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Relationship among specific leaf area, leaf nitrogen, leaf phosphorus and photosynthetic rate in herbaceous species of tropical dry deciduous in Vindhyan highlands

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Abstract: A range of leaf attributes was measured for 17 herbaceous species in four contrasting habitats fortnightly from July to September during 2996-2007. All herbaceous vegetation in 5 randomly located plots within each of four sites were clipped at ground level and analyzed fortnightly. Leaf area was recorded by the leaf area meter (Systronics; Leaf area meter-211). Fresh leaves were dried at 80° C for 48 hr to estimate their dry weight. Specific Leaf Area (SLA) was determined as ratio of leaf area to leaf dry weight. Leaf nitrogen was measured by Kjeldahl method and phosphorus by phosphomolybdic blue colorimetric method. The obtained values were subjected to Two- tailed Pearson correlation coefficients using SPSS (2004 ver. 13) package. SLA, leaf nitrogen, leaf phosphorus and photosynthetic rate show positive relationship with each other.

Key words: Leaf attributes; photosynthetic rate; specific leaf area; tropical dry deciduous forest.

Introduction

Understory plant species are often considered indicators of soil moisture and nutritional status (Ringius and Sims 1997) and contribute to the degree of biodiversity in forest ecosystems (Oian et al., 1997). Specific leaf area (the ratio of leaf area to leaf dry mass), leaf N and LPC are total the total amounts of N and P respectively, per unit of dry leaf mass, expressed in mg g-1. Specific leaf area (SLA) and leaf nitrogen (LN) concentration are important traits for plant growth and development because they provide information on main attributes such as relative growth rate and leaf gas exchange (Garnier et al., 1997). Specific leaf area describes the light capture area deployed per unit leaf mass (Wright and Westoby 2001) and increases as leaf thickness decreases (Meziane and Shipley 2001). Relationship between the growth capacity of a species and morphological and physiological leaf traits have been established (Poorter et al., 1990., Poorter and Bergkotte 1992; Cornelissen 1996, 1997; Grime et al., 1997). Combination of PFT, climate, and SLA explain approximately two-third of global variation in other leaf traits (Reich et al., 2007). The suggestion that incongruent plant species from different biomes may share similar leaf form and function has a long history in ecology, but has rarely been tested in a quantitative manner (Beadle 1966, Chabot and Hicks 1982). It is clear that leaf life span, specific leaf area (SLA), nitrogen (N) concentration, leaf diffusive conductance (G), and photosynthetic rate are fundamental plant traits that vary greatly among species, often by orders of magnitude (Field and Mooney 1986, Reich et al., 1992). This variation may represent adaptation to environmental heterogeneity that exists

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both locally and globally. It is well established that these leaf traits are generally correlated, based on examination of variation among and within species (Lugg and Sinclair 1981; Field and Mooney 1986; Korner 1989; Reich et al., 1992). Leaf nitrogen and photosynthetic rate are closely related with each other over a broad range as the bulk of nitrogen is directly involved in photosynthesis as a component of photosynthetic enzymes and chlorophyll related. Traditionally, ecologists have paid little attention to the understory component of the tropical dry deciduous forests. Studies from tropical dry forests show that key forests understory components can drive forests regeneration, belowground properties, and long term forest succession. Understanding understory vegetation ecology has important implications for conservations and production oriented management. Plant abilities to function are difficult to evaluate directely in the field. Therefore, a number of attempts have been made to determine easily measurable surrogates PFT. In particular, the value of PFTs as tool for predicting vegetation responses to management (i.e., grazing and moving) is the facus of the large number of studies. The relationship between leaf area per mass (SLA) and leaf N per area (LNCa) is of particular interest. SLA is a key component in, and index of, a species' growth strategy (Westoby 1998). At the leaf level, Specific leaf area and leaf nitrogen accuratevely predict maximum photosynthetic rate. SLA represents the light-intercepting area of a leaf per unit dry mass, related to net assimilation rate (Reich et al., 1992, 1997). A high SLA corresponds to a high competitive ability in terms of high mass -based stress tolerance (Grime 1979)





in terms of a short leaf life span (Reich et al., 1997; Wright et al., 2004). Plant strategies are sets of correlations that describe relationships among functional traits (Grime 1977, Chapin 1980). Consequently, plant strategies describe the patterns of trait variation that should be responsible for differential performance among species and have been used in attempts to help understand issues such as the relationship between biodiversity and ecosystem function (Tilman et al., 1997). A large fraction of leaf nitrogen is involved in the photosynthetic apparatus, and most of that in the part that determines photosynthetic capacity, at least in fastgrowing herbaceous plants (Evans 1989; Evans & Seemann 1989). Leaf N can thus be used as a proxy for photosynthetic capacity (photosynthetic saturating irradiances). Since plant strategies represent correlations of many traits across taxa, small sets of traits should be able to serve as surrogates for the larger plant strategies. If these traits are easily measured, this would facilitate the examination of large numbers of species and the relationship between plant strategies and ecological performance. For leaves specific leaf area (SLA), its components (leaf thickness and leaf tissue density) and leaf angle are relatively easy to measure and represent the principal traits that relate biomass investment in leaves and light interception (Ehleringer 1989, Witkowski and Lamont 1991, Ryser 1996, Reich et al. 1997, 1998a, b). The Photosynthetic capacity of leaves is related to the nitrogen content primarily because the proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen (Evans, 1989). Short-lived leaves can be cheaply build if nutrients are readily available, but do not withstand biotic and a biotic pressure. Such leaves have a high SLA with a high nitrogen concentration per unit area biomass invested (Reich et al., 2003). Significant nitrogen per unit mass accumulation would be required in leaves to achieve a high A_{mass} (Reich, 1999). Nitrogen accumulation requires thicker leaves i.e. lower SLA (Abrams et al., 1994; Niinemets, 1999). However thick leaves with low SLA show a low A_{mass}, probably due to limited diffusion of light and CO2 to the site of corboxylation (Lloyd et al., 1992; Terashima and Hikosaka 1995; Hanba et al., 1999). Thus, biophysical constraints place a limit on the maximum photosynthetic rate that can be achieved by the leaf with a given SLA or N mass. Leaf nitrogen productivity (LNP) was also strongly associated with RGR in most datasets, indeed to a similar extent as was SLA. Species with a lower A_{mass} for a given SLA or N_{mass} are possible from a biophysical point of view. However, they would be potentially less competitive (Reich et al., 1999). In general, although plant strategies have the potential to help predict the differential performance of species in different environments, there is a lack of data with which to examine the relationships of important functional traits that have been quantified independent of the gradients on which species performance will be examined (MacGillivray et al., 1995). Variation in leaf nitrogen explains much of the variation photosynthetic capacity, across a wide variety of plant communities, leaf nitrogen content was selected as a candidate predictor for A_{mass} (Vincent, 2001). Therefore, the aim of present study was to examine the relationship among four potentially ecologically important functional traits (specific leaf area, leaf nitrogen, phosphorus and photosynthetic rate).

Materials and Methods

Study site

The study area lies on the Vindhyan plateau in the Sonebhadra district of Uttar Pradesh (24° 13' to 24°19' N; 83°59' to 83°13'). The elevation above the mean sea level ranges between 315 and 485 m (Singh & Singh 1992). This area has been known as "Sonaghati" (golden valley) due to the richness of its natural resources (Singh et al., 2002). The climate is tropical with three seasons in a year, i.e. summer (March to mid June), rainy (mid June to September) and winter (October to February). October and March constitute the transition months between the rainy and winter seasons, and between winter and summer seasons, respectively. The long term (1981-1988) annual average rainfall varies between 926 mm at the Obra meteorological station and 1145 mm at the Renukoot meteorological station. About 85% of the annual rainfall occurs during the rainy season from the southwest monsoon (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 at 12°C in January and at 31°C in May. Red coloured and fine textured sandstone (Dhandraul orthoquartzite) is the most important rock of the area (Table-1). Sandstone is generally underlain by shale and limestone. The soils derived from these rocks are residual ultisols and are sandy-loam in texture (Raghubanshi 1992). These soils are part of the hyperthermic formation of typical plinthustults with ustorthents according to VII approximation of the USDA soil nomenclature (Singh et al., 2002). The potential natural vegetation of the region is tropical dry deciduous forest, which is locally dominated by species such as Anogeissus latifolia (Roxb. ex DC.) Wall. ex Beddome (Combretaceae), Boswellia serrata Roxb. ex (Burseraceae), Buchanania lanzan Colebr. (Anacardiaceae), Diospyros melanoxylon Ces., Passer & et Gibelli (Ebenaceae). Hardwickia binata Roxb. parviflora (Caesalpiniaceae), Lagerstroemia Roxb. cormendelica (Houtt.) (Lythraceae), Lannea Merr. (Anacardiaceae), Madhuca longifolia (J. Koenig ex L.) J.F. Macbr. (Sapotaceae), Shorea robusta C.F. Gaertn. (Dipterocarpaceae) and Terminalia tomentosa Wight & Arn. (Combretaceae). Herbaceous vegetation is dominanted by Hyptis suaveolens (L.) Poit. (Lamiaceae), Sporobolus diandra Retz. (Poaceae), Oplismenus composites (L.) P Beauv. (Poaceae) and Abutilon indicum (L.) Sweet (Malvaceae).

Method

Reconnaissance survey of the entire region was made and four sites (Hathinala, Ranitalli, Bokrakhari and Neuriuadamar) in the region were selected on the basis of soil moisture gradients. Hathinala and Ranitalli sites belong to Renukoot forest division Bokrakhari and Neuriuadamar sites belong to Obra forest division. At these sites, sampling was done for the year 2006 and

2007 in the wet season from July to September fortnightly. At each site, 5 quadrates each 1 x 1 m in size were sampled randomly for vegetation analysis. A total of 20 quadrates, were sampled for vegetation analysis from the entire study area. Photosynthetic rate and stomatal conductance was measured by LCpro. instrument, Sample were dried at 70 C for 48 hour leaf nitrogen was determined by micro-Kjeldahl method, for measurement of phosphorus Olsen's methods (1954) was applied and for measurement of specific leaf area of individual leaf area is divided by its oven dry mass.

Statistical analysis

Two- tailed Pearson correlation coefficients between SLA, leaf N, leaf P and photosynthetic rate were done. Statistical analyses was done using SPSS (2004 ver. 13) package.

Results

Soil is sandy loam in texture, slightly acidic and poor in nutrients. Mean annual soil moisture among sites, varied from 9.33 % to 13.42%; the Hathinala site was the moistest and the Ranitalli site the driest (Table 1). The soil cover at the Hathinala site was the deepest (21.11 cm) while that at Ranitalli site the shallowest (9.48 cm). Sand was the most preponderant soil particle, the sand content ranging from 40.56% (Bokrakhari site) to 48 % (Neruiyadamar site). Hathinala soil was richest in clay content (7.06%) and the Ranitalli site was the poorest (1.38%). Bulk density ranged from 1.30 to 1.38 g cm⁻³. Total soil carbon varied from 1.20% to 1.53% among sites, being maximum at Neruiyadamar and minimum at Bokrakhari site. Total soil nitrogen ranged from 0.11 % (Bokrakhari site) to 0.14 % (Neruiyadamar site). Total soil phosphorus content varied from 0.02 % to 0.04% among sites, Hathinala site showed the highest total soil phosphorus content. Litter depth among sites varied from 0.30 cm (Ranitalli site) to 4.75cm (Hathinala site). Available light for herbaceous vegetation as % of full sunlight was highest at Ranitalli site (84.5%) and lowest at Hathinala site (65.92%). According to pearson correlation SLA shows significant positive relationship with N mass (P<0.01), Pmass (P<0.01) and Aarea (P<0.01) (Table-2). Regression graph between SLA -N_{mass}(Figure.1), SLA -P_{mass}(Figure.2) and SLA- A_{area} (figure.3) show significant positive relationship.

Discussion

Leaf attributes were strongly intercorelated. SLA, P_{mass}, A_{area} would scale positively with one another at each site and also across all species. Higher SLA leaves tend to have less structural material relative to metabolic components, less internal shading and shorter gas diffusion paths (Parkhurst 1994; Terashima & Hikosaka 1995), presumably contributing to the association between A_{mass} and SLA at a given leaf N. Lower N mass is related to lower A_{mass} because of the central role of N in photosynthetic enzymes and pigments (Field and Mooney 1986). A number of studies have reported a positive association between SLA and leaf nitrogen concentration expressed on a dry mass basis (Sobrado and Medina 1981; Brown and Wilson 1983; Kull and Niinemets 1993). Thus, lower SLA is associated with greater tissue density and greater allocation of biomass to structural rather than metabolic components, enhancing leaf strength and durability, but also resulting in greater internal shading and potential diffusional limitations (Lloyd et al., 1992, Terashima and Hikosaka 1995, Parkhurst 1994). Thus, low N_{mass} and low SLA combine to promote low maximum rates of CO2 exchange. In species with the opposite leaf trait syndrome, the combination of a high N investment in photosynthetic enzymes and pigments and high SLA can provide high metabolism (gas exchange rates) and light harvesting per unit tissue mass (Field and Mooney 1986, Reich et al., 1992). The relationship between SLA and photosynthetic rate has not always been found to be consistent among studies (Werk et al., 1983; Wilhelm and Nelson 1985; Pammenter et al., 1986; Koerner & Diemer 1987). However, such tissues are also nutritionally desirable to herbivores (Coley et al., 1985) and less well defended physically against biotic (herbivory) and abiotic (physical weathering and stress) agents (Coley et al., 1985, Coley 1988, Reich et al., 1991a). High photosynthetic, SLA, and leaf N concentrations are generally associated with rapid growth, high allocation to photosynthetic tissue, early attainment of reproductive age, and regeneration in high resource habitats (Poorter & Remkes 1990; Reich et al., 1992; Coernelissen 1997; Wright et al., 1999). SLA can be considered the most important trait for the study of forest herbs, and can predict photosynthetic rate (hence productivity) and decomposability of herbaceous biomass.

Table 1: Site Characteristics

Parameters	Hathinala	Bokrakhari	Neruiyadamar	Ranitali
Average annual soil moisture (%)	13.42 (±1.11)	12.00 (±1.14)	11.39 (±1.09)	9.33 (±1.21)
Soil colour	Blackish brown	Reddish brown	Yellowish brown	Greyish brown
Soil pH	$6.52 (\pm 0.07)$	$6.40 (\pm 0.05)$	$6.45 (\pm 0.04)$	$6.90 (\pm 0.11)$
Total soil carbon (%)	$1.39 (\pm 0.18)$	$1.20 (\pm 0.10)$	$1.53 (\pm 0.08)$	$1.52 (\pm 0.08)$
Total soil nitrogen (%)	0.13 ± 0.01	0.11 ± 0.004	0.14 ± 0.008	0.13 ± 0.01
Total soil phosphorus (%)	0.04 ± 0.007	0.02 ± 0.001	0.03 ± 0.004	0.02 ± 0.002
Bulk density (g cm ⁻³)	1.30 ± 0.02	1.32 ± 0.02	1.38 ± 0.02	1.38 ± 0.02
Clay content (%)	7.06 ± 0.45	4.61 ± 0.40	3.22 ± 0.17	1.89 ± 0.16
Silt content (%)	23.33 ± 0.71	26.89 ± 0.81	29.11 ± 0.42	31.44 ± 0.47
Sand content (%)	44.33 ± 0.22	40.56 ± 0.38	48.00 ± 0.24	46.78 ± 0.32
Gravel content (%)	25.28 ± 0.55	27.83 ± 0.60	19.67 ± 0.49	19.78 ± 0.32
Rockiness (%)	$43.33 (\pm 2.76)$	$75.00 (\pm 4.17)$	65.56 (±5.68)	65.00 (±7.41)
Soil depth (cm)	21.11 (±2.42)	14.30 (±1.60)	11.85 (±1.07)	$9.48 (\pm 1.18)$
Litter depth (cm)	$4.75 (\pm 0.36)$	$1.23 (\pm 0.39)$	$1.87 (\pm 0.54)$	$0.30 (\pm 0.04)$
Incident light on ground (% sun light)	$65.92(\pm 0.94)$	$74.96(\pm 1.05)$	75.36((±0.63)	84.5(±1.01)

Leaf N is integral to the proteins of photosynthetic machinery, especially Rubisco. Whreas leaf P is integral to the nucleic acid, lipid membrane and ATP. Still P $_{\rm mass}$ showed a similar relationship to $A_{\rm mass}$, as did $N_{\rm mass}$, scaling together more steeply, than proportionally. Presumably photosynthetic capacity and leaf P are related because bioenergetic molecules such as ATP and NADPH play and integral part in metabolic processes such as photosynthesis and respiration (Atwell *et al.*, 1999).

Table 2: Pearson Correlation between SLA, leaf N_{mass},

		N mass	P mass	A area
	SLA	0.626**	0.628**	0.127**
Correlation is	significa	nt at the 0.0	1 level (2-ta	ailed)

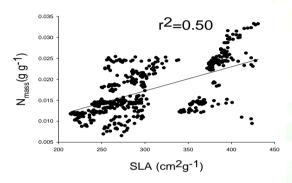


Figure 1: Relationship between specific leaf area and mass based nitrogen content.

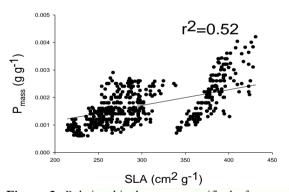


Figure 2: Relationship between specific leaf area and mass based phosphorus content.

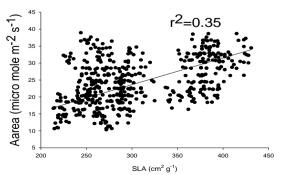


Figure 3: Relationship between specific leaf area and area based photosynthetic rate.

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