005, India

Abstract

Questions: How are leaf attributes and relative growth rate (RGR) of the dominant tree species of tropical deciduous forest (TDF) affected by seasonal changes in soil moisture content (SMC)? What is the relationship of functional attributes with each other? Can leaf attributes singly or in combination predict the growth rate of tree species of TDF?

Location: Sonebhadra district of Uttar Pradesh, India.

Methods: Eight leaf attributes, specific leaf area (SLA); leaf carbon concentration (LCC); leaf nitrogen concentration (LNC); leaf phosphorus concentration (LPC); chlorophyll concentration (Chl), mass-based stomatal conductance (Gs_{mass}); mass based photosynthetic rate (A_{mass}); intrinsic water use efficiency (WUEi); and relative growth rate (RGR), of six dominant tree species of a dry tropical forest on four sites were analysed for species, site and season effects over a 2-year period. Step-wise multiple regression was performed for predicting RGR from mean values of SMC and leaf attributes. Path analysis was used to determine which leaf attributes influence RGR directly and which indirectly.

Results: Species differed significantly in terms of all leaf attributes and RGR. The response of species varied across sites and seasons. The attributes were positively interrelated, except for WUEi, which was negatively related to all other attributes. The positive correlation was strongest between Gs_{mass} and A_{mass} and the negative correlation was strongest between Gs_{mass} and WUEi. Differences in RGR due to site were not significant when soil moisture was controlled, but differences due to season remained significant. The attributes showed plasticity across moisture gradients, which differed among attributes and species. Gs_{mass} was the most plastic attribute. Among the six species, *Terminalia tomentosa* exhibited the greatest plasticity in six functional attributes. In the step-wise multiple regression, A_{mass}, SLA and Chl among leaf attributes and SMC among environmental factors influenced the RGR of tree species. Path analysis indicated the importance of SLA, LNC, Chl and A_{mass} in determining RGR.

Conclusion: A_{mass}, SMC, SLA and Chl in combination can be used to predict RGR but could explain only three-quarters of the variability in RGR, indicating that other traits/factors, not studied here, are also important in modulating growth of tropical trees. RGR of tree species in the dry tropical environment is determined by soil moisture, whereas the response of mature trees of different species is modulated by alterations in key functional attributes such as SLA, LNC and Chl.

Introduction

According to Lugo & Murphy (1986), tropical dry forests (TDF) are seasonal, experiencing wet and dry periods within an annual cycle, with high ambient temperature and low relative humidity. Mooney et al. (1995) define TDFs as forests occurring in tropical regions characterized by pronounced seasonality in rainfall distribution, with

Doi: 10.1111/j.1654-1103.2011.01299.x

several months of drought. Tree species in these forests are subjected to water stress during the dry season (Eamus 1999). To survive in water stress conditions, plants change their morphological and/or physiological characteristics (functional attributes) to prevent excessive water loss (Schmidt & Levin 1985).

Tropical dry forests are characterized by functional attributes, such as deciduousness and drought tolerance. Deciduousness in TDF is a phenological attribute expressing adaptation to seasonality and drought, resulting in reduced activity during the unfavourable season and resumption of growth at variable rates of resource use during the short favourable season (Singh & Singh 1992). However, there are exceptions, such as *Cordia alliodora* in the neotropics (Choat et al. 2007) and *Faidherbia albida* in Africa (Roupsard et al. 1999), showing "reverse" leaf phenology by dropping their leaves in the wet season. Some TDFs contain essentially 100% deciduous species, while others may have several evergreen species (Condit et al. 2000). The northern Australian monsoon tropics are dominated by evergreen species despite having a strong dry season (Bowman & Prior 2005). There is also much diversity in attributes among various tree species and also within species due to characteristics such as rooting depth and degree of drought experienced by the trees (Van Schaik et al. 1993).

Leaves play a central role in the exchange of energy and nutrients between plants and their environment, therefore, particular attention has been paid to the enormous interspecific differences in leaf attributes (Wright et al. 2004). Specific leaf area (SLA) has strong positive relationships with leaf nutrient concentration, stomatal conductance, photosynthetic rate and leaf intrinsic water use efficiency (WUEi) (Hoffmann et al. 2005). There is a close relationship between SLA, chlorophyll concentration (Chl) and leaf nitrogen concentration (LNC) (Marenco et al. 2009). According to Le Maire et al. (2004), Chl is linked to LNC and hence to photosynthetic rate. Moreover, Chl provides information about the physiological state of the plant (Carter 1994; Lichtenthaler 1996). It is a direct indicator of photosynthetic capacity and plant productivity (Carter 1998; Zarco-Tejada et al. 2004). LNC and LPC affect photosynthetic rate, stomatal conductance, SLA and relative growth rate (RGR) (Jurik 1986; Reich et al. 1991; Cornelissen et al. 2003). LNC and LPC scale positively with one another and show similar relationships with photosynthetic rate (Wright et al. 2001). According to Schulze et al. (1994), stomatal conductance is linearly related to LNC for broad categories of vegetation types with variable leaf longevity. However, soil moisture content (SMC) may be equally or more important than LNC and LPC. Inadequate SMC lowers stomatal conductance, reduces photosynthetic rate (Freitas 1997), affects rate of evapotranspiration (Givnish & Vermeij 1976) and alters water use efficiency (Parkhurst & Loucks 1972). Water stress also decreases photosynthetic pigments (Yordanov et al. 2000) and relative water content, which induces stomatal closure in an attempt to conserve water (Castrillo et al. 2001).

Kattge et al. (2011) argued that plant traits play a key role in understanding and predicting vegetation responses to environmental changes. Niinemets et al. (2001) have shown intraspecific variability in seedling leaf attributes in response to light and water availability. Some studies have correlated growth rate of woody seedlings with leaf attributes such as A_{mass} and leaf mass per area (King 1991; Reich et al. 1992; Huante et al. 1995; Cornelissen et al. 1996; Wright & Westoby 1999). In natural forests, Reich et al. (1997) demonstrated a relationship between growth and leaf mass per area of mature trees, using data from temperate deciduous and coniferous forests in the USA. However, extensive studies relating leaf attributes to growth in mature trees under natural conditions, especially in TDFs, are scarce (see Prior et al. 2004).

This study includes eight leaf attributes and RGR (see abbreviations); collectively called here functional attributes. We have studied the relationships of the above functional attributes of six dominant tree species with change in SMC under field conditions in TDF of India. We hypothesized that leaf attributes such as SLA, LNC, LPC, Chl, Gs_{mass} and A_{mass} of the tree species in a dry tropical environment are primarily influenced by SMC, and are associated with RGR. We specifically address the following questions: (1) How are the functional attributes of the dominant tree species of TDF affected by seasonal changes in SMC in different habitats? (2) What is the relationship of functional attributes with each other? (3) How are the functional attributes and their plasticity affected by habitat conditions? (4) Can the functional attributes singly or in combination predict the growth rate of the tree species of TDF?

Methods

Study site

The present investigation included four sites, Hathinala West (24°18′07″N and 83°05′57″E, 291 m a.s.l.), Gaighat (24°24′13″N and 83°12′01″E, 245 m a.s.l.), Harnakachar East (24°18′33″N and 83°23′05″E, 323 m a.s.l.) and Ranitali (24°18′11″N and 83°04′22″E, 287 m a.s.l.). These sites are situated in Sonebhadra district of Uttar Pradesh, India (Fig. 1). They occupy a land area of 2555, 394, 1507 and 2118 ha, respectively. For the purpose of this study, three plots, each of 4 ha (200 m × 200 m), were established randomly at each site.

Doi: 10.1111/j.1654-1103.2011.01299.x

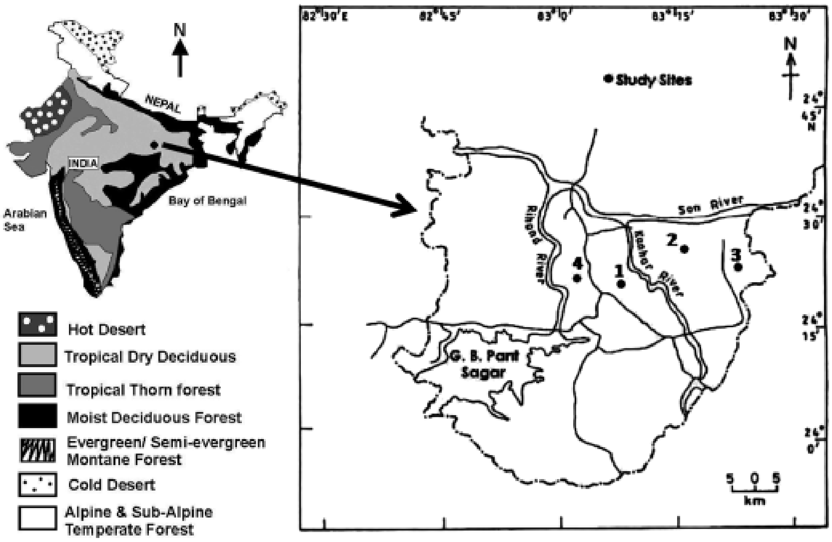

Fig. 1. Location of the study sites, numbers 1, 2, 3 and 4, respectively, indicate approximate location of Hathinala, Gaighat, Harnakachar and Ranitali sites. for the map of India (left) includes major biomes.

Climate

The area experiences a tropical monsoon climate. The year is divisible into four seasons: hot pre-monsoon (April–June), monsoon/rainy (July–September), early post-monsoon with gradually decreasing temperature (October–December) and late post-monsoon with gradually increasing temperature (January–March). About 85% of the annual rainfall occurs during the monsoon season from the southwest monsoon, and the remaining rainfall from the few showers in December and in May to June. There is an extended dry period of about 9 months in the annual cycle (Jha & Singh 1990). The ombrothermic diagrams for two localities in the study area, on the basis of 8 years of data, are given in Pandey & Singh (1992). The maximum monthly temperature varies from 20 °C in January to 46 °C in June, and the mean minimum monthly temperature reaches 12 °C in January and 31 °C in May. While the late post-monsoon period is characterized by leaf fall in most deciduous species, the pre-monsoon season represents the leaf-flushing period for all species.

Study species

Six dominant tree species (*Anogeissus latifolia*, *Buchanania lanzan*, *Diospyros melanoxylon*, *Lagerstroemia parviflora*, *Shorea robusta* and *Terminalia tomentosa* in the family Combretaceae, Anacardiaceae, Ebenaceae, Lythraceae, Dipterocarpaceae and Combretaceae, respectively), which occur on all the sites, were selected for the study. From each species, three individuals, above 30-cm girth, in each plot were marked. Therefore, nine individuals of a species per site were marked for the study of leaf attributes and RGR.

Soil measurements

SMC was measured in triplicate as percentage by volume every month at a distance of 1 m from the tree trunk on three sides, at a depth of 10 cm at 1-month intervals for 2 years (i.e. July 2005 to June 2007) using a theta probe instrument (type ML 1, Delta-T Devices, Cambridge, UK); these SMC values are called SMC_1. In addition, measurement of SMC (SMC_2) was done in five replicates at three random locations in each plot once in October 2005. During the same period, soil samples were also collected to a depth of 10 cm in five replicates at those locations in each plot, and the values were averaged to three readings per plot, i.e. nine observations per site. The soil samples were analysed for bulk density (Misra 1968), organic carbon (Walkley & Black 1934), nitrogen (Bremner & Mulvaney 1982) and phosphorus (Olsen & Sommers 1982) concentrations. Analyses of soil samples were also done for pH (Anderson & Ingram 1993) and texture (Sheldrick & Wang 1993).

Leaf measurements

In *S. robusta*, leaf emergence begins in the middle of the late post-monsoon period in March, and in the remaining five species, in the pre-monsoon period in May (*A. latifolia*, *B. lanzan*, *D. melanoxylon* and *L. parviflora*) or June (*T. tomentosa*). Further details on the phenology of these species are given in Singh & Singh (1992). Leaves of *S. robusta* were available throughout the year, whereas *D. melanoxylon* was leafless in March, *A. latifolia* and *B. lanzan* were leafless in February and March, and *L. parviflora* and *T. tomentosa* were leafless from February to April. Three twigs at mid-canopy height and having full sun exposure for at least part of the day, with healthy and fully expanded leaves, from each marked tree were sampled, and area-based stomatal conductance (Gs_{area}) and photosynthetic rate (A_{area}) were immediately measured in one randomly selected leaf from each twig (He et al. 2008) using an LC Pro Console Photosynthesis meter (model EN11 ODB, ADC Bioscientific Ltd., UK) between 09:30 h and 12:30 h (solar noon). From each twig, 30 healthy and fully expanded leaves were collected and their areas recorded with a leaf area meter (SYSTRONICS Leaf Area Meter-211, India). These leaves were marked and sealed in plastic bags containing damp paper towel and carried to the laboratory for further analysis. One leaf from each twig was kept separately in an ice box for estimation of Chl.

Chlorophyll was analysed by crushing 0.1 g of the leaf in 10 ml 80% acetone (Arnon 1949). The absorbance (D) of the extract was then measured at 645 and 663 nm using 80% acetone as blank. The concentrations of Chl *a* and Chl *b* were calculated from the following expressions: Chl $a = ([12.7 \times D663] - [2.6 \times D645]) \times$ vol. acetone/wt. leaf tissue; Chl $b = ([22.9 \times D645] - [4.68 \times D663]) \times$ vol. acetone/wt. leaf tissue; Chl = Chl a+Chl b.

Marked leaves were oven dried at 60 °C for 72 h to obtain dry weight. Using the area and dry weight, SLA was determined. SLA values from the leaves of each twig of a tree were averaged to obtain three values per individual tree. Dried leaf samples from each twig were ground separately in an electronic grinder for analysis of LCC, LNC and LPC. The above procedure was followed every month for 2 years in all nine marked individuals of each species at each site.

Among the eight leaf attributes, SLA, Chl, Gs_{area} and A_{area} were measured every month, whereas, LCC, LNC and LPC were estimated four times in a year (i.e. seasonal) by pooling the powdered leaf samples for 3 months in a season.

LNC was estimated using the Kjeldahl technique (Bradstreet 1965) and LPC using the phosphomolybdic blue colorimetric method (Anderson & Ingram 1993). Ground leaf samples were burned in an electric furnace at 400 °C, ash content (inorganic elements in the form of oxides) left after burning was weighed and carbon was calculated using the equation: Carbon (%) = 100 – (Ash weight+‴ molecular weight of O_2 (53.3) in $C_6H_{12}O_6$) (Negi et al. 2003). LNC and LPC are the total amounts of nitrogen and phosphorus, respectively, per unit dry leaf mass, expressed as percentage dry weight. The above-mentioned attributes were measured, in general, according to the protocol of Cornelissen et al. (2003).

Study of RGR

In each site, increases in girth for each season were measured for all the individuals of the selected species. Girth increments were measured with the help of metal dendrometer bands fitted at 1.3-m high in each tree (Cattelino et al. 1986; Keeland & Sharitz 1993). Girth was converted into cross-sectional area (CSA), and RGR was calculated using seasonal change in cross-sectional area (Prior et al. 2004). Unlike biomass estimates, this does not involve use of allometric equations (Prior et al. (2004).

Data analysis

The Gs_{area} and A_{area} were converted to Gs_{mass} and A_{mass} using SLA. WUEi was calculated as the ratio of A_{mass} and Gs_{mass}. It should be pointed out that in contrast to Wright et al. (2004), who defined photosynthetic capacity as "Photosynthetc assimilation rates measured under high light, ample soil moisture and ambient CO_2," we measured photosynthetic assimilation rates under high light, current soil moisture and ambient CO_2 and therefore, A_{mass}, Gs_{mass} and WUEi in this study represent the direct and immediate response of the plant to environmental conditions. Further, since WUE has been calculated as the ratio of A_{mass} to Gs_{mass} it is termed intrinsic water use efficiency (WUEi) following Santiago et al. (2004). RGR, SMC_1 and leaf attributes were averaged for each season. SMC_1, leaf attribute values and RGR obtained from each individual of a species in each plot were averaged to obtain three replicate values per species per plot in each site in each season in a year.

Data for leaf attributes and RGR were analysed using repeated measures ANCOVA with SMC_1 as covariate. Differences between the mean values of leaf traits were tested with Tukey's post-hoc test. Two-tailed Pearson correlation coefficients among functional attributes were calculated, where the three replicate values for each of the six species in each of the three plots, per site, per season in 2 years (n, $3 \times 6 \times 3 \times 4 \times 4 \times 2 = 1728$) were reduced to one value per species per plot, per site per season in 2 years (n, $1 \times 6 \times 3 \times 4 \times 4 \times 2 = 576$). For calculating correlations among soil characteristics, SMC_2 values were used ($n = 12$). Step-wise multiple regression was performed for predicting RGR from mean values of SMC_1 and leaf attributes. All the statistical analyses were done using the SPSS (v. 16) package. Effects of SMC_1 on the selected functional attributes of the six species were studied with the help of regression equations calculated using SigmaPlot (v.11).

We used path analysis (also known as covariance structure analysis) to determine which leaf attributes influence RGR directly and which indirectly. Path analysis is an analytical method based on multiple regression that permits determining pathways contributing to correlations between functional attributes and assessing causal

Doi: 10.1111/j.1654-1103.2011.01299.x

relationships within a defined network (Kingsolver & Schemske 1991). This approach allowed quantification of the degree to which each attribute contributed to variation in RGR. The path coefficients correspond to standardized partial regression coefficients. Amos (version 6.0; http://www.amosdevelopment.com/) was used to calculate path coefficients and to evaluate their significance level, and the fit of the structural model to the data.

Results

Soil physico-chemical characteristics

Physico-chemical properties of soils on the four sites are summarized in Table 1. Among the four study sites, Hathinala was the most moist site, having a mean annual SMC$_1$ of 13.0%, and Ranitali was the driest, with mean annual SMC$_1$ of 7.8%. Seasonal variation in SMC$_1$ was high; the values ranged from 25.8% in the monsoon season at Hathinala to 2.5% in the early post-monsoon season at Ranitali (Fig. 2).

Across the sites and plots, SMC$_2$ was positively correlated with clay, total pH, organic C, total N and total P, and negatively associated with sand. Bulk density was positively correlated with silt and negatively with sand. Clay was positively associated with silt, pH, organic C, total N and total P, and negatively with sand. Sand showed a significant negative relationship with pH. pH was positively related to organic C, total N and total P (Table 2). The relationship of organic C with clay had the highest *r*, total N showed the highest *r* with organic C, while total P had the highest *r* with pH (Table 2).

Functional attributes

Repeated measures ANCOVA with SMC$_1$ as covariate indicated significant effects of season and species on all functional attributes (Table 3). The interactions, season × site, season × species and site × species were also significant for all functional attributes. Effects of year, site and year × species were not significant for RGR (Table 3).

Mean values of SMC$_1$ at all four sites were higher in the second year as compared to the first year of measurement. Among the functional attributes, the mean values of Chl and Gs$_{\mathrm{mass}}$ were greater and those of LCC and WUEi lower in the second year as compared to the first year of estimation. Among the four sites, Hathinala was the most moist site, Ranitali the driest and the remaining two sites, Gaighat and Harnakachar, had intermediate levels of SMC. The mean values of SLA, LNC, LPC and Chl across years, seasons and species were greatest at Hathinala (SLA, 99.3 cm^2 g^{-1}; LNC, 1.7%; LPC, 0.16%; Chl, 0.76 mg g^{-1}) and mean LCC were highest at Ranitali (LCC, 42.3%) (Fig. 3). The analysis indicated that the effect of year and site on RGR was solely due to differences in soil moisture.

At all the sites, mean values of SMC$_1$ across years, sites and species were highest in the monsoon season and lowest in the early post-monsoon season, and among leaf traits across species, the highest mean values for LNC, LPC and Chl were recorded in the monsoon season (LNC, 2.2%; LPC, 0.19%; Chl, 1.3 mg g^{-1}), for SLA in the pre-monsoon and monsoon seasons, as compared to the early post-monsoon and late post-monsoon seasons (pre-monsoon, 117 cm^2 g^{-1}; late post-monsoon, 45.7 cm^2 g^{-1}), and for LCC in the late post-monsoon season (44.9%) (Fig. 3).

Among the six species, the mean values of SMC$_1$ across years, seasons and sites, recorded near *S. robusta* (11.6%) and *T. tomentosa* (11.8%) trees were higher, those near *A. latifolia* (10.0%), *B. lanzan* (10.4%) and *D. melanoxylon* (10.3%) were of intermediate level, and the SMC$_1$ was lowest near *L. parviflora* (9.3%). Species also differed in the values of leaf traits. The mean values of SLA (118 cm^2 g^{-1}), LNC (2.0%) and LPC (0.2%), were greatest for *S. robusta*, LCC (40.5%) was highest for *B. lanzan* and Chl (0.83 cm^2 g^{-1}) was maximum for *T. tomentosa*. LCC was lowest in *L. parviflora* (34.5%) and SLA (64.0 cm^2 g^{-1}), LNC (1.3%) and LPC (0.13%) were lowest in *B. lanzan*. Mean values of Chl (0.57 mg g^{-1}) were lowest for *D. melanoxylon* (Fig. 3).

Mean values for Gs$_{\mathrm{mass}}$, A_{mass} and RGR, across years and sites for all the six species, were greatest in the

Table 1. Physio-chemical properties of the five experimental sites located in the forest of the Vindhyan highlands. Values in parentheses are standard errors.

Parameters	Hathinala	Gaighat	Harnakachar	Ranitali
Soil moisture content (SMC$_2$) (%)	13.0 (± 1.87)	11.1 (± 1.94)	10.2 (± 1.07)	7.78 (± 1.70)
Bulk density (g cm^{-3})	1.30 (± 0.05)	1.32 (± 0.06)	1.27 (± 0.06)	1.26 (± 0.05)
Clay (%)	10.6 (± 1.85)	7.08 (± 1.37)	4.83 (± 0.69)	3.00 (± 0.84)
Silt (%)	31.9 (± 2.10)	32.1 (± 2.22)	26.2 (± 0.97)	26.8 (± 1.90)
Sand (%)	57.5 (± 0.90)	60.8 (± 1.54)	69.0 (± 0.97)	70.2 (± 1.33)
Soil pH	6.93 (± 0.16)	6.45 (± 0.11)	6.52 (± 0.20)	6.40 (± 0.14)
Organic carbon (%)	1.61 (± 0.15)	1.56 (± 0.25)	1.20 (± 0.27)	1.39 (± 0.50)
Total nitrogen (%)	0.13 (± 0.03)	0.13 (± 0.01)	0.12 (± 0.01)	0.12 (± 0.02)
Total phosphorus (%)	0.04 (± 0.02)	0.02 (± 0.00)	0.03 (± 0.01)	0.02 (± 0.01)

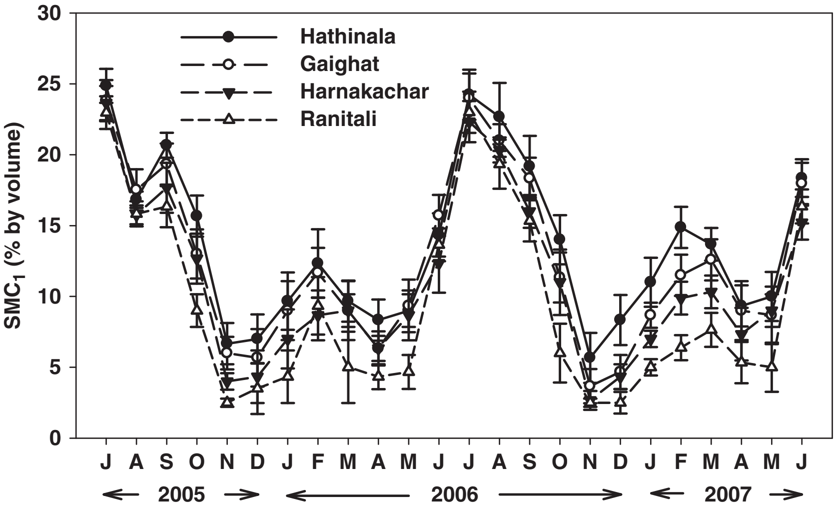

Fig. 2. Monthly soil moisture content (SMC$_1$) at the four experimental sites from July 2005 to June 2007.

Table 2. Pearson correlation coefficients between soil properties across experimental sites. $n = 36$, $^{ns}P > 0 \cdot 05$, $^{*}P < 0 \cdot 05$, $^{**}P < 0 \cdot 01$, $^{***}P < 0 \cdot 001$.

	SMC$_2$	Bulk density	Clay	Silt	Sand	pH	Organic C	Total N
Bulk density	0.04^{ns}							
Clay	0.87***	0.19^{ns}						
Silt	0.18^{ns}	0.51**	0.44**					
Sand	– 0.61***	– 0.42*	– 0.84***	– 0.86***				
pH	0.74***	0.04^{ns}	0.56***	0.20^{ns}	– 0.55**			
Organic C	0.49**	– 0.01^{ns}	0.75***	0.14^{ns}	– 0.30^{ns}	0.39*		
Total N	0.57***	0.07^{ns}	0.49**	0.02^{ns}	– 0.29^{ns}	0.35*	0.62***	
Total P	0.48**	– 0.12^{ns}	0.48**	– 0.16^{ns}	– 0.18^{ns}	0.61***	0.03^{ns}	0.33^{ns}

Table 3. Summary of repeated measures ANCOVA, with soil moisture content (SMC$_1$) as covariate, on functional attributes of six tropical dry forest tree species (only main effects and two-way interactions are shown). The residual *df* is 183. YR, year; ST, site; SS, season; SP, species; SLA, specific leaf area; LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; Chl, chlorophyll concentration; Gs$_{mass}$, mass-based stomatal conductance; A_{mass}, mass-based photosynthetic rate; WUEi, intrinsic water use efficiency; RGR, relative growth rate. $^{ns}P > 0 \cdot 05$, $^{*}P < 0 \cdot 05$, $^{**}P < 0 \cdot 01$, $^{***}P < 0 \cdot 001$.

Subject	*df*	SLA	LCC	LNC	LPC	Chl	Gs$_{mass}$	A_{mass}	WUEi	RGR
YR	1	0.11^{ns}	4.96*	3.56^{ns}	2.56^{ns}	7.32**	13.0***	0.91^{ns}	4.02*	0.18^{ns}
SS	1	45.5***	263***	104***	2.57^{ns}	53.4***	5.09*	22.3***	18.2***	8.53**
ST	3	19.6***	65.3***	45.4***	6.29***	16.7***	6.76***	20.8***	42.8***	0.50^{ns}
SP	5	620***	411***	507***	15.1***	27.5***	41.4***	167***	40.6***	12.5***
YR × SS	1	3.65^{ns}	1.25^{ns}	1.40^{ns}	0.25^{ns}	3.93*	11.1**	1.01^{ns}	0.21^{ns}	5.95*
YR × ST	3	7.33***	9.24***	11.0***	22.9***	3.22*	12.3***	6.48***	2.91*	34.7***
YR × SP	5	2.65*	22.3***	9.87***	25.3***	2.21^{ns}	11.2***	14.5***	2.68*	1.54^{ns}
SS × ST	3	15.6***	359***	76.0***	121***	47.7***	25.0***	21.4***	94.2***	3.16*
SS × SP	5	1964***	3001***	324***	235***	444***	73.2***	621***	85.9***	16.8***
ST × SP	14	7.00***	25.6***	25.3***	8.27***	8.24***	2.46**	11.9***	38.9***	2.07*

monsoon season (Gs$_{mass}$, 3.9 mmol g^{-1} s^{-1}; A_{mass}, 131 nmol g^{-1} s^{-1}; RGR; 0.07 cm^2 · cm^{-2} · yr^{-1}) and lowest in the late post-monsoon season (Gs$_{mass}$, 0.19 mmol g^{-1} s^{-1}; A_{mass}, 9.2 nmol g^{-1} s^{-1}; RGR, 0.008 cm^2 · cm^{-2} · yr^{-1}) except for *L. parviflora* whose RGR was lowest in the early post-monsoon season (Fig. 4). Generally, the WUEi was greater during the dry part of the year. Highest WUEi for *A. latifolia, B. lanzan, L. parviflora, S. robusta* and *T. tomentosa* was observed in the late post-monsoon season and that for *D. melanoxylon* in the pre-monsoon season. Lowest

Doi: 10.1111/j.1654-1103.2011.01299.x

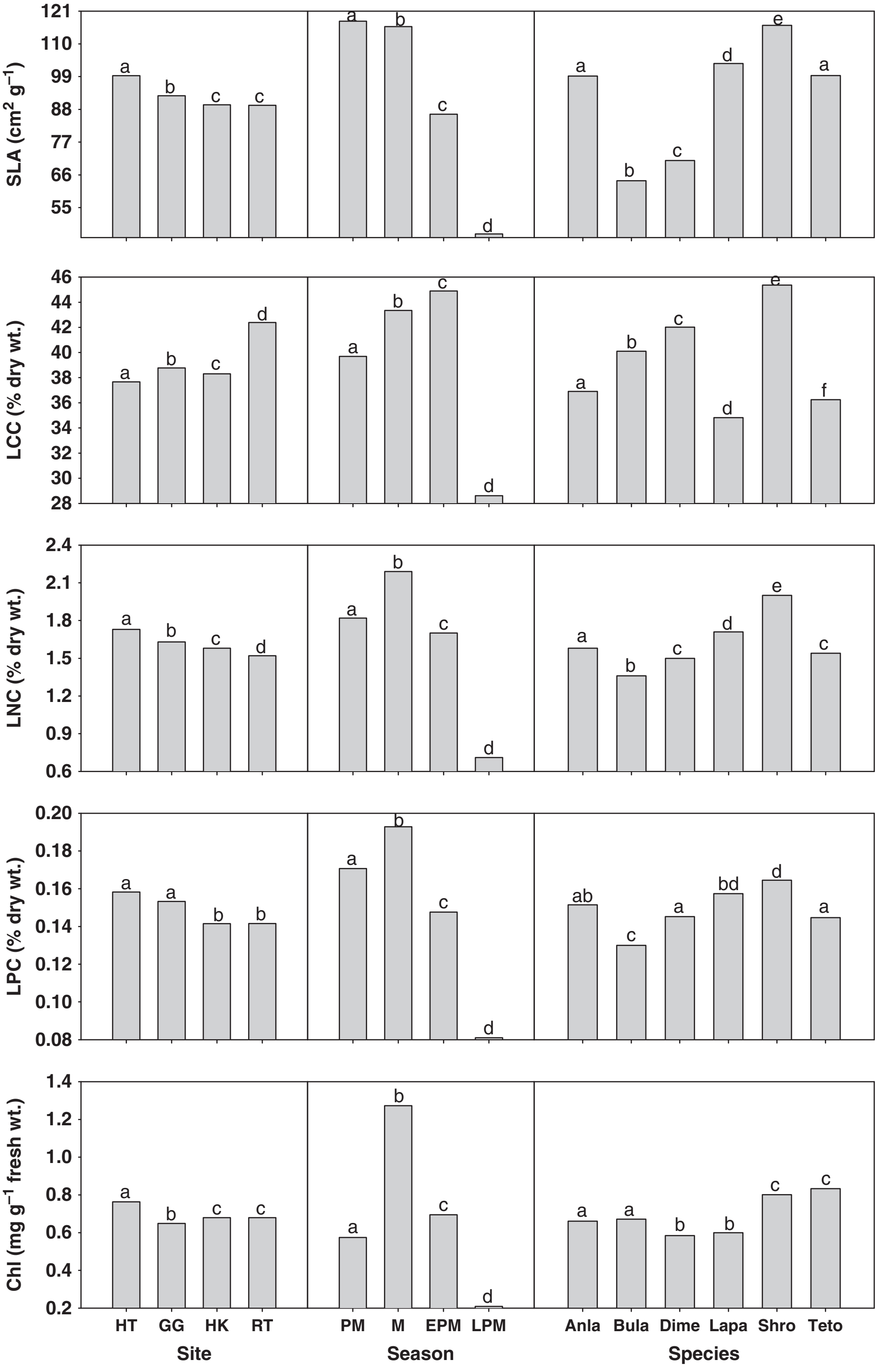

Fig. 3. Mean values of leaf traits across sites, seasons and species. SLA, specific leaf area; LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; Chl, chlorophyll concentration; HN, Hathinala; GG, Gaighat; HK, Harnakachar; RT, Ranitali; PM, pre-monsoon; M, monsoon; EPM, early post-monsoon; LPM, late post-monsoon; Anla, *Anogeissus latifolia*; Bula, *Buchanania lanzan*; Dime, *Diospyros melanoxylon*; Lapa, *Lagerstroemia parviflora*; Shro, *Shorea robusta*; Teto, *Terminalia tomentosa*. Different letters above bars indicate significant differences after Tukey's post-hoc test (α = 0.05).

WUEi for *A. latifolia* and *T. tomentosa* was recorded in the pre-monsoon season, for *B. lanzan, D. melanoxylon* and *S. robusta* in the monsoon season and for *L. parviflora* in the early post-monsoon season (Fig. 4).

In our study, functional attributes were positively interrelated, except for WUEi, which was negatively related to all other attributes (Table 4). The positive correlation was strongest between Gs_{mass} and A_{mass} and the negative correlation was strongest between Gs_{mass} and WUEi.

In the step-wise multiple regression, A_{mass}, SLA and Chl among functional attributes and SMC_1 among environmental factors were found to influence the RGR of tree species. The variation in A_{mass} alone accounted for 67% variation in RGR, A_{mass} and SMC together explained 71% variation in RGR, A_{mass}, SMC together with SLA accounted for 73% variation in RGR, and a combination of A_{mass}, SMC, SLA and Chl explained 74% variation in RGR. The final model was $RGR = 0.00 + 0.65\ A_{mass} + 0.23\ SMC_1 - 0.24\ SLA + 0.20\ Chl$.

Plasticity in functional attributes in relation to SMC

SLA (except for *B. lanzan*), LPC, A_{mass}, LNC, Gs_{mass} and RGR were significantly affected by SMC_1, while LCC and WUEi were affected by SMC_1 only in *S. robusta*. Among species, more variability in A_{mass} (71%) was explained by SMC_1 in *S. robusta* and *T. tomentosa*. The variability in SMC_1 explained most variability in SLA (54%), LCC (35%) and WUEi (23%) in *S. robusta*, maximum variability in LNC (40%), LPC (46%), Gs_{mass} (75%) and RGR (70%) in *T. tomentosa* and in Chl (66%) in *A. latifolia* (Table 5).

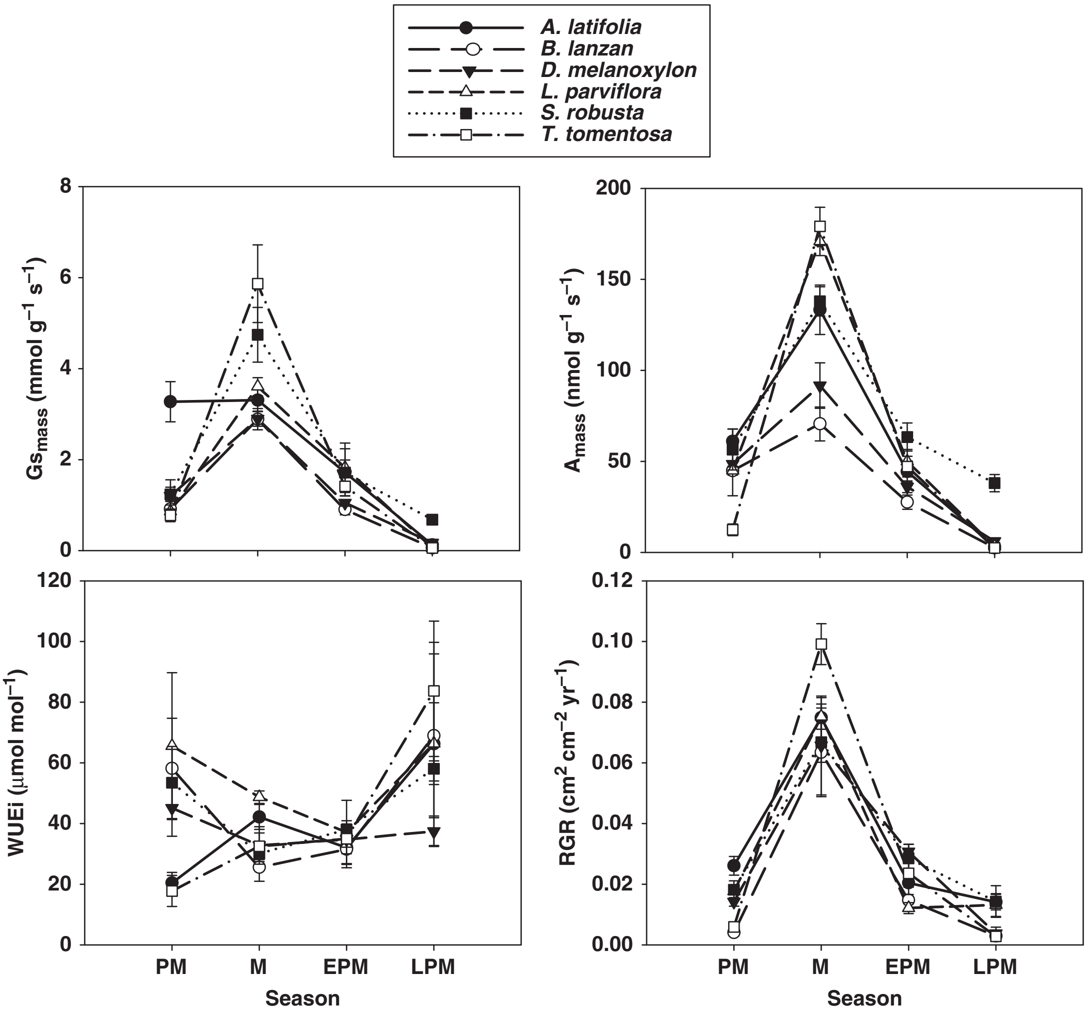

Fig. 4. Seasonal variations in leaf attributes and relative growth rates (RGR) in six dry tropical tree species across four sites. Gs_{mass}, mass-based stomatal conductance; A_{mass}, mass-based photosynthetic rate; WUEi, leaf water use efficiency; PM, pre-monsoon; M, monsoon; EPM, early post-monsoon; LPM, late post-monsoon.

Doi: 10.1111/j.1654-1103.2011.01299.x

Table 4. Pearson correlation coefficients between functional attributes across species, sites and seasons. SLA, specific leaf area; LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; Chl, chlorophyll concentration; Gs_{mass}, mass-based stomatal conductance; A_{mass}, mass-based photosynthetic rate; WUEi, intrinsic leaf water use efficiency; RGR, relative growth rate. $n = 576$, $^{*}P < 0 \cdot 05$, $^{**}P < 0 \cdot 01$, $^{***}P < 0 \cdot 001$.

	RGR	WUEi	A_{mass}	Gs_{mass}	Chl	LPC	LNC	LCC
SLA	0.41***	– 0.24***	0.69***	0.68***	0.63***	0.68***	0.81***	0.56***
LCC	0.31***	– 0.13**	0.49***	0.46***	0.59***	0.55***	0.70***	
LNC	0.57***	– 0.26***	0.78***	0.70***	0.74***	0.72***		
LPC	0.44***	– 0.27***	0.62***	0.67***	0.63***			
Chl	0.72***	– 0.27***	0.81***	0.82***				
Gs_{mass}	0.70***	– 0.42***	0.84***					
A_{mass}	0.76***	– 0.10*						
WUEi	– 0.16***							

We observed remarkable variation in the slope of the relationships of functional attributes with SMC_1 among species. The highest values of the slope for SLA, LPC, Gs_{mass}, A_{mass}, and RGR occurred for *T. tomentosa*. *T. tomentosa* together with *A. latifolia* also had a greater slope for LPC. The maximum slope for LCC was observed in *L. parviflora*, for LNC in *A. latifolia, B. lanzan* and *L. parviflora*, and for WUEi in *B. lanzan*. The species having minimum slope for the functional attributes were *D. melanoxylon* for SLA, LNC, Gs_{mass}, WUEi and RGR, *S. robusta* for LNC, LPC, Chl and RGR, *B. lanzan* for SLA, Gs_{mass}, A_{mass} and RGR, *L. parviflora* for Chl and Gs_{mass}, and *A. latifolia* for Gs_{mass} and RGR (Table 5).

Path analysis

Path analysis helped to identify the basis of RGR variation observed across the four study sites. The model fit index was 0.99, indicating a reasonable fit for our path model to the data. The attributes in the model explained 68% of the variation in RGR (Fig. S1). While A_{mass} and Chl had significant paths to RGR, a greater proportion of the variance in RGR was attributed to variation in A_{mass} compared to Chl. Variations in LNC and LCC explained 60% variation in Chl, which in turn, together with LNC and SLA, accounted for 72% variation in A_{mass}.

Discussion

The six tree species studied varied significantly in terms of leaf attributes and RGR. Among the leaf attributes, A_{mass}, Gs_{mass} and WUEi are expected to respond directly and quickly to environmental conditions, while the other attributes (SLA, LNC, LPC, LCC and Chl) may change more slowly. Among species, SLA varied 1.8-fold, LCC 1.4-fold, LNC 1.5-fold, LPC 1.3-fold, Chl 1.5-fold, Gs_{mass} 1.8-fold, A_{mass} twofold, WUEi 1.5-fold and RGR 1.6-fold. These variations were smaller than found by Reich et al. (1999) and Prior et al. (2003) for SLA and A_{mass}, and Reich et al. (1999) for LNC and Gs_{mass}, probably because of the lower number of species studied here. The tree species also showed strong seasonality in these functional attributes. Among the four seasons, SLA varied 2.6-fold, LCC 1.6-fold, LNC 3.1-fold, LPC 2.4-fold, Chl 6.2-fold, Gs_{mass} 20.2-fold, A_{mass} 14.2-fold, WUEi 1.8-fold and RGR 8.7-fold. SLA peaked during pre-monsoon season, LCC and WUEi in the post-monsoon season, while the rest of the attributes assumed maximum values in the monsoon season. It should be mentioned that the effect of seasonality on leaf attributes can, to some extent, be confounded with leaf phenology. For example, the pre-monsoon peak in SLA coincided with leafing in that season; new leaves are reported to have greater SLA than older leaves, presumably because of a build-up of cell wall material and chloroplasts as leaves age (Poorter et al. 2009). Mean values of SLA and LNC were within the range reported by Reich et al. (1999) for desert shrubland and woodland vegetation in New Mexico, Prior et al. (2003) for seasonally dry forests in Australia and Santiago & Wright (2007) for tropical plant species in Panama. LPC was within the range reported by Prior et al. (2003) and Santiago & Wright (2007), Gs_{mass} within the range reported by Reich et al. (1999) and Santiago & Wright (2007). A_{mass}, on the other hand, was generally larger than that reported by Reich et al. (1999), but comparable to values reported by Prior et al. (2003). The monsoon season A_{mass} was within the range of values measured by Eamus et al. (1999) in the wet season for eight Australian savanna tree species. In contrast, species such as *Cordia alliodora* in the neotropics are wet season deciduous, although in drier forests leaf flush occurs in June, i.e. early in the wet season (Borchert 1994; Choat et al. 2007).

Intrinsic water use efficiency (WUEi) was lower at Hathinala (moist site) compared to Ranitali (driest site). Marshall & Zhang (1994), in their carbon isotope discrimination analysis, showed that the WUEi of either evergreen or deciduous species increased with altitude, which followed a decreasing rainfall gradient, indicating that WUEi increased with site dryness. The seasonal pattern

Table 5. Parameters of regression equations (in the form: $y = a + bx$) relating functional attributes (y) of the six dominant tree species with SMC_1 (x). SLA, specific leaf area; LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; Chl, chlorophyll concentration; Gs_{mass}, mass-based stomatal conductance; A_{mass}, mass-based photosynthetic rate; WUEi, intrinsic water use efficiency; RGR, relative growth rate. $^{ns}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	a	b	R^2	a	b	R^2	a	b	R^2
	SLA			LCC			LNC		
A. latifolia	62.3	3.50	0.23^{**}	32.8	0.39	0.04^{ns}	1.00	0.10	0.24^{**}
B. lanzan	47.0	1.60	0.11^{ns}	38.9	0.15	0.01^{ns}	0.70	0.10	0.24^{**}
D. melanoxylon	53.1	1.60	0.15^{*}	39.8	0.18	0.03^{ns}	1.00	0.04	0.21^{**}
L. parviflora	57.3	4.20	0.37^{***}	28.4	0.55	0.09^{ns}	1.00	0.10	0.35^{**}
S. robusta	91.5	2.50	0.43^{***}	47.6	− 0.21	0.35^{***}	1.60	0.04	0.33^{**}
T. tomentosa	47.7	4.90	0.38^{***}	32.1	0.39	0.04^{ns}	0.60	0.09	0.40^{***}
	LPC			Chl			Gs_{mass}		
A. latifolia	0.100	0.010	0.19^{*}	0.02	0.10	0.66^{***}	0.40	0.20	0.38^{***}
B. lanzan	0.100	0.004	0.14^{*}	0.10	0.10	0.62^{***}	− 0.60	0.20	0.74^{***}
D. melanoxylon	0.100	0.003	0.12^{*}	0.10	0.10	0.59^{***}	− 0.30	0.20	0.72^{***}
L. parviflora	0.100	0.003	0.18^{*}	0.20	0.04	0.47^{***}	− 0.40	0.20	0.52^{***}
S. robusta	0.100	0.002	0.19^{*}	0.40	0.04	0.49^{***}	− 0.70	0.30	0.73^{***}
T. tomentosa	0.030	0.010	0.46^{***}	− 0.10	0.10	0.59^{***}	− 0.20	0.40	0.75^{***}
	A_{mass}			WUEi			RGR		
A. latifolia	− 17.2	7.40	0.68^{***}	51.5	− 1.10	0.03^{ns}	− 0.80	0.30	0.59^{***}
B. lanzan	− 0.90	3.50	0.54^{***}	63.8	− 1.70	0.08^{ns}	− 1.60	0.30	0.56^{***}
D. melanoxylon	− 2.20	4.50	0.58^{***}	41.7	− 0.40	0.03^{ns}	− 0.50	0.30	0.37^{***}
L. parviflora	− 34.5	9.70	0.68^{***}	60.5	− 0.60	0.01^{ns}	− 1.50	0.40	0.63^{***}
S. robusta	7.80	6.30	0.71^{***}	59.9	− 1.40	0.23^{**}	− 0.50	0.30	0.69^{***}
T. tomentosa	− 55.2	10.9	0.71^{***}	58.6	− 1.50	0.07^{ns}	− 2.80	0.50	0.70^{***}

of WUEi showed that it was lower during the dry period as compared to the wet period. According to Medrano et al. (2009), under drought conditions, plants optimize carbon assimilation and minimize water loss by decreasing stomatal conductance, thereby increasing WUEi during the period of low soil water availability.

In our study, roughly 50 to 80% of mean annual tree growth (RGR) occurred during the monsoon season; the average monsoon season growth of *S. robusta*, *A. latifolia*, *D. melanoxylon*, *L. parviflora*, *B. lanzan* and *T. tomentosa* accounted for, respectively 52, 55, 57, 64, 75 and 76% of annual RGR. Prior et al. (2004), for the savanna trees of northern Australia, also reported maximum stem growth during the wet season. Rossatto et al. (2009), for forest and savanna trees in the cerrado of central Brazil, also reported maximum radial stem growth in wet season. In another study, Schöngart et al. (2002), for Venezuelan semi-deciduous forest, reported that diameter growth of tree species was prolonged, occurring for 9 to 10 months of the year, which could be because this forest experiences a less severe dry season. However, maximum annual tree growth in our study during the monsoon season was not solely related to water availability. Our analysis indicated that differences in RGR due to sites were not significant when soil moisture was controlled, but differences due to season remained significant. Thus, season is a complex situation representing a combination of several abiotic variables, such as temperature, humidity, photoperiod, etc. Singh & Singh (1992) reported that leaf flushing in tree species of the Vindhyan highlands is not correlated with the onset of the rainy season but rather precedes it, begins with the rise in temperature and peaks in the hottest and driest month (May).

Leaf carbon concentration was also higher during the dry post-monsoon season, and among sites was higher at Ranitali. Van de Water et al. (2002) analysed variability in leaf carbon isotope ratio with elevation, slope aspect and precipitation in the southwest United States and reported a negative correlation of leaf carbon isotope ratio with precipitation and soil water availability due to changes in leaf morphology and biochemical processes.

S. robusta, which is semi-evergreen, exhibited a 70% decline in A_{mass} during the dry season (i.e. late post-monsoon season), whereas the other five species, which are deciduous, showed $> 90\%$ decline in A_{mass} during the dry season. Eamus et al. (1999) reported a 30 to 75% loss in photosynthetic activity in semi-deciduous species and 100% in the deciduous species. Gs_{mass} is also reported to be low during the dry season (O'Grady et al. 2009). Our study showed a 86% decline in Gs_{mass} during the dry season for *S. robusta*, which reached $> 90\%$ in the other five species.

The slope of the relationship between a plant functional attribute and an environmental variable is traditionally taken as a measure of plasticity, i.e. the steeper the slope, the greater the plasticity (Valladares et al. 2006). Our study indicated that the degree of phenotypic plasticity across the gradient of soil moisture differed among functional attributes and species. Stomatal conductance (Gs_{mass}) was the most plastic trait. Among the six species, *T. tomentosa* had the highest plasticity in six functional attributes, and is among the best-distributed species throughout tropical dry forest in India (Champion & Seth 1968). Phenotypic plasticity is also argued to help species to adjust to community composition, promoting coexistence and community diversity (Callaway et al. 2003). It is considered a method of adapting to variable environments (Callaway et al. 2003; Valladares et al. 2005).

We found significant correlations among the functional attributes. Westoby & Wright (2006) found that pairs of traits are often co-ordinated but that the correlation does not prove a direct causal link. Correlations between leaf attributes have been reported (Reich et al. 1992, 1999; Prior et al. 2003), and trait relationships have been explained in terms of trade-offs between leaf structural and metabolic functions (Reich et al. 1999; Read & Stokes 2006). Witkowski et al. (1992) reported that leaves of two Australian tree species growing in drier and more nutrient-poor soils had thicker leaves, with more dense tissues, resulting in a lower SLA. Thick leaves with dense tissues also have a high LCC (Kloeppel et al. 1998). SLA was lower and LCC higher for the tree species at our Ranitali site, compared to those growing at the moist Hathinala site. According to Wright et al. (2004), a lower SLA is associated with a low A_{mass}, Gs_{mass}, LNC, LPC, SLA and RGR. Photosynthetic capacity is influenced both by Gs_{mass} and by drawdown of CO_2 inside the leaf, i.e. carboxylation capacity, which is a process affected by leaf structure (Wright et al. 2004). Rossatto et al. (2009) found a significant positive correlation of radial growth with SLA but not with A_{mass}, while our study showed a stronger positive correlation between RGR and A_{mass} compared to that between RGR and SLA.

Step-wise multiple regression for predicting RGR on the basis of studied functional attributes indicates that A_{mass} accounted for the greatest variability (67%) in RGR, as also found by Pons (1977) and Pattison et al. (1998). It could be argued that A_{mass} mediates the direct influence of SMC_1 on RGR, rather than being a leaf characteristic, like Chl, which represents photosynthetic capacity. However, a combination of four factors (A_{mass}, SMC_1, SLA and Chl) only explained 74% variability in RGR, indicating that other traits/factors, not studied by us, are also important in modulating the growth of tropical trees.

Path analysis indicates that the influence of SLA on RGR is through its capacity to influence LNC. LNC decides the level of chlorophyll in the leaves, which ultimately modulates photosynthetic capacity. In our study, A_{mass} was positively correlated with LNC and SLA, as also found by Poorter et al. (1990) and Reich et al. (1994, 1997). According to Reich et al. (1999), these patterns are common to all species, because significant nitrogen per unit mass accumulation is required in leaves to achieve a high A_{mass}. SLA has been shown to be directly and strongly correlated with RGR across species (Poorter et al. 1990; Lambers & Poorter 1992; Cornelissen et al. 1996; Atkin et al. 1998; Poorter & Van der Werf 1998; Reich et al. 1998; Wright & Westoby 2000). Any change in SLA relates to actual changes in leaf structure and chemical composition. A lower SLA may be associated with slower intercellular diffusion of CO_2 (Parkhurst 1994; Hikosaka et al. 1998; Poorter & Evans 1998) or with increased internal shading of chloroplasts passing through the lamina (Terashima & Hikosaka 1995), either of which could decrease the photosynthetic rate of a leaf. SLA is also associated with nitrogen allocation to photosynthesis (Poorter & Evans 1998). Feng et al. (2008) showed that nitrogen allocation to carboxylation and bioenergetics increased significantly with increasing SLA. Hikosaka et al. (1998) and Takashima et al. (2004) also found that SLA is positively correlated with the fraction of leaf nitrogen in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), a key enzyme of photosynthesis. This is because about 60% of leaf soluble protein consists of Rubisco, which is the most limiting factor for biomass production (Nijs et al. 1995). Other studies also demonstrate that increasing leaf nitrogen parallels increasing investment in photosynthetic compounds (thylakoid proteins, enzymes of the Calvin cycle) (Mooney et al. 1981; Field & Mooney 1986; Reich et al. 1991; Nijs et al. 1995; Reich et al. 1997). Therefore, alterations in the carbon capture efficiency of leaves, due to changes in SLA influence RGR of the species in the dry tropical environment.

Conclusions

Leaf attributes and RGR are significantly different among tree species and show distinct seasonal variations. All functional attributes are interrelated. A_{mass}, SMC_1, SLA and Chl in combination explained about three-quarters of the variability in RGR, indicating that other traits/factors, not studied by us, are also important in modulating the growth of tropical trees. RGR of tree species in the dry tropical environment is determined by soil moisture, whereas the response of other tree species is modulated by alterations in key functional attributes, such as SLA, LNC and Chl. This conclusion, however, applies only to mature trees.

Acknowledgements

The authors thank the Ministry of Environment and Forests, Government of India for financial support. JSS is supported under a NASI senior scientist scheme. Dr. Toby Marthews and Dr. Jens Kattge are also thanked for reviewing the manuscript and offering helpful suggestions.

References

Anderson, J.M. & Ingram, J.S.I. 1993. *Tropical soil biology and fertility: a handbook of methods*. CAB International, Wallingford, UK.

Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts: polyphenol oxidases in *Beta vulgaris*. *Plant Physiology* 24: 1–15.

Atkin, O.K., Schortemeyer, M., McFarlane, N. & Evans, J.R. 1998. Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments. *Plant, Cell and Environment* 21: 1007–1017.

Borchert, R. 1994. Water status and development of tropical trees during seasonal drought. *Trees, Structure and Function* 8: 115–125.

Bowman, D.M.J.S. & Prior, L.D. 2005. Why do evergreen trees dominate the Australian seasonal tropics? *Australian Journal of Botany* 53: 379–399.

Bradstreet, R.B. 1965. *The Kjeldahl method for organic nitrogen*. Academic Press, New York, NY, US.

Bremner, J.M. & Mulvaney, C.S. 1982. Nitrogen total. In: Page, A.L., Miller, R.H. & Keeney, D.R. (eds.) *Methods of soil analysis: Part 2. Chemical and microbiological properties. Agronomy Monograph No. 9. (Second edition)*. pp. 595–624. American Society of Agronomy and Soil Science Society of America, Madison, WI, US.

Callaway, R.M., Pennings, S.C. & Richards, C.L. 2003. Phenotypic plasticity and interactions among plants. *Ecology* 84: 1115–1128.

Carter, G.A. 1994. Ratios of leaf reflectances in narrow wavebands as indicators of plant stress. *International Journal of Remote Sensing* 15: 697–703.

Carter, G.A. 1998. Reflectance wavebands and indices for remote estimation of photosynthesis and stomatal conductance in pine canopies. *Remote Sensing of Environment* 63: 61–72.

Castrillo, M., Fernandez, D., Calcagno, A.M., Trujillo, I. & Guenni, L. 2001. Responses of ribulose-1, 5-bisphosphate carboxylase, protein content and stomatal conductance to water deficit in maize, tomato, and bean. *Photosynthetica* 39: 221–226.

Cattelino, P.J., Becker, C.A. & Fuller, L.G. 1986. Construction and installation of homemade dendrometer bands. *Northern Journal of Applied Forestry* 3: 73–75.

Champion, H.G. & Seth, S.K. 1968. *General Silviculture for India*. Publication Division, Government of India, Delhi, IN.

Choat, B., Sack, L. & Holbrook, N.M. 2007. Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytologist* 175: 686–698.

Condit, R., Watts, K., Bohlman, S.A., Pérez, R., Hubbell, S.P. & Foster, R.B. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science* 11: 649–658.

Cornelissen, J.H.C., Castro-Diez, P. & Hunt, R. 1996. Seedling growth allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84: 755–765.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Duthie, J.F. 1903-1929. *Flora of the Upper Gangetic Plain and of the adjacent Siwalik and Sub-Himalayan tracts*. Government Press, Calcutta, IN.

Eamus, D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* 14: 11–16.

Eamus, D., Myers, B., Duff, G. & Williams, D. 1999. Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiology* 19: 665–671.

Feng, Y.L., Fu, G.L. & Zheng, Y.L. 2008. Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. *Planta* 228: 383–390.

Field, C. & Mooney, H.A. 1986. The photosynthesis–nitrogen relationships in wild plants. In: Givnish, T.J. (ed.) *On the economy of plant form and function*. pp. 25–55. Cambridge University Press, Cambridge, UK.

Freitas, H.M.O. 1997. Drought. In: Prasad, N.K. (ed.) *Plant ecophysiology*. pp. 129–147. John Wiley & Sons, New York, NY, US.

Givnish, T.J. & Vermeij, G.J. 1976. Sizes and shapes of Liana leaves. *American Naturalist* 110: 743–778.

He, C., Li, J., Guo, M., Wang, Y. & Chen, C. 2008. Changes in leaf photosynthetic characteristics and water use efficiency along with tree height of 4 tree species. *Acta Ecologica Sinica* 28: 3008–3016.

Hikosaka, K., Hanba, Y.T., Hirose, T. & Terashima, I. 1998. Photosynthetic nitrogen-use efficiency in leaves of woody and herbaceous species. *Functional Ecology* 12: 896–905.

Hoffmann, W.A., Franco, A.C., Moreira, M.Z. & Haridasan, M. 2005. Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Functional Ecology* 19: 932–940.

Huante, P., Rincón, E. & Acosta, I. 1995. Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Functional Ecology* 9: 849–858.

Jha, C.S. & Singh, J.S. 1990. Composition and dynamics of dry tropical forest in relation to soil texture. *Journal of Vegetation Science* 1: 609–614.

Jurik, T.W. 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *American Journal of Botany* 73: 1083–1092.

Kattge, J., Ogle, K., Bönisch, G., Díaz, S., Lavorel, S., Madin, J., Nadrowski, K., Nöllert, S., Sartor, K. & Wirth, C. 2011. A genetic structure for plant trait databases. *Methods in Ecology and Evolution* 2: 202–213.

Keeland, B.D. & Sharitz, R.R. 1993. Accuracy of tree growth measurements using dendrometer bands. *Canadian Journal of Forest Research* 23: 2454–2457.

King, D.A. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecology* 5: 485–492.

Kingsolver, J. & Schemske, D.W. 1991. The measurement of natural selection by path analysis. *Trends in Ecology and Evolution* 6: 276–280.

Kloeppel, B.D., Gower, S.T., Treichel, I.W. & Kharuk, S. 1998. Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison. *Oecologia* 114: 153–159.

Lambers, H. & Poorter, H. 1992. Inherent variation in growth rate between higher plants: a search for ecological causes and consequences. *Advances in Ecological Research* 23: 187–261.

Le Maire, G., François, C. & Dufrêne, E. 2004. Towards universal broad leaf chlorophyll indices using PROSPECT simulated database and hyperspectral reflectance measurements. *Remote Sensing of Environment* 89: 1–28.

Lichtenthaler, H.K., Gitelson, A.A. & Lang, M. 1996. Nondestructive determination of chlorophyll content of leaves of a green and an aurea mutant of tobacco by reflectance measurements. *Journal of Plant Physiology* 148: 483–493.

Lugo, A.E. & Murphy, P. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. *Journal of Tropical Ecology* 2: 55–72.

Marenco, R.A., Antezana-Vera, S.A. & Nascimento, H.C.S. 2009. Relationship between specific leaf area, leaf thickness, leaf water content and SPAD-502 readings in six Amazonian tree species. *Photosynthetica* 47: 184–190.

Marshall, J.D. & Zhang, J. 1994. Carbon isotope discrimination and water use efficiency in native plants of the north-central Rockies. *Ecology* 75: 1887–1895.

Medrano, H., Flexas, J. & Galmés, J. 2009. Variability in water use efficiency at the leaf level among Mediterranean plants with different growth forms. *Plant Soil* 317: 17–29.

Misra, R. 1968. *Ecology work book*. Oxford and IBH Publishing, Calcutta, IN.

Mooney, H.A., Field, C., Gulmon, S.L. & Bazzaz, F.A. 1981. Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. *Oecologia* 50: 109–112.

Mooney, H.A., Bullock, S.H. & Medina, E. 1995. Introduction. In: Bullock, S.H., Mooney, H.A. & Medina, E. (eds.) *Seasonally dry tropical forests*. pp. 146–194. Cambridge University Press, Cambridge, UK.

Negi, J.D.S., Manhas, R.K. & Chauhan, P.S. 2003. Carbon allocation in different components of some tree species of India: a new approach for carbon estimation. *Current Science* 85: 1528–1531.

Niinemets, Ü., Ellsworth, D.S., Lukjanova, A. & Tobias, M. 2001. Site fertility and the morphological and photosynthetic acclimation of *Pinus sylvestris* needles to light. *Tree Physiology* 21: 1231–1244.

Nijs, I., Behaeghe, T. & Impens, I. 1995. Leaf nitrogen content as a predictor of photosynthetic capacity in ambient and global change conditions. *Journal of Biogeography* 22: 177–183.

O'Grady, A.P., Cook, P.G., Eamus, D., Duguid, A., Wischusen, J.D.H., Fass, T. & Worldege, D. 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia* 160: 643–655.

Olsen, S.R. & Sommers, L.E. 1982. Phosphorus, chemical and microbiological properties. In: Page, A.L., Miller, R.H. & Keeney, D.R. (eds.) *Methods of soil analysis: Part 2 Agronomy Monograph No. 9 (Second edition)*. pp. 403–430. American Society of Agronomy and Soil Science Society of America, Madison, WI, US.

Pandey, C.B. & Singh, J.S. 1992. Influence of rainfall and grazing on herbage dynamics in a seasonally dry tropical savanna. *Vegetatio* 102: 107–124.

Parkhurst, D.F. 1994. Diffusion of CO_2 and other gases inside leaves. *New Phytologist* 126: 449–479.

Parkhurst, D.F. & Loucks, O.L. 1972. Optimal leaf size in relation to environment. *Journal of Ecology* 60: 505–537.

Pattison, R.R., Goldstein, G. & Ares, A. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rain-forest species. *Oecologia* 117: 449–459.

Pons, T.L. 1977. An ecophysiological study in field layer of ash coppice. II. Experiments with *Geum urbanum* and *Cirsium palustre* in different light intensities. *Acta Botanica Neerlandica* 26: 29–42.

Poorter, H. & Evans, J.R. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* 116: 26–37.

Poorter, H. & Van der Werf, A. 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers, H., Poorter, H. & Van Vuuren, M.M.I. (eds.) *Inherent variation in plant growth*. pp. 309–336. Backhuys Publishers, Leiden, NL.

Poorter, H., Remkes, C. & Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94: 621–627.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta analysis. *New Phytologist* 182: 565–588.

Prior, L.D., Eamus, D. & Bowman, D.M.J.S. 2003. Leaf attributes in the seasonally dry tropics: a comparison of four habitats in northern Australia. *Functional Ecology* 17: 504–515.

Prior, L.D., Eamus, D. & Bowman, D.M.J.S. 2004. Tree growth rates in north Australian savanna habitats: seasonal patterns and correlations with leaf attributes. *Australian Journal of Botany* 52: 303–314.

Read, J. & Stokes, A. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* 93: 1546–1565.

Reich, P.B., Uhl, C., Walters, M.B. & Ellsworth, D.S. 1991. Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86: 16–24.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365–392.

Reich, P.B., Walters, M.B., Ellsworth, D.S. & Uhl, C. 1994. Photosynthesis–nitrogen relations in Amazonian tree species 1. Patterns among species and communities. *Oecologia* 97: 62–72.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13730–13734.

Reich, P.B., Walters, M.B., Tjoelker, M.G., Vanderklein, D. & Buschena, C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* 12: 395–405.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.

Rossatto, D.R., Hoffmann, W.A. & Franco, A.C. 2009. Differences in growth patterns between co-occurring forest and savanna trees affect the forest–savanna boundary. *Functional Ecology* 23: 689–698.

Roupsard, O., Ferhi, A., Granier, A., Pallo, F., Depommier, D., Mallet, B., Joly, H. & Dreyer, E. 1999. Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agro-forestry parkland of Sudanese West Africa. *Functional Ecology* 13: 460–472.

Santiago, L.S. & Wright, S.J. 2007. Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology* 21: 19–27.

Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543–550.

Schmidt, K.P. & Levin, D.A. 1985. The comparative demography of reciprocally sown populations of *Phlox drummondii* Hook. I. Survivorships, fecundities, and finite rates of increase. *Evolution* 33: 1210–1218.

Schöngart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V. & Worbes, M. 2002. Phenology and stem-growth periodicity of the tree species in Amazonian floodplain forests. *Journal of Tropical Ecology* 18: 581–597.

Schulze, E.D., Kelliher, F.M., Korner, C., Lloyd, J. & Leuning, R. 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. *Annual Review of Ecology and Systematics* 25: 629–660.

Sheldrick, B.H. & Wang, C. 1993. Particle-size distribution. In: Carter, M.R. (eds.) *Soil sampling and methods of analysis*. pp. 499–511. Canadian Society of Soil Science, Lewis Publishers, Ann Arbor, MI, US.

Singh, J.S. & Singh, V.K. 1992. Phenology of seasonally dry tropical forest. *Current Science* 63: 684–689.

Takashima, T., Hikosaka, K. & Hirose, T. 2004. Photosynthesis or persistence: nitrogen allocation in foliage of evergreen and deciduous *Quercus* species. *Plant, Cell and Environment* 27: 1047–1054.

Terashima, I. & Hikosaka, K. 1995. Comparative ecophysiology of leaf and canopy photosynthesis. *Plant, Cell and Environment* 18: 1111–1128.

Valladares, F., Arrieta, S., Aranda, I., Lorenzo, D., Sánchez-Gómez, D., Tena, D., Huárez, F. & Pardos, J.A. 2005. Shade tolerance, photoinhibition sensitivity and phenotypic plasticity of *Ilex aquifolium* in continental-Mediterranean sites. *Tree Physiology* 25: 1041–1052.

Valladares, F., Sánchez-Gómez, D. & Zavala, M.A. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* 94: 1103–1116.

Van de Water, P.K., Leavitt, S.W. & Betancourt, J.L. 2002. Leaf δ^{13}C variability with elevation, slope aspect, and precipitation in the southwest United States. *Oecologia* 132: 332–343.

Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary producers. *Annual Review of Ecology and Systematics* 24: 353–377.

Walkley, A. & Black, I.A. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science* 37: 29–38.

Westoby, M. & Wright, I.J. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21: 261–268.

Witkowski, E.T.F., Lamont, B.B., Walton, C.S. & Radford, S. 1992. Leaf demography, sclerophylly and ecophysiology of two *Banksias* with contrasting leaf life spans. *Australian Journal of Botany* 40: 849–862.

Wright, I.J. & Westoby, M. 1999. Differences in seedling growth behavior among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* 87: 85–97.

Wright, I.J. & Westoby, M. 2000. Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. *Functional Ecology* 14: 97–107.

Wright, I.J., Reich, P.B. & Westoby, M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* 15: 423–434.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, F.S., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. 2004. The world-wide leaf economics spectrum. *Nature* 428: 821–827.

Yordanov, I., Velikova, V. & Tsonev, T. 2000. Plant responses to drought, acclimation and stress tolerance. *Photosynthetica* 38: 171–186.

Zarco-Tejada, P.J., Miller, J.R., Morales, A., Berjón, A. & Agüera, J. 2004. Hyperspectral indices and model simulation for chlorophyll estimation in open-canopy tree crops. *Remote Sensing of Environment* 90: 463–476.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Photograph S1. Photograph of the experimental site during dry season in the tropical deciduous forest of Vindhyan highlands, India.

Photograph S2. Photograph of the dry site in the tropical deciduous forest of Vindhyan highlands, India.

Photograph S3. Photograph of the moist site in the tropical deciduous forest of Vindhyan highlands, India.

Photograph S4. Photograph of the moist site in the tropical deciduous forest of Vindhyan highlands, India.

Photograph S5. Photograph of the moist site in the tropical deciduous forest of Vindhyan highlands, India.

Fig. S1. Path analysis model showing five leaf attributes and RGR. The path coefficients are standardized partial regression coefficients. LNC, leaf nitrogen concentration; SLA, specific leaf area; LCC, leaf carbon concentration; A_{mass}, mass-based photosynthetic rate; Chl, chlorophyll concentration; RGR, relative growth rate.