Species and site effects on leaf traits of woody vegetation in a dry tropical environment

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Selected leaf traits (leaf area, leaf weight, specific leaf area and chlorophyll content) from eight woody species at four sites in the dry tropical Vindhyan forest were investigated in order to assess their variability across species and site conditions. The morphological traits such as leaf area and leaf weight were more variable than biochemical traits such as chlorophyll content. There was significant effect of species and site, and the site × species interaction was also significant for all traits. These traits were correlated except for specific leaf area, which was independent of leaf area. A combination of traits could discriminate between the sites. Between-site variability in leaf traits was smaller (1.3–1.5-fold) than between-species variability (1.7–12.5 fold). The larger inter-species variability reflects marked genotypic variability in the leaf traits, while the smaller between-site variability reflects phenotypic plasticity leading to adaptation to site conditions.

Keywords: Dry tropical forest, inter-species variability, leaf traits, woody species.

LEAF traits are often cited as the principal traits to relate plant resource use, biomass and ecosystem functioning[1–4]. In addition, these traits are easy to quantify and convenient to compare among a large number of plant species. Leaf traits may be divided into two groups: functional traits and structural traits. Functional traits reflect the index of plant growth and metabolism. On the other hand, structural traits are indexes of biological characteristics of different plant species, and reflect the adaptation strategies of plants to the environment. These traits, among others, include leaf area, leaf dry weight, specific leaf area (SLA) and chlorophyll content. SLA is the ratio of leaf area to leaf dry weight and, being strongly correlated with relative growth rate, maximum rate of photosynthesis[3] and competitive ability, is often considered a key trait linked to plant functioning[5–8]. It has been argued that SLA can provide important clues regarding future changes in community composition due to global change, if dryness is going to be altered in much of the tropics. The high-SLA leaves are productive[6,9] but are necessarily also short-lived and vulnerable to herbivory[10,11]. On the other hand, low-SLA leaves perform better in resource-poor environments[7].

Leaf area plays an important role in light interception, water and nutrient use, growth and yield potential[12–14]. Leaf size and SLA decline along gradients of decreasing moisture and/or nutrient availability[15–20]. Lower SLA, due to thicker and/or denser leaves contributes to long leaf survival, nutrient retention, and protection from desiccation[21], whereas small leaf size reduces boundary layer resistance, and helps maintain favourable leaf temperatures and higher photosynthetic water-use efficiency under the combination of high solar radiation and low water availability[22,23].

Chlorophyll is the most important pigment for photosynthesis[24–26]. Chlorophyll concentration in leaves and canopies can be an indicator of photosynthetic capacity, developmental stage, plant productivity, environmental stress and nutrient management[27–30]. Measurement of leaf chlorophyll content is also an indirect approach to estimate soil nitrogen[31–33].

Since the leaf traits are considered important for understanding vegetation response to a broad range of environmental factors, we examined four leaf traits, viz. leaf area, leaf weight, SLA and chlorophyll content in eight woody species on four sites of a dry tropical forest in the Vindhyan highland. We addressed the questions: (i) How much do the woody species occurring in a dry tropical environment differ in these leaf traits and how much are these leaf traits affected by site conditions? (ii) Can a combination of these leaf traits across species discriminate between the sites?

The study was conducted on four sites, viz. Ranitalli, Neruiadamar, Bokrakhari and Hathinala of the Vindhayan dry tropical region (21°29′–25°11′N lat.; 78°15′–84°15′E long.), Sonbhadra District, Uttar Pradesh in 2008. The elevation above the mean sea level ranges between 313 and 483 m. The area experiences a tropical monsoon climate. The sites are located between two meteorological stations, Obra and Renukut. Ranitalli site is nearest to Obra and Hathinala site is nearest to Renukoot. Mean annual rainfall is 926 mm at Obra and 1146 mm at Renukoot[34]. The soils are residual ultisols, sandy loam in texture, reddish to dark grey in colour and are extremely poor in nutrients[35]. Among the four sites, the mean rainy

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season gravimetric soil water content was highest at Hathinala site and lowest at Ranitalli site (Table 1).

Shorea robusta, *Buchanania lanzan*, *Diospyros melanoxylon*, *Lagerstroemia parviflora*, *Lannea coromandelica*, *Terminalia tomentosa*, *Holarrhena antidysenterica* and *Lantana camara* were selected for the study as these species occurred on all the four sites. Five fully grown leaves from each of the five individual plants were sampled ($n = 800$) for each species in September 2008. The leaves were collected from the unshaded mid-canopy region. After measuring the leaf area by a portable leaf area meter (SYSTRONICS, Leaf Area Meter-211), the leaves were oven-dried at 70°C for 72 h to obtain the dry mass with a precision electronic balance, to the nearest 0.001 g. SLA was calculated as the ratio of leaf area to leaf dry weight. For determination of chlorophyll content, five leaf samples were collected at the same time from the same five individuals and locations as above. The leaf samples were homogenized in 80% acetone, and absorbance at 663 and 645 nm was measured. The chlorophyll concentration was then calculated following Arnon[36]. Data were subjected to multivariate ANOVA. Tukey's test was used to differentiate between means. Two-tailed Pearson correlation coefficients among leaf traits were calculated. All statistical analyses were done using SPSS (ver. 10) package. Species and sites were ordinated by correspondence analysis (CA) using the combination of leaf traits through Biodiversity-Pro (ver. 2).

All leaf traits examined had wide variability across species and sites (Table 2). The coefficient of variation was maximum for leaf weight (86%) followed by leaf area (82%), SLA (57%) and total chlorophyll content (46%). Thus total chlorophyll concentration had the least variation. The leaf traits across species and sites were significantly correlated with each other (Table 3), except for SLA which was independent of leaf area, although leaf weight which accounted for 75.3% variability in leaf area (Figure 1), showed a significant negative relationship with SLA. The positive relationship between leaf area and chlorophyll concentration is particularly meaningful for the seasonally dry tropics, as the canopies have to perform photosynthetically at their best during the short growth period. Many leaf traits have been found to be correlated in other studies also[7,37]. At the species level, comparative studies of woody plants from a range of environments, however, suggest that leaf size and SLA may not be closely linked[20,38]. The lack of correlation between leaf area and SLA as observed in our study suggests that these two traits could be associated with different ecophysiological strategies or environmental factors, as argued by Ackerly *et al.*[39]. SLA, for example, could be correlated with sclerophylly or thickness of cuticle, while leaf area could be related to boundary-layer resistance and photosynthetic water-use efficiency[39].

ANOVA indicated that all the four leaf traits had a significant species effect (Table 4). The mean leaf area varied from 26.39 cm^2 in *H. antidysentrica*, which had the minimum total chlorophyll concentration (0.72 mg/g), to 143.05 cm^2 in *T. tomentosa* (Table 5). On the other hand, mean leaf weight was minimum for *L. camara* (0.11 g/leaf), which had the greatest SLA (269.35 cm^2/g), and maximum for *T. tomentosa* (1.38 g/leaf). Minimum SLA was exhibited by *D. melanoxylon* (88.15 cm^2/g), which had the maximum total chlorophyll concentration (1.26 mg/g). Thus there was a marked interspecific variation in leaf traits: leaf area 5.4-fold, leaf weight 12.5-fold, SLA three-fold and chlorophyll content 1.7-fold. Other studies also indicate that the morphological traits such as leaf area and leaf mass are more variable than biochemical traits such as chlorophyll content[40]. However, Tukey's test indicated that several species overlapped in individual leaf traits, except for *T. tomentosa* which was significantly different from all other species in terms of leaf area and leaf weight, *L. camara* in terms of leaf weight and SLA, *L. coromandelica* in terms of SLA and *D. melanoxylon* in total chlorophyll concentration (Table 5).

ANOVA also indicated a significant site effect on all four traits (Table 4). When the data on leaf traits were averaged for each site across the eight species, the overall

Table 1. Mean gravimetric soil water, total soil nitrogen and total soil carbon for the different sites, as recorded for the rainy season (R.K. Chaturvedi, unpublished)

Site	Gravimetric soil water (%)	Total soil nitrogen (%)	Total soil carbon (%)
Ranitalli	16.10 ± 1.21	0.11 ± 0.01	1.52 ± 0.08
Neruiadamar	17.70 ± 1.09	0.11 ± 0.01	1.53 ± 0.08
Bokarakhari	18.10 ± 1.14	0.07 ± 0.01	1.20 ± 0.1
Hathinala	19.80 ± 1.11	0.09 ± 0.01	1.39 ± 0.18

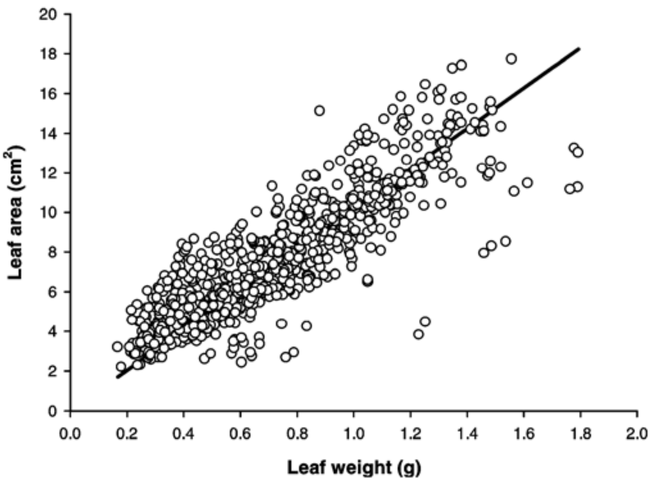

Figure 1. Relationship between leaf area and leaf weight across the eight species at the four sites. The values were square-root transformed for the analysis. The regression line represents the equation $y = 1.574 + 8.4x$ ($r^2 = 0.753$, $P < 0.0001$, $n = 800$), where y is square-root leaf area and x is square-root leaf weight.

Table 2. Minimum, maximum, mean and standard deviation values for leaf traits across species and sites ($n = 800$)

Descriptive statistics	Minimum	Maximum	Mean	Standard deviation
Leaf area (cm^2)	4.90	314.30	70.26	57.81
Leaf weight (g)	0.03	3.21	0.65	0.56
Specific leaf area (cm^2/g)	9.74	546.81	133.34	76.10
Chlorophyll (mg/g)	0.21	2.54	0.91	0.42

Table 3. Pearson's correlation coefficients between leaf traits. The values for leaf traits were square-root transformed ($n = 800$)

	Leaf area	Leaf weight	Specific leaf area
Leaf weight (cm^2)	0.868**		
Specific leaf area (cm^2/g)	–0.015^{NS}	–0.449**	
Chlorophyll content (mg/g)	0.154**	0.149**	–0.081*

*$P < 0.05$; **$P < 0.01$; NS, Not significant.

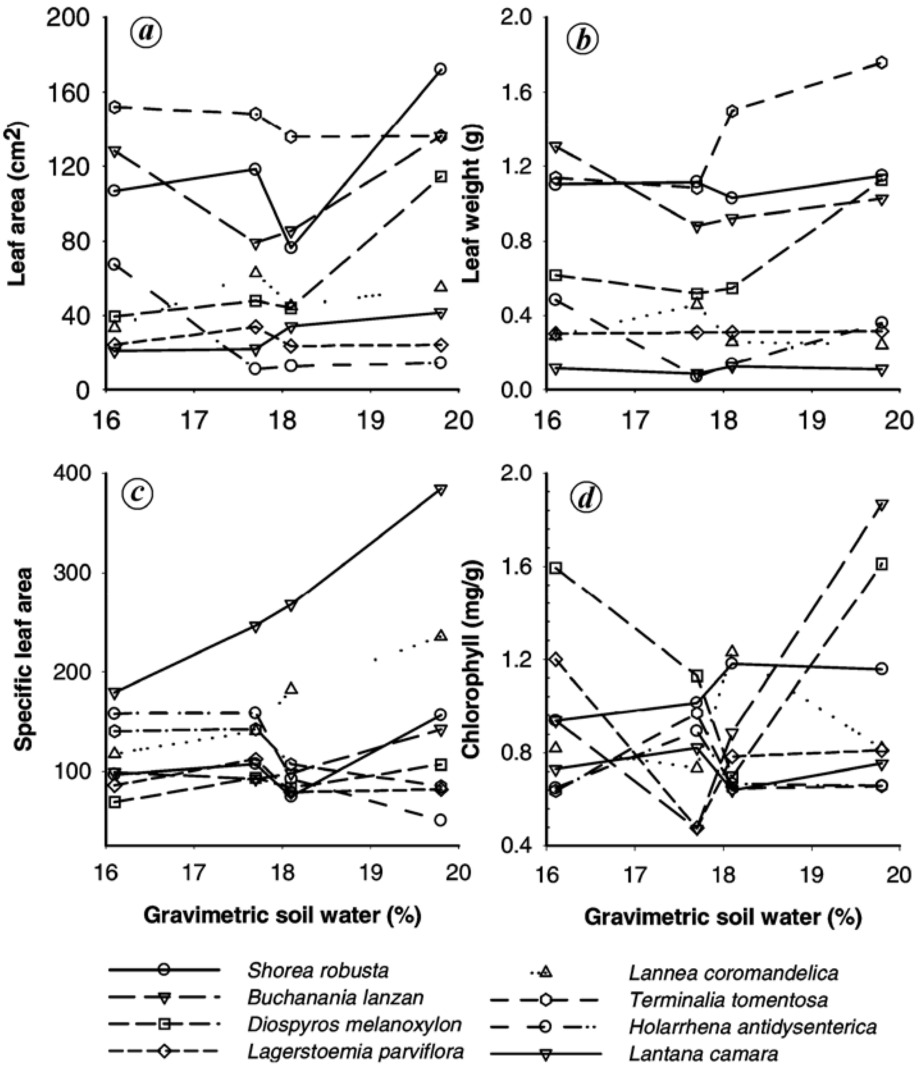

Figure 2. Plots of leaf traits against sites; the sites are scaled according to gravimetric soil water content: ***a***, Leaf area; ***b***, Leaf weight; ***c***, Specific leaf area; ***d***, Chlorophyll concentration.

variation was reduced (Table 6). Mean leaf area ranged from 57.21 cm^2 for the Bokarakhari site to 86.73 cm^2 for the Hathinala site (1.5-fold), mean leaf weight from 0.57 g/leaf at Neruiadamar to 0.77 g/leaf at Hathinala (1.3-fold), mean SLA from 123.10 cm^2/g on Bokarakhari to 155.15 cm^2/g at Hathinala (1.3-fold), and total chlorophyll concentration from 0.81 mg/g at Neruiadamar to 1.04 mg/g at Hathinala site (1.3-fold). The Hathinala site had the highest mean leaf trait values and was significantly different from all other sites. The Neruiadamar site was also significantly different from all other sites in terms of SLA and the Ranitalli site in terms of chlorophyll concentration (Table 6).

Table 4. Summary of ANOVA on leaf traits

Main effect	Traits	*df*	*F*
Site	LA	3	29.47
	LW	3	13.74
	SLA	3	46.30
	CHL	3	27.85
Species	LA	7	202.67
	LW	7	206.93
	SLA	7	310.29
	CHL	7	50.90
Site × species	LA	21	12.02
	LW	21	7.02
	SLA	21	41.09
	CHL	21	30.14
Error	Each trait	768	

All F values were significant at $P < 0.001$. LA, leaf area; LW, Leaf weight; SLA, Specific leaf area; CHL, Chlorophyll content.

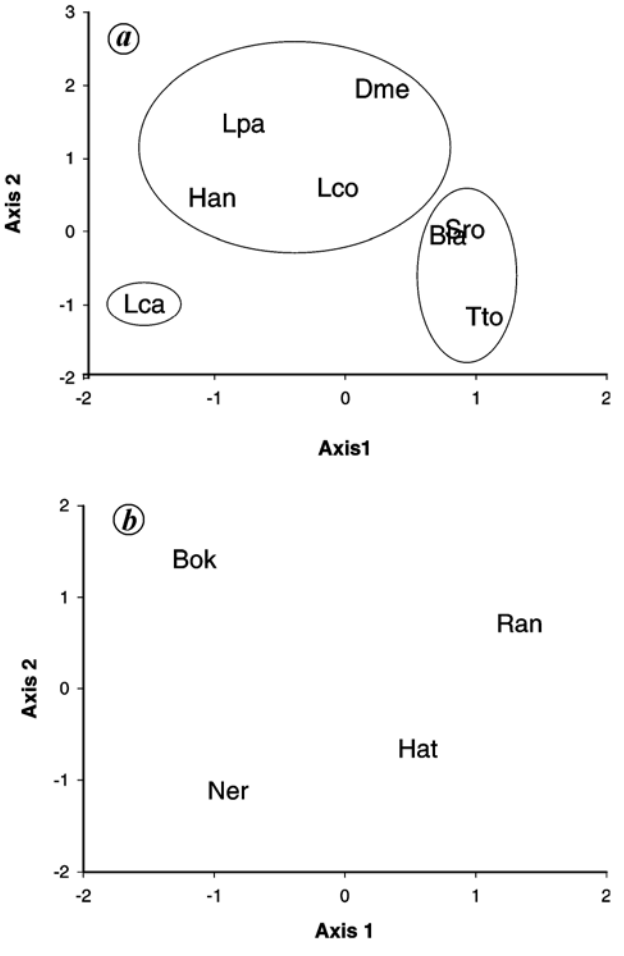

Figure 3. ***a***, Correspondence analysis (CA) ordination of species on the basis of leaf traits: *Bla*, *Buchanania lanzan*; *Dme*, *Diospyros melanoxylon*; *Han*, *Holarrhena antidysenterica*; *Lca*, *Lantana camara*; *Lco*, *Lannea coromandelica*; *Lpa*, *Lagerstroemia parviflora*; *Sro*, *Shorea robusta* and *Tto*, *Terminalia tomentosa*. ***b***, CA ordination of four sites on the basis of leaf traits: *Bok*, Bokarakhari; *Hat*, Hathinala; *Ner*, Neruiadamar; *Ran*, Ranitalli.

Interaction between species and site yielded significant differences in all the leaf traits (Table 4). The effect of site × species interaction was not consistent across leaf traits and majority of the species did not show marked dynamics with respect to sites (Figure 2). On the wettest site (Hathinala), *S. robusta* and *D. melanoxylon* showed clear peaks in mean leaf area, *T. tomentosa* and *D. melanoxylon* in leaf weight; *L. camara*, *L. coromandelica* and *S. robusta* in SLA, and *B. lanzan* and *D. melanoxylon* in chlorophyll concentration. On the other hand, *H. antidysenterica* showed peaks in leaf area and SLA on the driest site (Ranitalli).

CA on the basis of the set of leaf traits indicated three broad groups of species (Figure 3 *a*). The groups generally corresponded to leaf size (large leaf size, ≥ 107 cm^2: *T. tomentosa*, *S. robusta* and *B. lanza*; smaller leaf size, 26.37–61.48 cm^2: *H. antidysenterica*, *L. parviflora*, *D. melanoxylon* and *L. coromandelica*), except for *L. camara* having small leaf size (29.77 cm^2) but high SLA (269.35 cm^2/g), which stood alone. It is important to note that *L. camara* is a non-native invasive species in the dry tropical forests of India and is spreading fast in open-canopy areas. Global-scale comparisons also show that exotic invasive species generally have significantly higher values of SLA compared to native species[41]. Leaves that have high SLA can produce large or more assimilatory surfaces for a given amount of carbon fixed[42]. Also, SLA is positively related to plant growth and efficiency because it relates to leaf thickness and longevity[43]. Thus exotic species like *Lantana* achieve a greater C gain for a given investment in leaves, resulting in an even greater return on investment and hence faster growth.

A similar analysis on site based-leaf traits indicated that a combination of leaf traits can discriminate between the sites. The sites remained scattered and distinct in the ordination space (Figure 3 *b*). Between-site variability in leaf traits was smaller (1.3–1.5-fold) than between-species variability (1.7–12.5-fold). The larger inter-species variability reflects marked genotypic variability in the leaf traits, while the smaller between-site variability reflects phenotypic plasticity leading to adaptation to site conditions. For example, smallest cross-species SLA on the driest Ranitalli site may reflect water stress, which is known to reduce SLA[44]. The relationships among the leaf traits could contribute to the relative consistency of com-

Table 5. Mean leaf area, leaf weight, specific leaf area and chlorophyll content of eight species across four sites

Species	Leaf area (cm^2)	Leaf weight (g)	Specific leaf area (cm/g)	Chlorophyll (mg/g)
Shorea robusta	118.33[a]	1.09[a]	108.86[a]	1.07[a]
Buchanania lanzan	107.39[a]	1.031[a]	108.27[a]	1.04[a]
Diospyros melanoxylon	61.48[b]	0.70[b]	88.15[b]	1.26[b]
Lagerstroemia parviflora	26.51[c]	0.30[c]	89.67[b]	0.82[dc]
Lannea coromandelica	49.13[b]	0.31[c]	168.92[c]	0.90[d]
Terminalia tomentosa	143.05[d]	1.38[d]	118.42[a]	0.73[c]
Holarrhena antidysenterica	26.39[c]	0.26[c]	114.90[a]	0.72[c]
Lantana camara	29.77[c]	0.11[e]	269.35[d]	0.74[c]

Values suffixed with the same letter in a column were not significantly different from each other.

Table 6. Mean leaf area, leaf weight, specific leaf area and chlorophyll content of plants on a site across species

Site	Leaf area (cm^2)	Leaf weight (g)	Specific leaf area (cm^2/g)	Chlorophyll (mg/g)
Ranitalli	71.67[a]	0.66[a]	118.48[a]	0.93[a]
Neruiadamar	65.41[ba]	0.56[b]	136.53[b]	0.81[b]
Bokarakhari	57.21[b]	0.60[ba]	123.10[a]	0.84[b]
Hathinala	86.73[c]	0.76[c]	155.15[c]	1.04[c]

Values suffixed with the same letter in a column were not significantly different from each other.

bined traits at the site level. For example, as SLA increases, leaf weight and chlorophyll concentration decrease. Thus there is a trade-off between the leaf traits.

In conclusion, we suggest that a combination of cross-species leaf traits indeed reflects site conditions in the dry tropical environment. The SLA and chlorophyll concentration are more stable traits than leaf area or leaf weight, because of their lower inter-species and inter-site variability.

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