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Predominant phenotypic traits of disturbed tropical dry deciduous forest vegetation in northern India

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Abstract: The study examined the vegetation composition and phenotypic traits at five sites, differing in degree of disturbance, in a tropical dry deciduous forest of India. A total of 49 species and 4033 individuals (≥ 9.6 cm dbh) were enumerated in the cumulative 15-ha permanently protected area. The study revealed that the five sites represented five more or less different communities (species combinations with different dominants). On the basis of phenotypic traits, these communities or sites could not be discriminated, either by proportion of species belonging to different trait categories or by the cumulative importance value of the trait categories. As a result, disturbance did not affect the predominant traits. Evidently, all the communities shared the major phenotypic traits of the dry deciduous forest. Small leaf size, medium leaf texture, rough bark texture and medium deciduousness characterized the dry deciduous forest vegetation. Both the percent of species and importance values were larger for medium or less deciduous trait categories than for highly deciduous trait, representing a trade-off between water loss and the period of dry matter synthesis.

Nomenclature: Verma et al. (1985).

Introduction

Plant functional groups or types (PFTs) are defined as groups of plant species with similar traits and functions with respect to multiple environmental factors (Skarpe 1996, Lavorel et al. 1997). Current global alterations in atmospheric composition, nitrogen cycling and human-induced land-cover changes (Vitousek 1994), and the anticipated global climatic change (Cramer and Leemans 1993) warrant an understanding of the interactions between environment and plants on a broad scale. For such purposes, it may be more efficient to work with a functional classification of plants opposed to a species classification (Skarpe 1996).

A need for global datasets of such plant functional groups has been recognised by the International Geosphere Biosphere Programme in order to evaluate and predict the nature of vegetation responses to future global change (Box 1996, Woodward and Cramer 1996). Since the impact of climatic change on ecosystems over large areas cannot usually be assessed on a species basis, plant functional groups, an alternative to species, representing ecosystem structure (Aguiar et al. 1996), may facilitate this task (Bugmann 1996). Palaeoecological investigations have shown that vegetation has changed in time with climate through changes in the distribution of species according to their environmental tolerance (Skarpe 1996). Different plant functional types are expected to play different roles in terms of matter and energy processes in ecosystems (Diaz Barradas et al. 1999). Therefore, their identification and the estimation of their abundance is highly relevant to the assessment of ecosystem function (Gitay and Noble 1997).

Plant functional types based on morphology can potentially link ecophysiological traits with ecosystem processes (Chapin 1993). Information on functional diversity represented by PFTs may facilitate making decisions about the viability of the conservation areas (Nicholls and Margules 1993, Pressey et al. 1993). Despite the fact that the dry deciduous forest accounts for about 46% of the forested land in India (Singh and Singh 1988), data on phenotypic traits from dry tropical forest are lacking. The present study aims to investigate the relative importance value and diversity of different plant phenotypic traits and their ability to detect disturbance in the dry tropical forest region in northern India.

Materials and methods

Study area

The canopy of the northern tropical dry deciduous forest is formed entirely of deciduous trees, and is irregular and often broken due to human activities. Most trees have relatively short boles with low spreading crowns (Champion and Seth 1968). The climate of the dry deciduous forest, in general, is characterized by high temperatures (mean monthly minimum 17^{o}C and mean monthly maximum over 30^{o}C), and low annual rainfall (900-1150 mm) with a dry period of about 8 months within the year (Champion and Seth 1968).

The present study was conducted on five sites viz. Hathinala (HT), Khatabaran (KH), Majhauli (MJ), Bhawani Katariya (BK) and Kota (KT) (24^{o}6'52"-24^{o}26'16" N and 83^{o}1'86"-83^{o}9'60" E) in the northern dry tropical forest region of India in the years 1998-2000. The sites were selected on the basis of satellite images using LISS-III sensor of IRS-1D, and field observations to represent the entire range of conditions in terms of canopy cover and disturbance. The altitude varies from 313 to 483 m above mean sea level. The soils are ultisols, sandy loam in texture and reddish to dark grey in colour, and are extremely poor in nutrients (Singh et al. 1989). The area experiences a tropical monsoon climate with mean annual rainfall of 821 mm, of which about 86% is received from southwest monsoons during June-August. The region is facing large scale anthropogenic forcing in the form of mining, thermal power generation and the cement industry. In addition, illegal sporadic tree felling, widespread lopping and extraction of nontimber resources such as gum, resin, fibre, tannin materials, etc. are occurring (Singh et al. 1991).

The sites experience anthropogenic as well as natural disturbances with varying intensity. The disturbance regimes with estimated relative impact are summarized in Table 1. The sites nearer to roads, agricultural lands, human habitations and market experience enhanced utilization pressure. The anthropogenic disturbances include grazing and browsing and removal of ground cover by scraping for collection of grasses, cutting and lopping of trees and shrubs for fodder and fuel wood. Natural disturbances include soil erosion, wild animals and rockiness. The site with maximum distance from road, agricultural land, habitation or market was given the impact factor 1. Impact factors for other sites were calculated as ratios of the distance of this site to the distance of other sites, e.g., distance of the Khatabaran site from the road was maximum, i.e., 6000 m. The distance of the Hathinala site from the road was 1000 m. The impact of road for Khatabaran was 1, and that for Hathinala was 6 (6000/1000). In a similar way, impact of cutting and lopping was relativised with the help of tree basal area, and that of grazing and browsing by sapling density. Other impacts were determined through visual estimation. The total score of disturbance increased in degree from Hathinala to Kota site (Table 1).

Sampling and data analysis

At each of the five sites, three one-hectare contiguous permanent plots were established. Each hectare (100 m x 100 m) was divided into 100 sub-plots, each 10 m x 10 m in size, as workable units. All individuals ≥ 9.6 cm diameter at breast height (dbh) were enumerated by species and the dbh of all the individuals was measured to the nearest mm.

Four phenotypic traits (viz. leaf size, leaf texture, leaf longevity and bark texture) were used in the analysis. Each trait was classified into three categories. Species yielding 201-400 cm^2 leaf area were grouped in medium leaf size (MLS) while those below and above this range were grouped in small (SLS) and large leaf categories (LLS), respectively. On the basis of the presence or absence of scales and hair, thickness and degree of co-

Table 1. Disturbance regimes (scores for relative impact) at each of the five dry tropical forest sites.

Sites	Source of impact										Total score of relative impact
	Road	Agricultural land	Habitation	Merket	Cutting and lopping	Grazing and browsing	Scraping	Soil erosion	Rockiness	Wild animals	
Hathinala	6	1	1	1	2	2	0	2	3	4	22
Khatabaran	1	2	3	3	1	5	0	3	5	5	28
Majhauli	8	3	3	1	2	1	1	4	4	3	30
Bhawani Katariya	75	3	3	1	2	3	0	5	2	2	96
Kota	60	8	8	9	11	4	5	1	1	1	108

riaceousness of lamina, the species were grouped into rough (RLT), medium (MLT) and smooth (SLT) leaf texture categories. On the basis of the foliage duration, the species were grouped into three classes, viz. highly deciduous (HD, 7-8 mo. foliage duration), medium (MD, 9-10 mo. foliage duration) and less deciduous (LD, 10 mo. foliage duration) categories. The bark texture trait was divided into three types, viz. rough (RBT), medium (MBT) and smooth (SBT) on the basis of thickness and presence or absence of grooves and fissures in different intensity.

The relative importance value (= [relative frequency + relative density + relative basal area] / 3) (Curtis 1959) for each species was determined and summed across the phenological trait categories. Analysis of Variance (ANOVA) was used to identify the effect of degree of disturbance on importance value and per cent species contributed by different trait categories. Tukey's test was used to differentiate the means. Simple correlation coefficients were also calculated between pairs of trait categories. All statistical analyses were accomplished by using the statistical software package SPSS (SPSS 1997).

Results

A total of 49 species with 4033 stems were recorded in the 15-ha area. The number of stems for various species in the entire study area varied from 1-655 (Table 2).

On the basis of relative importance values (see Appendix), the Hathinala site represented *Acacia catechu-Shorea robusta* community; Khatabaran site, *Tectona grandis-Anogeissus latifolia* community; Majhauli site, *Shorea robusta – Terminalia tomentosa* community; Bhawani Katariya site, *Hardwickia binata – Shorea robusta* community; and the Kota site, *Hardwickia binata – Butea monosperma* community.

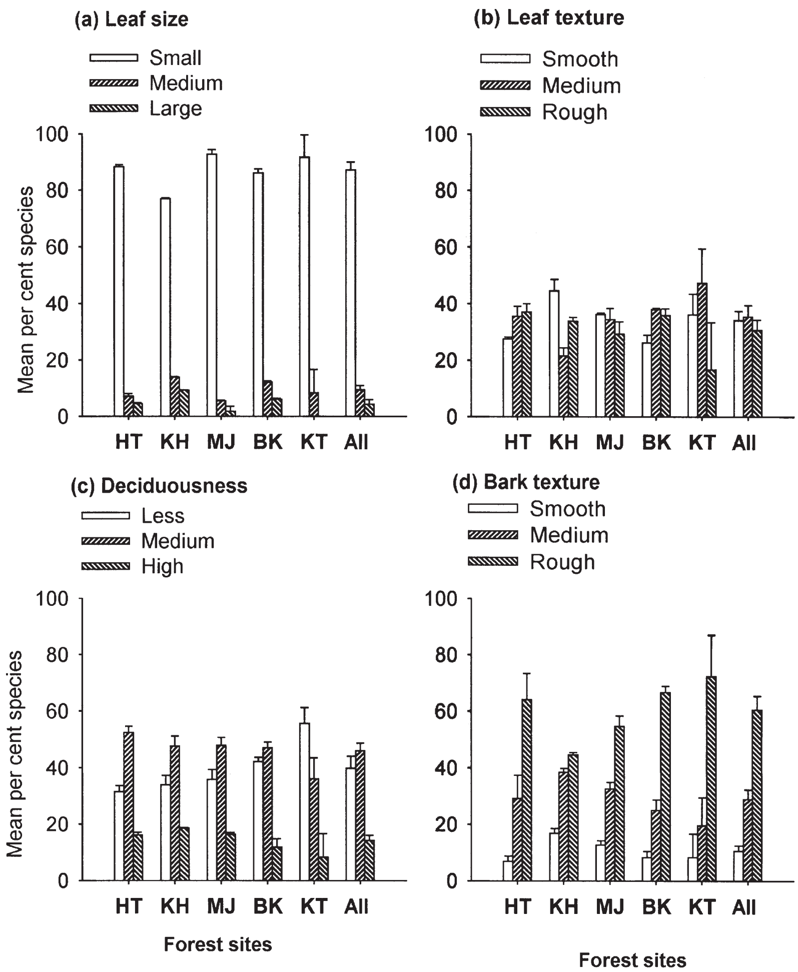

Figure 1. Distribution of species into various phenotypic traits; (a) leaf size, (b) leaf texture, (c) deciduousness, (d) bark texture. Thin bars represent 1 SE. HT, KH, MJ, BK, KT and All, respectively, stand for Hathinala, Khatabaran, Majhauli, Bhawani Katariya, Kota and all sites.

Table 2. List of adult tree species (family), in decreasing order of abundance and the number of sites as well as morphological characters of occurrence in the 15-ha permanent plot of Vindhyan dry tropical forest of India, HT = Hathinala, KH = Khatabaran, MJ = Majhauli, BK = Bhawani Katariya, KT = Kota, SLS = Small leaf size, MLS = medium leaf size, LLS = large leaf size, RLT = rough leaf texture, MLT = medium leaf texture, SLT = smooth leaf texture, HD = high deciduous, MD = medium deciduous, LD = less deciduous, RBT = rough bark texture, MBT = medium bark texture and SBT = smooth bark texture.

Species	Family	Total density in 15-ha area	No. of sites occupied	Morphological characters
Shorea robusta	Dipterocarpaceae	655	4,KH,HT,MJ,BK	SLS,MLT,LD,RBT
Acacia catechu	Mimosaceae	514	All	SLS, SLT, MD, RBT
Terminalia tomentosa	Combretaceae	371	4,KH,HT,MJ,BK	MLS,RLT,MD,RBT
Hardwickia binata	Caesalpinaceae	360	4,HT,MJ,BK,KT	SLS,MLT,LD,RBT
Lagerstroemia parviflora	Lythraceae	274	4,KH,HT,MJ,BK	SLS,MLT,MD,RBT
Buchanania lanzan	Anacardiaceae	248	All	SLS,RLT,LD,RBT
Lannea coromandelica	Anacardiaceae	233	All	SLS,SLT,HD,SBT
Diospyros melanoxylon	Ebenaceae	207	All	SLS,RLT,LD,RBT
Tectona grandis	Verbenaceae	165	1,KH	LLS,RLT,HD,SBT
Anogeissus latifolia	Combretaceae	163	All	SLS,MLT,LD,MBT
Holarrhena antidysenterica	Apocynaceae	161	4,KH,HT,MJ,BK	SLS,SLT,HD,MBT
Emblica officinalis	Euphorbiaceae	99	4,KH,HT,MJ,BK	SLS,MLT,MD,MBT
Briedelia retusa	Euphorbiaceae	82	2,HT,MJ	SLS,MLT,MD,RBT
Boswellia serrata	Burseraceae	63	3,HT,MJ,BK	SLS,SLT,HD,MBT
Soymida febrifuga	Meliaceae	61	3,HT,MJ,BK	LLS,MLT,LD,MBT
Miliusa tomentosa	Annonaceae	56	3,HT,MJ,BK	SLS,MLT,MD,RBT
Zizyphus glaberrima	Rhamnaceae	50	4,KH,HT,MJ,BK	SLS,RLT,LD,MBT
Butea monosperma	Fabacae	49	2,KH,KT	MLS,RLT,MD,RBT
Cassia fistula	Caesalpinaceae	37	3,KH,HT,MJ	SLS,SLT,MD,SBT
Elaeodendron glaucum	Celastraceae	26	4,KH,HT,MJ,BK	SLS,RLT,MD,MBT
Pterocarpus marsupium	Fabaceae	22	3,HT,MJ,BK	SLS,RLT,LD,RBT
Cassia siamea	Caesalpinaceae	16	1,BK	MLS,SLT,LD,RBT
Carissa spinarum	Apocynaceae	15	1,KH	SLS,MLT,MD,RBT
Casearia elliptica	Flacourtiaceae	14	1,KH	SLS,SLT,LD,MBT
Nyctanthes arbortristis	Oleaceae	12	2,KH,HT	SLS,RLT,MD,RBT
Adina cordifolia	Rubiaceae	10	2,KH,MJ	SLS,SLT,LD,MBT
Terminalia chebula	Combretaceae	9	3,HT,MJ,BK	SLS,RLT,MD,RBT
Flacourtia indica	Flacourtiaceae	7	2,HT,BK	SLS,RLT,MD,MBT
Hymenodictyon excelsum	Rubiaceae	6	1,KH	MLS,SLT,HD,RBT
Ougeinia oojeinsis	Fabaceae	6	1,HT	SLS,RLT,MD,MBT
Semecarpus anacardium	Anacardiaceae	6	1,KH	LLS,SLT,MD,MBT
Bauhinia racemosa	Caesalpinaceae	5	2,HT,MJ	SLS,SLT,LD,RBT
Gardenia turgida	Rubiaceae	4	3,KH,HT,BK	SLS,MLT,MD,MBT
Eriolaena quinqueolocularis	Sterculiaceae	4	2,HT,MJ	SLS,RLT,MD,RBT
Gardenia latifolia	Rubiaceae	3	2,HT,BK	MLS,SLT,MD,SBT
Grewia serrulata	Rubiaceae	3	1,HT	SLS,RLT,HD,MBT
Aegle marmelos	Rutaceae	2	1,KH	SLS,MLT,LD,SBT
Dalbergia sissoo	Fabaceae	2	1,KT	SLS,MLT,LD,RBT
Holoptelia integrifolia	Ulmaceae	2	1,KH	SLS,MLT,LD,MBT
Mimosa himalayana	Mimosaceae	2	1,HT	SLS,RLT,MD,RBT
Albizia odoratissima	Mimosaceae	1	1,HT	SLS,SLT,MD,RBT
Bombax ceiba	Bombacaceae	1	1,KH	SLS,SLT,MD,MBT
Chloroxylon swietenia	Rutaceae	1	1,KH	SLS,SLT,MD,RBT
Ficus benghalensis	Fabaceae	1	1,KH	SLS,RLT,LD,MBT
Randia dumetorum	Rubiaceae	1	1,KH	SLS,SLT,LD,MBT
Schrebera swietenioides	Oleaceae	1	1,KH	SLS,MLT,MD,MBT
Syzygium heyneanum	Myrtaceae	1	1,KH	SLS,SLT,LD,SBT
Papra (unidentified)		1	1,HT	MLS, MLT,MD,MBT
Rij (unidentified)		1	1,MJ	SLS,MLT,MD,SBT

Table 3. Summary of ANOVA on per cent species in different trait categories.

Source	Dependent variable	df	F	Significance
Site	Leaf size	4	0.118	0.975
	Leaf texture	4	0.000	1.000
	Deciduousness	4	0.001	1.000
	Bark texture	4	0.000	1.000
Trait	Leaf size	2	1085.424	0.000
	Leaf texture	2	0.810	0.455
	Deciduousness	2	94.251	0.000
	Bark texture	2	80.537	0.000
Site x trait	Leaf size	8	3.211	0.009
	Leaf texture	8	2.751	0.021
	Deciduousness	8	4.893	0.001
	Bark texture	8	2.380	0.041
Error	Leaf size	30		
	Leaf texture	30		
	Deciduousness	30		
	Bark texture	30		

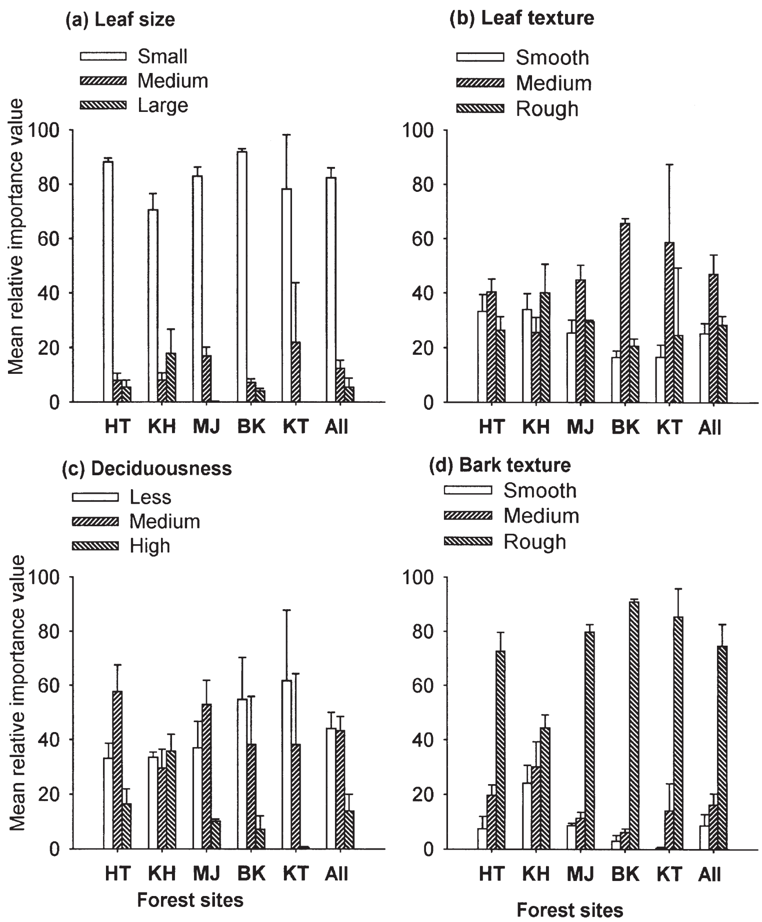

Figure 2. Mean relative importance values for various phenotypic traits; (a) leaf size, (b) leaf texture, (c) deciduousness, (d) bark texture. Thin bars represent 1 SE. HT, KH, MJ, BK, KT and All, respectively stand for Hathinala, Khatabaran, Majhauli, Bhawani Katariya, Kota and all sites.

Table 4. Summary of ANOVA on IVI of different trait categories.

Source	Dependent variable	df	F	Significance
Site	Leaf size	4	0.027	0.999
	Leaf texture	4	0.006	1.000
	Deciduousness	4	0.024	0.999
	Bark texture	4	0.003	1.000
Trait	Leaf size	2	121.547	0.000
	Leaf texture	2	5.946	0.007
	Deciduousness	2	9.305	0.001
	Bark texture	2	212.598	0.000
Site x trait	Leaf size	8	1.105	0.387
	Leaf texture	8	1.582	0.172
	Deciduousness	8	1.549	0.183
	Bark texture	8	8.178	0.000
Error	Leaf size	30		
	Leaf texture	30		
	Deciduousness	30		
	Bark texture	30		

Data on per cent of species displaying different phenotypic traits are summarized in Fig. 1. Analysis of variance indicated that different morphological traits were significantly different, in terms of distribution of species among different trait categories, except for leaf texture (Table 3). However, differences between sites on account of the proportional distribution of species in different trait categories were not significant. Most predominant traits were small leaf size (87% species), medium deciduousness (46% species), and rough bark texture (60% species). Species were almost equally divided between the three leaf texture classes. ANOVA also showed significant interaction between sites and trait categories (Table 3), indicating that species distribution among different trait categories was not consistent across sites. For example, at the Kota site about 92% species displayed small leaf size but at Khatabaran site only 77% species had small leaves. Similarly, 72% species at the Kota site had rough bark texture against 45% at the Khatabaran site.

Considering all sites, the different traits realized different importance values (Fig. 2). The small leaf size, medium leaf texture, and rough bark texture types exhibited highest dominance. Medium and less deciduousness were equally important. Minimum importance value was exhibited by large leaf size, smooth leaf texture, highly deciduous and smooth bark texture trait categories (Fig. 2). ANOVA again indicated that the sites were not significantly different from each other in terms of importance values of different trait categories, while the trait categories differed significantly in importance values (Table 4). However, Tukey's test indicated that differences in importance values between medium and large leaf size, rough and smooth leaf texture, medium and less deciduousness, and medium and smooth bark texture trait categories were not significant. The site and trait interaction was significant only for bark texture.

The correlations between different functional types based on the number of species at each forest site are shown in Table 5. There were as many as 21 significant positive correlations, with $r > 0.9$, between number of species in pairs of traits. The small leaf size had maximum correlation with medium leaf texture, large leaf size with smooth bark texture, and high deciduousness with medium bark texture. The rough bark texture accounted for 91% relative importance value at the Bhawani Katariya site against 44% at the Khatabaran site.

Discussion

Plants change evolutionarily and with environmental conditions, through modification of functions such as water economy, CO_2 assimilation, biomass allocation, reproductive rate, etc. Some of these functional modifications involve consequent modifications of phenotypic

Table 5. Correlation matrix of different morphological features using number of species of each forest site (total 5 sites) in the Vindhyan dry tropical forests of India. Only the highest *r* values for each pair with r > 0.9 is given. The values in parentheses show the significance level.

	Medium leaf texture	Smooth leaf texture	Highly deciduous	Medium deciduous	Less deciduous	Rough bark texture	Medium bark texture	Smooth bark texture
Small leaf size	0.993 (0.001)	-	0.987 (0.002)	0.991 (0.001)	0.982 (0.003)	0.969 (0.007)	0.965 (0.008)	-
Medium leaf size	-	0.919 (0.028)	-	-	0.929 (0.023)	-	0.938 (0.018)	-
Large leaf size	-	0.982 (0.003)	-	-	0.982 (0.003)	-	-	0.999 (0.000)
Rough leaf texture	-	-	-	0.987 (0.002)	-	0.984 (0.002)	-	-
Medium leaf texture	-	-	0.985 (0.002)	-	-	-	0.966 (0.008)	-
Smooth leaf texture	-	-	-	-	0.977 (0.004)	-	-	0.982 (0.003)
Highly deciduous	-	-	-	-	-	-	0.994 (0.001)	-
Medium deciduous	-	-	-	-	-	0.982 (0.003)	-	-
Less deciduous	-	-	-	-	-	-	-	0.982 (0.003)

traits. According to Keddy (1992), the concept of trait-environment linkages refers to sets of plant attributes associated with certain environmental conditions, irrespective of the species involved. Local conditions filter traits from a regional species pool, rather than taxa (Woodward and Diament 1991, Diaz et al. 1999). Therefore, plant traits and, hence, plant functions are the subject of environmental filtering processes. It may, however, be noted that morphological characters may not have one-to-one relationship with function because in biotic systems processes do not operate in isolation (Hogeweg 2002). Nevertheless, plant functional types or phenotypic trait categories are considered essential for reducing the complex characteristics of species diversity when attempting to project the nature and function of species assemblages into future environments (Woodward and Cramer 1996). According to Walker (1992), the enormous complexity of individual species and populations can be summarized into a relatively small number of general recurrent patterns, with the help of PFTs.

Phytosociological analysis indicated that the five sites of the dry tropical forest studied represented different combinations of species with different dominants and co-dominants. Jha and Singh (1990) reported that the dry tropical forest is composed of a mosaic of noncontiguous patches representing different plant communities. However, when phenotypic traits are considered, neither the sites nor the communities could be discriminated, either by proportions of species belonging to different trait categories or by the cumulative importance value of the trait categories. Nevertheless, distribution of species among the trait categories was not consistent across the sites. The present sites represented different levels of disturbance, and evidently disturbance did not affect the predominant traits, although species composition and relative importance of individual species varied along the disturbance gradient. Evidently, the major phenotypic traits of the forest were shared by all communities, however different they may be in terms of species composition. The sites may have different species composition but there may still be phylogenetic similarities which constrain the phenotypic characters.

The predominant phenotypic traits exhibited by the dry deciduous forest, notwithstanding site characteristics such as disturbance, were small leaf size, rough bark texture, medium leaf texture, and medium deciduousness. Correlation coefficients between the number of species showing these traits were also high. These trait categories appear to be most ideal for the dry deciduous forest species. It is likely that interrelationships in plant traits occur through a series of linkages to influence species distribution patterns (Suding et al. 2003).

Small leaf size is an important trait for light interception, heat balance, CO_2 diffusion and water balance; particularly in phanerophytes. Leaf size generally decreases with decreasing water availability and with increasing temperature during the growth period (Werger and Ellenbroeck 1978). Smaller leaves have less boundary layer resistance hence heat convection is more rapid. At the same time, in such leaves transpiration and convection are less closely coupled permitting leaves to cool down as well as conserve water. Reduced leaf size is efficient in controlling water loss (Box 1996). Small size of leaf or pinnatified blade also prevents drought necrosis. In large leaves, the marginal parts, especially those lying between the larger veins, die when exposed to severe atmospheric drought. Therefore, the dominance of small leaf PFT with highest proportional species characterize the dry deciduous forest, which are poor in water availability and experience relatively higher temperatures.

Medium or rough leaf texture is associated with thick cuticles, sunken stomata (often of high density), hairiness, more sclerenchyma, better developed palisade mesophyll and wax or resin layers. Smaller specific leaf area (SLA) is associated with an increase in leaf thickness (Burslem et al. 1996), a large number of mesophyll cell layers (Bjorkman 1981) and a thick layer of leaf hair (Ehleringer 1988). For several species pairs, SLA decreased from wet to dry habitats due to reinforcement of vasculture or epidermis which decreases the susceptibility to wilting (Wright and Westoby 1999). Lambers and Poorter (1992) concluded that the trade-offs between investment in photosynthetic machinery and the degree to which a plant is defended against leaf damage due to drought are likely to have occurred mainly by adaptations which decrease SLA. The extra construction costs would be recovered only if they reduce the losses to the environment, e.g., loss of water (Orians and Solbrig 1977). The highest proportion of species as well as dominance of medium leaf texture PFT characterize the tropical dry deciduous forest.

Deciduousness is a phenological attribute (McIntyre et al. 1999). Changes such as leaf fall and leaf expansion were found to cause changes in tree water status, and tree water stress accelerates leaf senescence and hence leaf shedding, ultimately resulting in reduced water loss (Reich and Borchert 1984). However, shorter duration of foliage would also result in a shorter span of time for photosynthesis. Therefore, instead of highly deciduous trait, both the per cent of species or importance value was larger for medium to less deciduous trait categories, representing a trade-off between water loss and period of dry matter synthesis.

The dry deciduous forest experiences frequent fires (Champion and Seth 1968). According to Levit (1972), thin barked trees are highly susceptible to heat injury. Thick and rough bark texture permits the species to escape from fire injury and fungal attack. It is not surprising, therefore, that the dry deciduous forest is dominated by the rough bark texture trait.

The study also indicated that the trade-offs between phenotypic traits and plant function have a limit. For example, although all species possessed one or more of these ideal traits (viz. small leaf size, rough bark texture, medium leaf texture, and medium deciduousness, only five species possessed all four of the most desirable traits and none of these species dominated a site. As many as 13 species possessed a combination of three most desirable characters and 15 species possessed a combination of two of these characteristics. Thus a considerable amount of redundancy (i.e., species richness), which is a main-stay of community stability/resilience, occurs within a phenotypic trait category.

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References

Aguiar, M.R., J.M. Paruelo, O.E. Sala and W.K. Lauenroth. 1996. Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. *J. Veg. Sci.* 7: 381-390.

Bjorkman, O. 1981. Responses to different quantum flux densities. In: O.L. Lang, P.S. Nobel, C.B. Osmond and H. Ziegler (eds), *Encyclopedia of Plant Physiology,* vol. 12A. Springer-Verlag, Berlin, pp. 57-107.

Box, E.O. 1996. Plant functional types and climate at global scale. *J. Veg. Sci.* 7: 309-320.

Bugmann, H. 1996. Functional types of trees in temperate and boreal forests: classification and testing. *J. Veg. Sci.* 7: 359-370.

Burslem, D.F.R.P., P.J. Grubb and I.M. Turner. 1996. Responses to stimulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* 28: 636-648.

Champion, H.G. and S.K. Seth. 1968. *A Revised Survey of the Forest Types of India*. Government of India Publication, New Delhi.

Chapin, F.S. 1993. Functional role of growth forms in ecosystem and global processes. In: J.R. Ehleringer and C.B. Field (eds.), *Scaling Physiological Processes: Leaf to Globe*. Academic Press, San Diego, CA, pp. 287-312.

Cramer, W.P. and R. Leemans. 1993. Assessing impact of climate change on vegetation using climate classification systems. In: A.M. Solomon and H.H. Shugart (eds), *Vegetation Dynamics and Global Change*. Chapman and Hall, London, pp. 190-217.

Curtis, J.T. 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press, Madison.

Diaz Barradas, M.C., M. Zunzunegui, R. Tirado, F. Ain-Lhout and F. Garcia Novo. 1999. Plant functional types and ecosystem function in Mediterranean shrubland. *J. Veg. Sci.* 10: 709-716.

Diaz, S., M. Cabido and F. Casanoves. 1999. Functional implications of trait-environment linkages in plant communities. In: E. Weiher and P.A. Keddy (eds), T*he Search for Assembly Rules in Ecological Communities*. Cambridge University Press, Cambridge, pp. 338-362.

Ehleringer, J.R. 1988. Comparative ecophysiology of *Encelia farinose* and *Encelia frutescens*. I. Energy balance considerations. *Oecologia* 76: 553-561.

Gitay, H. and I.R. Noble. 1997. What are functional types and how should we seek them? In: T.M. Smith, H.H. Shugart and F.I. Woodward (eds), *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge, pp. 3-19.

Hogeweg, P. 2002. Computing an organism: on the interface between informatic and dynamic processes. *Biosystems* 64: 97-109.

Jha, C.S. and J.S. Singh. 1990. Composition and dynamics of dry tropical forest in relation to soil texture. *J. Veg. Sci.* 1: 609-614.

Keddy, P.A. 1992. Assembly and response rules: two goods for predictive community ecology. *J. Veg. Sci.* 3: 157-164.

Lambers, H. and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for ecological causes and consequences. *Adv. Ecol. Res*. 23: 187-261.

Lavorel, S., S. McIntyre, J. Landsberg and T.D.A. Forbes. 1997. Plant functional classification: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol*. 12: 474-478.

Levit, J. 1972. *Responses of Plants to Environmental Stress*. Academic Press, New York.

McIntyre, S., S. Lavorel, J. Landsberg and T.D.A. Forbes. 1999. Disturbance response in vegetation towards a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.

Nicholls, A.O. and C.R. Margules. 1993. An upgraded reserve selection algorithm. *Biol. Conserv*. 64: 165-169.

Orians, G.L. and O.T. Solbrig. 1977. A cost-income model of leaves and roots with special reference to arid and semiarid areas. *Am. Nat*. 111: 677-690.

Pressey, R.L., C.J. Humpheries, C.R. Margules, R.I. Vane-Wright and P.H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends Ecol. Evol*. 8: 124-128.

Reich, P.R. and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol*. 72: 61-74.

Skarpe, C. 1996. Plant functional types and climate in a southern African savanna. *J. Veg. Sci.* 7: 397-404.

Singh, J.S., A.S. Raghubanshi, R.S. Singh and S.C. Srivastava. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forests and savanna. *Nature* 238: 499-500.

Singh, J.S., K.P. Singh and M. Agrawal. 1991. Environmental degradation of the Obra-Renukoot-Singrauli area, India, and its impact on natural and derived ecosystems. *The Environmentalist* 11: 171-180.

SPSS. 1997. *SPSS Base 7.5 Applications Guide*. SPSS Inc., Chicago.

Suding, K.N., D.E. Gordberg and K.M. Hartman. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1-16.

Verma, D.M., P.C. Pant and M.I. Hanfi. 1985. *Flora of Raipur, Durg and Rajnandgaon*. Botanical Survey of India, Howrah.

Vitousek, P.M. 1994. Beyond global warming: Ecology and global change. *Ecology* 75: 1861-1876.

Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conserv. Biol*. 6: 18-23.

Werger, M.J.A. and G.A. Ellenbraek. 1978. Leaf size and leaf consistence of a riverine forest formation along a climatic gradient. *Oecologia* 34: 297-308.

Woodward, F.I. and D.A. Diament. 1991. Functional approaches to predicting the ecological effects of global change. *Func. Ecol*. 5: 202-212.

Woodward, F.I. and W. Cramer. 1996. Plant functional types and climatic changes: Introduction. *J. Veg. Sci.* 7: 306-308.

Wright, I.J. and M. Westoby. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *J. Ecol*. 87: 85-97.

Appendix

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Appendix EA4-3. Mean relative importance values for tree species at five sites of dry tropical forest.