

Plant functional traits with particular reference to tropical deciduous forests: A review

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Functional traits (FTs) integrate the ecological and evolutionary history of a species, and can potentially be used to predict its response as well as its influence on ecosystem functioning. Study of inter-specific variation in the FTs of plants aids in classifying species into plant functional types (PFTs) and provides insights into fundamental patterns and trade-offs in plant form and functioning and the effect of changing species composition on ecosystem functions. Specifically, this paper focuses on those FTs that make a species successful in the dry tropical environment. Following a brief overview, we discuss plant FTs that may be particularly relevant to tropical deciduous forests (TDFs). We consider the traits under the following categories: leaf traits, stem and root traits, reproductive traits, and traits particularly relevant to water availability. We compile quantitative information on functional traits of dry tropical forest species. We also discuss trait-based grouping of plants into PFTs. We recognize that there is incomplete knowledge about many FTs and their effects on TDFs and point out the need for further research on PFTs of TDF species, which can enable prediction of the dynamics of these forests in the face of disturbance and global climate change. Correlations between structural and ecophysiological traits and ecosystem functioning should also be established which could make it possible to generate predictions of changes in ecosystem services from changes in functional composition.

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1. Introduction

Plant functional traits (FTs) can be defined as ‘plant characteristics that respond to the dominant ecosystem processes’ (Gitay and Noble 1997). Examples of FTs are leaf size, toughness and longevity, seed size and dispersal mode, canopy height and structure, ability to resprout and capacity for symbiotic fixation of nitrogen (Díaz and

Cabido 2001). In recent years, the possible effects of terrestrial plant diversity on ecosystem processes and services are increasingly being documented (see Díaz *et al.* 2003; Mooney *et al.* 2009; Mooney 2010), and ecologists are trying to develop functional classifications of species to comprehend the complex diversity of life on earth (McIntyre *et al.* 1999; Weiher *et al.* 1999). Garnier *et al.* (2007) presented a standardized methodology that used FTs to assess

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Abbreviations: A_{area} , area-based leaf maximum photosynthetic rate; A_{mass} , mass-based leaf maximum photosynthetic rate; ANPP, above ground net primary production; ATP, adenosine triphosphate; Ca_{mass} , mass-based calcium concentration; CC, leaf construction cost; Chl, chlorophyll concentration; C_{mass} , mass-based carbon concentration; DBH, diameter at breast height; E, leaf transpiration rate; FT, functional trait; g_c , leaf stomatal conductance, K_{mass} , mass-based potassium concentration; LA, leaf area; LAI, leaf area index; LDMC, leaf dry matter content; LL, leaf life-span; LMA, leaf mass per area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; LSC_{max} , maximum leaf specific hydraulic conductivity; LWC, leaf water content; Na_{mass} , mass-based sodium concentration; N_{mass} , mass-based nitrogen concentration; PFT, plant functional type; P_{mass} , mass-based phosphorus concentration; Rd_{area} , area-based dark respiration rate; Rd_{mass} , mass-based dark respiration rate; Rd_{max} , maximum rate of dark respiration; SLA, specific leaf area; SSD, specific stem density; TDF, tropical deciduous forest; TDMC, twig dry matter content; WUEi, intrinsic water use efficiency

the impacts of land-use changes on vegetation and ecosystem functioning. They studied 16 traits describing plant stature, leaf characteristics and reproduction for the most dominant species at 11 sites representing various types of land-use changes occurring in marginal agro-ecosystems across Europe and Israel. According to their results, the functional traits were able to describe adequately the functional response of vegetation to land-use changes. Thus, a consideration of FTs makes it possible to seek general explanations for differences in functioning of climatically and edaphically diverse environments (Pakeman 2004).

Understanding the mechanisms through which species traits determine community structure is also a priority area of research (Lavorel *et al.* 2007). A recent trait based approach to community assembly helped to integrate functional ecology and gradient analysis with community ecology and coexistence theory (Ackerly and Cornwell 2007). Kraft *et al.* (2008) examined the co-occurrence patterns of over 1100 tree species in a 25-hectare Amazonian forest plot in relation to field measured functional traits and showed that inter-specific differences in trait-based ecological strategies contribute to the maintenance of diversity in one of the most diverse tropical forests in the world.

The complexity and diversity of natural systems makes grouping of species essential for deriving general principles of succession and ecosystem recovery following human impact (Keddy 1992; Grime *et al.* 1997; Westoby 1998; Aubin *et al.* 2009). Traditionally, species have been grouped into plant functional types (PFTs) on the basis of their physiological/ecological functions and common evolutionary history (Noble and Gitay 1996). However, there has also been a search for the functional description of vegetation based on FTs that show a common response to the environment, independent of phylogeny (Rusch *et al.* 2003). Mouchet *et al.* (2010) have inferred that in combination with phylogenetic and taxonomic diversity, functional diversity will 'improve our understanding of how biodiversity interacts with ecosystem processes and environmental constraints'. In many poorly described plant communities where taxonomic knowledge is limited, an FT approach can be used to understand and predict plant responses to changing management factors and environment (Díaz *et al.* 2001). Plant functional groupings are also potentially useful communication tools for land managers, who may not necessarily relate to taxonomic units, particularly when dealing with species-rich ecosystems (Díaz *et al.* 2002).

According to Holdridge (1967), tropical forests comprise about 52% of the global forest cover, and tropical dry forests comprise 42% of tropical forests. In India, tropical dry forests account for 38.2% of the total forest cover (MoEF 1999). Tropical deciduous forests (TDFs) are forests occurring in tropical regions which are characterized by pronounced seasonality in rainfall distribution with several

months of drought (Mooney *et al.* 1995). TDFs are typically dominated by deciduous trees where at least 50% of trees present are drought deciduous, the mean annual temperature is $>25^{\circ}\text{C}$, total annual precipitation ranges between 700 and 2000 mm, and there are 3 or more dry months (with precipitation < 100 mm) every year (Sánchez-Azofeifa *et al.* 2005). Pennington *et al.* (2006) use a wider interpretation of TDF which includes vegetation that experiences a minimum dry season period of 5–6 months, resulting in strongly seasonal ecological processes and functions.

TDFs have historically supported high human population densities because their climatic and edaphic characteristics are attractive for human settlement and development (Tosi and Voertman 1964; Sánchez-Azofeifa *et al.* 2005). Dry forests are more threatened and less protected than moist and wet forests (Gerhardt 1993; Powers and Tiffin 2010) and have decreased in area considerably during the past decades. In central India they are threatened by lopping, burning, overgrazing and clearing for cultivation (Jha and Singh 1990), and as a result, the forest cover in most regions is being converted, over the past several decades, into dry deciduous scrub, savanna and grasslands that are progressively species-poor (Champion and Seth 1968; Sagar and Singh 2003). These forests are vulnerable to stress during successional processes as they experience a severe and less predictable environment (Murphy and Lugo 1986).

Plant species in TDFs are subjected to water stress during the dry season (Eamus 1999), and the length of dry season is the controlling factor of vegetation structure and patterns (Gritti *et al.* 2010). Due to locational differences in the extent and intensity of seasonal drought, TDFs are composed of a mosaic of different PFTs showing varying adaptations to seasonal drought (Borchert 2000).

In the present article, following a brief background, we review the literature on plant FTs which are particularly relevant to TDFs in order to understand the relationship between FTs and functioning of plants in tropical deciduous forest ecosystems. We consider the traits under following categories: leaf traits, stem and root traits, reproductive traits and traits particularly relevant to water availability and discuss their relevance to functioning of tropical deciduous forest ecosystems. We also discuss trait-based grouping of plants into PFTs. Finally, this article compiles information on FTs of TDF species, and recognizes that there is incomplete knowledge about many FTs and suggests the need for further research on FTs and their effects on TDFs. We suggest that a major focus of research should be to evaluate those FTs that make a species successful in relation to moisture gradient.

2. Plant functional traits and ecosystem processes

Functional traits are directly or indirectly linked to plant population and ecosystem processes (Hillebrand and

Matthiessen 2009). The correlations between structural and ecophysiological traits and ecosystem functioning, including primary productivity, decomposition and nutrient cycling, and water availability could make it possible to predict changes in ecosystem services from changes in functional composition. Changing species composition can change FT composition, which in turn affects the ecosystem functioning that depends both on the traits of species that decline or disappear and the traits of species that replace them (Díaz *et al.* 2003; Suding *et al.* 2006; Lavorel *et al.* 2007).

There is much variation in plant traits among species (Wardle *et al.* 1998; Kooyman and Westoby 2009) and across groups of species (Garnier 1991). The relative importance of FTs in determining ecosystem processes changes across plant groups (Cornelissen and Thompson 1997; McLaren and Turkington 2010). Further, plant effects on any ecosystem process can be mediated by multiple traits, and many of these traits vary independently from one another (Eviner and Chapin 2003). Specific processes could be affected by a combination of traits, while particular key traits could simultaneously control multiple processes (de Bello *et al.* 2010). A consideration of inter-specific variation in FTs provides insights into the patterns and trade-offs in plant form and functioning (e.g. Poorter and Bergkotte 1992; Reich *et al.* 1992; Von Willert *et al.* 1992; Grime *et al.* 1997; Lambers *et al.* 1998; Craine *et al.* 2001) and reveals the effects of (changing) species composition on ecosystem functions (e.g. Schulze and Mooney 1994; MacGillivray *et al.* 1995; Wardle *et al.* 1998; Díaz *et al.* 1999).

Geber and Griffen (2003) defined a functional trait as any phenotypic character that influences an organism's fitness and reported that the influence of FTs on final fitness can be complex because of the interrelationships among FTs. They also argued that FTs affect fitness through performance measures such as growth rate, competitive ability, herbivore resistance to tolerance, attractiveness to pollinators, etc. The performance measures, in turn, affect fitness components such as age-specific rates of survival, growth, fertility, or mating success, and, eventually, lifetime fitness. Violle *et al.* (2007) consider functional traits as morpho-physio-phenological traits that affect fitness indirectly through their effects on growth, reproduction and survival.

Currently, the construction of a large database of FTs is gaining high priority in the research agenda of plant ecology (e.g. Westoby and Wright 2006; TraitNet: <http://traitnet.ecoinformatics.org/>) because it appears as a fundamental step both to understand and to predict the distribution of species in the present and future environments (Grime *et al.* 1988; Keddy 1992; Westoby 1998), and to relate the functioning of species to that of ecosystems (Grime 1997; Chapin *et al.* 2000).

3. Tropical deciduous forest functional traits

As mentioned above, tropical deciduous forests are characterized by warm temperatures and a dry period of 3 or more months. Deciduousness is a phenological attribute expressing adaptation to seasonality and drought, resulting in reduced activities during the unfavourable season and resumption of growth with variable rates of resource use during the short favourable season (Singh and Singh 1992). The deciduousness of TDF species is affected by rainfall, temperature and solar radiation and affects intra- and inter-annual pattern of water, carbon and energy balance in TDFs (Bohlman 2010).

FTs that enable acquisition of limiting nutrients and water are important for TDF species. Plant water uptake patterns from different soil depths, which often vary spatially and temporally between different plant functional groups or types, can directly influence soil water dynamics during the growing season (Ryel *et al.* 2008; Schwinning 2010). Apart from water, nutrient supply also limits growth rates in TDFs (Hedin *et al.* 2009) and may determine spatial variation in growth of individual species in these forests (Swaine *et al.* 1987). According to Yuan *et al.* (2006), the efficiency of whole-plant nitrogen use, uptake and response increase monotonically with decreasing soil nitrogen and water, and it is higher on infertile (dry) habitats than on fertile (wet) habitats.

There are a number of FTs that can influence ecosystem processes in TDFs. Starting with vegetative traits, various growth forms represent adaptations in response to grazing by different herbivores. Life forms with perennating tissues help in the survival of plant species from unpredictable disturbances. Plant height is associated with competitive vigour and whole plant fecundity (Cornelissen *et al.* 2003). Clonality, spinescence and flammability are also important vegetative traits of plant species in TDFs (Saha and Howe 2003; Raheison and Grouzis 2005).

A high priority goal to help reduce the measuring effort is the identification of relationships between tree physiology and tree (or leaf) morphological and phenological traits. Examples are leaf lifespan – photosynthesis or leaf conductance relations, specific leaf area – photosynthesis relationships (e.g. Reich *et al.* 1998), and tree height – photosynthesis relations (Zhang *et al.* 2009; Brien *et al.* 2010). Data are now available on tropical deciduous trees with respect to selected physiological attributes or functional relationships such as (i) nitrogen and water use efficiency (Sobrado 1991), (ii) photosynthetic characteristics and associated traits (Kitajima *et al.* 1997; Niinemets and Tenhunen 1997; Niinemets 1999; Niinemets *et al.* 2009; Posada *et al.* 2009), (iii) water and trait relations (Olivares and Medina 1992; Medina and Francisco 1994; Franco *et al.*

2005; Wright *et al.* 2007; Gotsch *et al.* 2010), (iv) light-dependent leaf trait variations (Rozendaal *et al.* 2006; Markesteijn *et al.* 2007), (v) nitrogen fixation and nitrate/ammonium assimilation capacities (Schulze *et al.* 1991; Högberg 1992; Högberg and Alexander 1995; Freitas *et al.* 2010), (vi) drought effects on leaf conductance, leaf water status and photosynthesis (Eamus 1999; Brodribb *et al.* 2003; Brodribb and Holbrook 2003a,b), (vii) herbivore damage (Janzen 1970; Coley and Barone 1996; Coley 1998; Arnold and Asquith 2002; Campo and Dirzo 2003; Brenes-Arguedas *et al.* 2009) and (viii) leaf flushing and flowering phenology (Opler *et al.* 1980; Seghieri *et al.* 2009; Hayden *et al.* 2010; Fallas-Cedeño *et al.* 2010). However, despite rapid progress in the field of dry tropical tree ecophysiology, most studies (a) do not consider more than two or three FTs (which makes a multivariate analysis of tree character sets difficult), (b) refer to tree saplings instead of adults (which do not reveal the complete picture, because there are changes in many biological processes as organisms grow and age, leading to increased structural complexity) and (c) are related to the neotropics, therefore limiting generalizations about the pattern of functional trait relationships worldwide (Díaz *et al.* 2004; Wright *et al.* 2007). In the following subsections, we review our understanding of functional traits in TDFs.

3.1 Leaf traits

Leaf habit (i.e. deciduousness/evergreenness) has been traditionally considered as an important FT for grouping species into ecologically relevant PFTs. However, Powers and Tiffin (2010) analysed the potential of leaf habit as a trait for defining ecologically meaningful groups of tropical dry forest species, and concluded that leaf habit alone has little utility in distinguishing PFTs in the Costa Rican TDFs. It has been rightly argued that a database of FTs must include all traits that are relevant to acquisition and use of resources (Westoby 1998; Weiher *et al.* 1999). Three such traits are SLA (specific leaf area, i.e. the ratio of leaf area to dry mass), LDMC (leaf dry matter content, i.e. the ratio of leaf dry mass to saturated fresh mass) and LNC (leaf nitrogen concentration) (Cunningham *et al.* 1999; Reich *et al.* 1999; Wilson *et al.* 1999; Markesteijn *et al.* 2007). Two of these traits (SLA and LNC) have already been compiled into a database (Wright *et al.* 2004). SLA and LNC of component species may have a significant impact on primary productivity and nutrient cycling at the ecosystem level (Reich *et al.* 1992; Cornelissen *et al.* 1999; Aerts and Chapin 2000). This is because a combination of SLA and LNC, which are related to leaf lifespan, can predict accurately the maximum photosynthetic rate of a wide range of species (Reich *et al.* 1997). A similar argument has been made for LDMC (Ryser and Urbas 2000). The above traits are involved in a trade-off between rapid biomass production and efficient nutrient conservation at

the whole plant level (Grime *et al.* 1997; Poorter and Garnier 1999; Lavorel *et al.* 2007).

Data available on various leaf traits of tree species in TDFs are limited, and summarized in table 1. There are marked inter-specific and inter-regional variations in the values of most of the traits. Inter-specific variation in a majority of cases was larger than the inter-regional variation (table 1). For example, while mean SLA of TDF species among six countries varied between 8.5 mm² mg⁻¹ (Panama) to 20.7 mm² mg⁻¹ (Bolivia), within a region (e.g. Argentina) the maximum value of SLA was more than six times the minimum value. The desert, tropical evergreen, temperate evergreen and tundra species usually have lower SLA than the TDF species. For example, SLA ranged between 6.2 and 4.7 mm² mg⁻¹ in desert species (Reich *et al.* 1998; Vendramini *et al.* 2002), 5.9 and 9.7 mm² mg⁻¹ in tropical evergreen (Vendramini *et al.* 2002; Santiago 2003), 4.2 and 4.8 mm² mg⁻¹ in temperate evergreen (Reich *et al.* 1995; Reich *et al.* 1998) and 3.3 and 7.0 mm² mg⁻¹ in tundra species (Körner *et al.* 1986; Reich *et al.* 1998) compared to the TDF range of 8.5 to 18.6 mm² mg⁻¹ (table 1). While some leaf trait values of TDF species are similar to those of tropical evergreen species (e.g. CC; Villar and Merino 2001), values of other traits differ between the species of these two leaf habits. In the TDF, broad-leaved deciduous trees are reported to have greater SLA, LNC and photosynthetic rates as compared to broad-leaved evergreen trees (see references in Powers and Tiffin 2010). The mean values of leaf life-span (LL) for desert (14 mo), tropical evergreen (20 mo), temperate evergreen (44 mo), temperate deciduous (13 mo) and tundra (7 mo) species (Reich *et al.* 1998) are greater than the value (6 mo) observed by Prior *et al.* (2003) for deciduous species of Australia. Thus, mean LL is shorter and LMA is lower in TDF species compared to evergreen woody species (Wright *et al.* 2004a). In Argentina, the desert species showed greater average leaf thickness (1.9 mm) and LWC (80%) as compared to the average leaf thickness (0.3 mm) and LWC (60%) of deciduous species (Vendramini *et al.* 2002). Among ecophysiological traits, g_c of TDF species also varied substantially among the regions and species (table 1). The reported values for g_c from desert (329 mmol m⁻² s⁻¹; Horton *et al.* 2001), tropical evergreen (90 mmol m⁻² s⁻¹; Ishida *et al.* 2006) and temperate deciduous (190 mmol m⁻² s⁻¹; Kubiske and Abrams 1993) are lower compared to the values for TDF species (205 to 680 mmol m⁻² s⁻¹; table 1). On the contrary, A_{area} , N_{mass} , P_{mass} and C_{mass} exhibited little variation among regions and species (table 1). Generally, deciduous trees maintain greater N_{mass} than evergreen species and consequently maintain larger light saturated assimilation rate (Eamus 1999). Rd_{area} of TDF species (0.6–1.9 μ mol m⁻² s⁻¹; table 1) is lower than that of desert species (2.4 μ mol m⁻² s⁻¹; Reich *et al.* 1998) but is within

Table 1. List of leaf traits of tree species in tropical deciduous forests

Species/Forest	Mean Value	Range	±1SE	References
SLA (mm ² mg ⁻¹)				
Dry forest of Panama	8.5 (n=7)	5.0 to 12.5	0.9	Santiago 2003
Deciduous forest of Australia	9.9 (n=2)	9.0 to 10.7	0.8	Eamus and Prichard 1998
Dry forest of Costa Rica	10.2 (n=87)	5.5 to 23.0	3.6	Powers and Tiffin 2010
Deciduous forest of India	10.9 (n=54)	6.4 to 19.1	0.4	Lal <i>et al.</i> 2001
Deciduous forest of central-western Argentina	11.2 (n=16)	4.2 to 25.4	1.5	Vendramini <i>et al.</i> 2002
Deciduous forest of India	11.7 (n=6)	7.6 to 14.4	1.3	Chaturvedi <i>et al.</i> 2011
Dry forest of Panama	12.6 (n=6)	7.3 to 21.9	1.1	Kitajima <i>et al.</i> 1997
Deciduous forest of India	11.4 (n=7)	8.8 to 16.9	1.0	Pandey <i>et al.</i> 2009
Deciduous forest of central-western Argentina	15.0 (n=23)	nk	1.2	Cornelissen <i>et al.</i> 1999
Dry forest of Venezuela	18.6 (n=6)	11.6 to 26.8	2.9	Sobrado 1991
Dry deciduous forest of Bolivia	20.7 (n=12)	11.5 to 26.9	6.0	Markesteyn <i>et al.</i> 2011
LA (cm ²)				
Dry monsoon forest of Australia	40.0 (n=4)	31.0 to 64.0	8.0	Prior <i>et al.</i> 2004
Dry deciduous forest of Bolivia	45.1 (n=12)	2.5 to 201	13.0	Markesteyn <i>et al.</i> 2011
Deciduous forest of India	75.9 (n=7)	26.4 to 143	17.6	Pandey <i>et al.</i> 2009
Chl (mg g ⁻¹)				
Deciduous forest of India	0.93 (n=7)	0.72 to 1.26	0.08	Pandey <i>et al.</i> 2009
Deciduous forest of India	1.27 (n=6)	1.04 to 1.83	0.12	Chaturvedi <i>et al.</i> 2011
LDMC (% saturated wt.)				
Deciduous forest of central-western Argentina	35.9 (n=13)	13.4 to 47.4	3.6	Vaieretti <i>et al.</i> 2007
Dry deciduous forest of Bolivia	32.2 (n=12)	23.0 to 48.0	9.3	Markesteyn <i>et al.</i> 2011
N _{mass} (%)				
Savanna of Africa	1.3 (n=4)	1.2 to 1.6	0.2	Manlay <i>et al.</i> 2002
Deciduous forest of Australia	1.4 (n=2)	1.2 to 1.6	0.2	Eamus and Prichard 1998
Dry forest of Brazil	1.8 (n=3)	1.4 to 2.1	0.3	Geßler <i>et al.</i> 2005
Deciduous forest of Australia	1.8 (n=27)	0.8 to 4.0	0.3	Roderick <i>et al.</i> 1999
Deciduous forest of India	2.0 (n=54)	0.9 to 3.2	0.1	Lal <i>et al.</i> 2001
Deciduous forest of Central Ethiopia	2.1 (n=7)	1.7 to 3.2	0.3	Kindu <i>et al.</i> 2006
Deciduous forest of India	2.2 (n=6)	1.9 to 2.5	0.1	Chaturvedi <i>et al.</i> 2011
Dry forest of Panama	2.3 (n=8)	nk	0.2	Santiago 2003
Dry forest of Costa Rica	2.3 (n=87)	1.2 to 3.6	0.7	Powers and Tiffin 2010
Deciduous forest of Australia	2.4 (n=6)	1.1 to 3.2	0.4	Prior <i>et al.</i> 2003
Dry forest of Panama	2.4 (n=6)	1.5 to 3.8	0.3	Kitajima <i>et al.</i> 1997
LL (mo)				
Deciduous forest of Australia	6.3 (n=6)	4.8 to 8.2	0.5	Prior <i>et al.</i> 2003
Dry forest of Venezuela	8.4 (n=6)	6.0 to 10.0	1.3	Sobrado 1991

Table 1 (continued)

Species/Forest	Mean Value	Range	±1SE	References
A_{area} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)				
Lowland forest of Panama	12.9 (n=16)	9.7 to 18.3	0.7	Santiago 2003
Dry forest of Panama	13.4 (n=6)	7.8 to 19.9	1.8	Kitajima <i>et al.</i> 1997
Deciduous forest of Australia	13.9 (n=6)	9.6 to 18.7	1.3	Prior <i>et al.</i> 2003
Deciduous forest of Australia	14.8 (n=2)	14.0 to 15.6	0.8	Eamus and Prichard 1998
A_{mass} ($\text{nmol g}^{-1}\text{s}^{-1}$)				
Dry forest of Panama	122.3 (n=7)	58.1 to 200.4	17.5	Santiago 2003
Deciduous forest of India	130.6 (n=6)	70.6 to 179.1	17.5	Chaturvedi <i>et al.</i> 2011
Deciduous forest of Australia	143.8 (n=2)	126.4 to 161.3	17.5	Eamus and Prichard 1998
Deciduous forest of Australia	175.8 (n=6)	129.0 to 250.0	16.7	Prior <i>et al.</i> 2003
R_{darea} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)				
Deciduous forest of Australia	0.61 (n=2)	0.62 to 0.60	0.01	Eamus and Prichard 1998
Dry forest of Panama	1.90 (n=6)	2.90 to 0.80	0.20	Kitajima <i>et al.</i> 1997
g_c ($\text{mmol m}^{-2}\text{s}^{-1}$)				
Dry forest of Venezuela	204.8 (n=5)	140.7 to 274.8	23.0	Sobrado 1991
Deciduous forest of India	337.2 (n=6)	252.1 to 406.2	26.2	Chaturvedi <i>et al.</i> 2011
Dry forest of Panama	456.6 (n=7)	199.3 to 670.2	91.4	Santiago 2003
Dry forest of Panama	573.4 (n=6)	249.1 to 1306.6	127.5	Kitajima <i>et al.</i> 1997
Deciduous forest of Australia	680.0 (n=2)	620.0 to 750.0	65.0	Eamus and Prichard 1998
WUE_i ($\mu\text{mol mol}^{-1}$)				
Deciduous forest of India	35.3 (n=6)	25.6 to 48.7	3.5	Chaturvedi <i>et al.</i> 2011
Savanna of central Venezuela	37.5 (n=3)	30.4 to 46.0	4.6	Medina and Francisco 1994
Tropical dry forest of Venezuela	44.8 (n=6)	36.0 to 53.0	2.7	Sobrado 1991
P_{mass} (%)				
Savanna of Africa	0.07 (n=4)	0.05 to 0.09	0.01	Manlay <i>et al.</i> 2002
Dry forest of Costa Rica	0.11 (n=87)	0.06 to 0.20	0.04	Powers and Tiffin 2010
Deciduous forest of Australia	0.15 (n=6)	0.08 to 0.19	0.02	Prior <i>et al.</i> 2003
Deciduous forest of Central Ethiopia	0.18 (n=7)	0.15 to 0.30	0.03	Kindu <i>et al.</i> 2006
Deciduous forest of India	0.19 (n=6)	0.16 to 0.26	0.01	Chaturvedi <i>et al.</i> 2011
Deciduous forest of India	0.21 (n=54)	0.08 to 0.52	0.01	Lal <i>et al.</i> 2001
LSC_{max} ($\text{mmol m}^{-1}\text{s}^{-1}\text{MPa}^{-1}$)				
Lowland forest of Panama	53.8 (n=16)	15.8 to 120.7	6.8	Santiago 2003
Dry deciduous forest of Bolivia	42.7 (n=12)	8.0 to 81.0	12.3	Markestijn <i>et al.</i> 2011
Dry tropical forest of Costa Rica	19.3 (n=3)	15.0 to 25.0	11.2	Brodribb and Holbrook 2003a

Table 1 (continued)

Species/Forest	Mean Value	Range	±1SE	References
E (mmol m ⁻² s ⁻¹)				
Dry forest of Venezuela	6.5 (n=4)	5.2 to 7.7	0.5	Sobrado 1991
Deciduous forest of Australia	17.2 (n=2)	16.9 to 17.5	0.3	Eamus and Prichard 1998
CC (g glu.g ⁻¹)				
Deciduous forest of Australia	1.2 (n=2)	1.1 to 1.3	0.05	Eamus and Prichard 1998
Dry forest of Charallave, Venezuela	1.5 (n=7)	1.4 to 1.6	0.02	Villar and Merino 2001
LWC (%)				
Dry forest of Costa Rica	58.8 (n=87)	40.2 to 73.9	8.0	Powers and Tiffin 2010
Deciduous forest of central-western Argentina	60.4 (n=16)	38.0 to 83.0	3.0	Vendramini <i>et al.</i> 2002
C _{mass} (%)				
Savanna of Africa	37.3 (n=4)	35.8 to 39.7	1.3	Manlay <i>et al.</i> 2002
Deciduous forest of India	42.8 (n=54)	32.0 to 47.7	0.4	Lal <i>et al.</i> 2001
Dry forest of Brazil	43.0 (n=2)	42.7 to 43.3	0.6	Geßler <i>et al.</i> 2005
Deciduous forest of India	43.3 (n=6)	41.6 to 44.3	0.4	Chaturvedi <i>et al.</i> 2011
Dry forest of Costa Rica	45.9 (n=87)	37.6 to 52.3	3.3	Powers and Tiffin 2010
Deciduous forest of India	46.3 (n=8)	44.8 to 47.4	0.7	Negi <i>et al.</i> 2003
Dry forest of Panama	49.0 (n=8)	nk	0.8	Santiago 2003
Deciduous forest of Australia	49.2 (n=27)	0.41 to 57.6	1.4	Roderick <i>et al.</i> 1999
Na _{mass} (%)				
Deciduous forest of India	0.07 (n=25)	nk	0.01	Singh and Singh 1991
K _{mass} (%)				
Deciduous forest of Central Ethiopia	1.4 (n=7)	1.0 to 1.9	0.2	Kindu <i>et al.</i> 2006
Ca _{mass} (%)				
Deciduous forest of India	1.2 (n=8)	0.6 to 2.3	0.3	Negi <i>et al.</i> 2003
Thickness (mm)				
Deciduous forest of Australia	0.3 (n=6)	0.2 to 0.5	0.04	Prior <i>et al.</i> 2003
Deciduous forest of central-western Argentina	0.4 (n=16)	0.2 to 0.6	0.03	Vendramini <i>et al.</i> 2002

n=number of species, nk=not known. SLA (specific leaf area); LA (leaf area); Chl (chlorophyll concentration); LDMC (leaf dry matter content); LSC_{max} (maximum leaf specific hydraulic conductivity); A_{area} (area-based leaf maximum photosynthetic rate); A_{mass} (mass-based leaf maximum photosynthetic rate); Rd_{area} (area-based dark respiration rate); E (leaf transpiration rate); g_c (leaf stomatal conductance); WUEi (intrinsic water use efficiency); CC (leaf construction cost); LWC (leaf water content); N_{mass} (mass-based nitrogen concentration); LL (leaf life-span); P_{mass} (mass-based phosphorus concentration); C_{mass} (mass-based carbon concentration); Na_{mass} (mass-based sodium concentration); K_{mass} (mass-based potassium concentration); Ca_{mass} (mass-based calcium concentration).

the range of 0.8–1.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ observed for tropical evergreen, temperate evergreen, temperate deciduous and tundra species (Reich *et al.* 1998). Santiago (2003) observed greater mean value of LSC_{max} in evergreen species (83.4 $\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) than the deciduous species (19.3 $\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) of Costa Rica.

Growth potential of a species is an integrated outcome of responses of various traits and is particularly determined by its leaf traits. A study in an abandoned grazing land in Australia proved SLA as the best predictor of response to land-use change (Meers *et al.* 2008). Bertiller *et al.* (2006) have studied leaf strategies and soil nitrogen across a regional humidity gradient in Patagonia and reported that the leaf traits related to carbon fixation and the decomposition pathway significantly varied with humidity. Wright *et al.* (2004b) identified six leaf traits that together capture many essentials of carbon economy of the leaf: LMA, A_{mass} , leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), rate of dark respiration (Rd_{max}) and leaf lifespan (LL). LMA measures investment of dry matter per unit of light-intercepting leaf area deployed. LMA can be calculated as $1/\text{SLA}$. High LMA means a thicker leaf blade or denser tissue, or both. A_{mass} is the photosynthetic assimilation rate measured under high light, ample soil moisture and ambient CO_2 . Stomatal conductance and the drawdown of CO_2 concentration inside the leaf (carboxylation capacity) influence A_{mass} . While A_{mass} in deciduous species is zero during the dry period when trees are leafless, the decline in A_{mass} is much less under low water conditions in mature evergreen tree species (15–50%) and semi-deciduous species (25–75%) (Eamus 1999). Leaf nitrogen is integral to the proteins of photosynthetic machinery, especially RuBisCo, which is responsible for drawdown of CO_2 inside the leaf. The drawdown of CO_2 is also affected by leaf structure. Phosphorus occurs in nucleic acids, lipid membranes and bioenergetic molecules such as ATP. According to Westoby and Wright (2006), leaf N:P ratio increases with temperature, and species with lower absolute LNC and LPC tend to have higher N:P ratio, which in turn is associated with slow leaf-specific growth rates. The mean N:P ratio of tree leaves for deciduous woody species is lower than that for evergreens (Wright *et al.* 2004a). Leaf dark respiration rate per unit mass (Rd_{mass}) reflects metabolic expenditure of photosynthate, especially protein turnover and phloem-loading of photosynthates and is related to LMA (Reich *et al.* 1997). LL describes the average duration of the revenue stream from each leaf constructed. Long LL requires robust construction in the form of high LMA.

There are other leaf traits that are either directly or indirectly associated with the above-mentioned traits. According to Vendramini *et al.* (2002), variation in SLA depends on changes in leaf tissue density or leaf water content (LWC), which is closely correlated with tissue

density and leaf thickness. LWC, although not typically considered as a plant functional trait, is important for properties such as flammability and can be quantified through remote sensing (Powers and Tiffin 2010). Leaf-area-based maximum photosynthetic rate (A_{area}) and stomatal conductance are positively correlated with maximum specific hydraulic conductivity (LSC_{max}) of leaf (Santiago *et al.* 2004). Chl is highly correlated with LNC (Marino *et al.* 2010). According to Loranger and Shipley (2010), thicker leaves have high stomatal density and low Chl. Many studies have shown that the photochemical part of the photosynthetic apparatus increases relative to the biochemical part at low light to enhance light harvesting and provide the energy for carbon fixation (see Kull 2002 for a review). This acclimation pattern is expected to lead to an increased chlorophyll-to-nitrogen ratio in low light (Hallik *et al.* 2009). Leaf area (LA), the one-sided projected surface area of the leaf, is an essential component of plant growth analysis and evapotranspirational studies. It also has large influence on transpiration rate (E) (Enoch and Hurd 1979). It is useful in the analysis of canopy architecture as it allows determination of LAI. It is related to canopy light interception and photosynthetic efficiency and contributes to the carbohydrate metabolism, dry matter accumulation, yield and RGR (Leith *et al.* 1986, Williams 1987; Centritto *et al.* 2000). Leaf construction cost (CC) is considered as the energy invested by plants to synthesize carbon skeletons and nitrogenous compounds (Baruch and Goldstein 1999). Indirectly CC can also be related to efficiency of resource utilization (Williams *et al.* 1987; Lambers and Poorter 1992; Griffin 1994).

According to Chapin (1980), low LNC and LPC are characteristics of plants having relatively high nutrient-use efficiency. In unproductive habitats, plant species increase leaf carbon content (C_{mass}) by accumulating many carbon-based secondary compounds including lignin and tannins (Coley *et al.* 1985; Lambers and Poorter 1992), and it has been suggested that leaves of species accumulating these compounds have high CC (Miller and Stoner 1979). In other studies, concentration of nutrients such as nitrogen, phosphorus, sodium, potassium and calcium in leaves control retranslocation of nitrogen and phosphorus from senescing leaves (Loneragan *et al.* 1976). Plants having high nutrient concentration in leaves retranslocate larger proportions of nitrogen and phosphorus than do plants with low nutrient status (Miller *et al.* 1976; Turner and Olson 1976). All the above-mentioned traits exhibit plasticity. Plasticity is particularly high along moisture gradients, being the least in the dry forest and greatest in the moist forest tree species (Markesteyn *et al.* 2007). Studies also indicate that there is no substantial change in species ranking for these traits in time or across different environments (Jurik 1986; Thompson *et al.* 1997; Garnier *et al.* 2001).

3.2 Stem and root traits

For the maintenance of physiological activity of dry forest species, the minimum seasonal water potential is ecologically relevant (Bhaskar and Ackerly 2006). Wright *et al.* (2006) studied many leaf and stem traits and found that their coordinated effect is very important for a plant's water use efficiency. Therefore, study of stem and root traits along with leaf traits are important to detect the effect of water stress on the physiology of dry tropical plant species. Also, FTs which enable acquisition of limiting nutrients such as extensive root foraging and/or association with mycorrhizal fungi may be important for C dynamics (de Deyn *et al.* 2008).

Stem FTs include specific stem density (SSD) or wood-specific gravity, which is directly associated with soil water availability (Preston *et al.* 2006), and above-ground wood productivity along with species maximum height (Baker *et al.* 2008). Increasing wood density is associated with decline in wood water content, and hence its potential for water storage (Borchert 1994). SSD has been emphasized for studying the rehydration processes in species showing variable duration of deciduousness (Eamus and Prior 2001) – it is a good predictor of resistance to drought-driven embolism (Sperry 2003). Higher SSD appears to be related to smaller leaf and twig sizes (Westoby and Wright 2006). Other stem FTs include twig dry matter content (TDMC) and bark thickness, which helps plants survive lethally high temperature associated with fire. Since aboveground and belowground plant traits involved in C cycling are weakly coupled, identification of easily measurable, cost-effective, aboveground traits that may capture belowground C dynamics is an important area of research (de Deyn *et al.* 2008).

Among other structural traits, plant stature (herb, shrub, tree), leaf area index (LAI) or crown depth, bark thickness, rooting depth, tree/root architecture, tree lifespan, plant architecture (DBH to height curve), maximum size/height may be important for the drought tolerance capability in TDF trees. Other stem and root traits such as nitrogen content (N_{mass}), phosphorus content (P_{mass}), carbon content (C_{mass}), sodium content (Na_{mass}), potassium content (K_{mass}) and calcium content (Ca_{mass}) are also associated with the physiology of TDF tree species; however, the work on these aspects of plant traits in TDF is scarce (tables 2 and 3). Compared to other traits listed in tables 2 and 3, SSD is highly variable among regions ($0.37\text{--}0.73\text{ g cm}^{-3}$) and among species (e.g. dry forest of Costa Rica, $0.19\text{--}1.20\text{ g cm}^{-3}$). Borchert (1994) reported a greater mean value of SSD in deciduous trees (0.73 g cm^{-3}) compared to evergreen trees (0.60 g cm^{-3}). The limited data in table 2 indicate about threefold difference in stem N_{mass} among TDF species. The significance of these variations, however, remains to be examined.

Regenerative traits especially resprouting capacity after major natural or anthropogenic disturbance could prove an

important trait in the TDF facing a high population load (pers. observation).

3.3 Reproductive traits

A large number of reproductive traits are important for the success of a tree species in dry tropical environment. Some of these are fruit number, fruit mass, seed weight, seed viability, time period for seed germination (table 4), number of seeds, dispersal distance, specialized pollination/dispersal, maturity age/size, seed production and reproductive phenology. Dispersal ability is strongly influenced by the seed size of a species (Khurana *et al.* 2006). Smaller seeds have greater dispersal ability as compared to heavier and larger seeds but the seedlings produced by heavier, larger seeds have greater competitive ability, enabling them to establish and survive under various stresses such as competition, moisture, shading, disturbances, defoliation and herbivory (Khurana *et al.* 2006). The above advantages of the seed size cause the structure of the TDF to be largely determined by the medium- to large-seeded species (Khurana *et al.* 2006).

3.4 Functional traits syndrome for maintaining growth in seasonally dry environments

The total amount of rainfall sets limits to distribution of forests in the tropics (Holdridge 1967; Walter 1979; White 1983; Woodward 1987; Portillo-Quintero and Sánchez-Azofeifa 2010). Research indicates that spatial and temporal variation in soil water availability determines intra- and inter-annual patterns of growth, productivity and survival within seasonal forests (Baker *et al.* 2003a; Baker *et al.* 2003b; Urbeita *et al.* 2008; Sánchez-Coronado *et al.* 2007; Namirembe *et al.* 2008). The annual girth increment of deciduous species correlates positively with rainfall during the middle of the wet season (Bullock 1997) and also with total rainfall during the previous 2 years (Whigham *et al.* 1990). This observation is also verified by tree ring studies in seasonal forests of Panama (Devall *et al.* 1995).

It is evident that TDF species maintain a set of FTs which leads to their survival in seasonally dry environments by conserving water. They may achieve this by reducing their LL and modulating leaf FTs in such a way that a higher rate of photosynthesis is maintained during the brief period of water availability favourable for the physiological processes essential for the plant growth during that period. However, there is incomplete knowledge about many FTs involved and further research efforts are needed to study these and to develop a database of FTs of TDF species. Our review of FTs indicates that TDF species generally have a higher SLA, LNC, N_{mass} , g_c and light saturated photosynthetic rate and a

Table 2. List of stem traits of tree species in tropical deciduous forests

Species/Forest	Mean Value	Range	±1SE	References
SSD (g cm ⁻³)				
Dry deciduous forest of Bolivia	0.37 (n=12)	0.19 to 0.52	0.11	Markesteijn <i>et al.</i> 2011
Dry forest of Costa Rica	0.40 (n=18)	0.16 to 0.78	0.04	Wiemann and Williamson 1989
Deciduous forest of Panama	0.51 (n=16)	0.35 to 0.70	0.02	Santiago 2003
Deciduous forest of India	0.58 (n=7)	0.37 to 0.75	0.04	Chaturvedi <i>et al.</i> 2010
Dry forest of Costa Rica	0.72 (n=26)	0.19 to 1.20	0.05	Borchert 1994
Deciduous forest of Mexico	0.73 (n=21)	0.27 to 1.39	0.09	Huante <i>et al.</i> 1995
N _{mass} (%)				
Dry forest of Brazil	0.25 (n=2)	0.20 to 0.30	0.10	Geßler <i>et al.</i> 2005
Savanna of Africa	0.25 (n=4)	0.16 to 0.45	0.10	Manlay <i>et al.</i> 2002
Deciduous forest of Central Ethiopia	0.28 (n=7)	0.20 to 0.34	0.03	Kindu <i>et al.</i> 2006
P _{mass} (%)				
Deciduous forest of Central Ethiopia	0.02 (n=7)	0.01 to 0.03	0.04	Kindu <i>et al.</i> 2006
Savanna of Africa	0.03 (n=4)	0.02 to 0.04	0.01	Manlay <i>et al.</i> 2002
C _{mass} (%)				
Savanna of Africa	37.6 (n=4)	36.5 to 38.8	0.31	Manlay <i>et al.</i> 2002
Dry forest of Brazil	43.0 (n=2)	42.7 to 43.3	0.61	Geßler <i>et al.</i> 2005
Deciduous forest of India	47.3 (n=8)	46.5 to 49.2	0.41	Negi <i>et al.</i> 2003
Na _{mass} (%)				
Deciduous forest of India	0.08 (n=25)	nk	0.03	Singh and Singh 1991
K _{mass} (%)				
Deciduous forest of Central Ethiopia	0.22 (n=7)	0.14 to 0.46	0.06	Kindu <i>et al.</i> 2006
Ca _{mass} (%)				
Deciduous forest of India	0.35 (n=8)	0.07 to 1.12	0.16	Negi <i>et al.</i> 2003
Bark C _{mass} (%)				
Deciduous forest of India	38.8 (n=8)	34.4 to 41.2	1.13	Negi <i>et al.</i> 2003
Bark Ca _{mass} (%)				
Deciduous forest of India	2.17 (n=8)	1.00 to 4.30	0.54	Negi <i>et al.</i> 2003

n=number of species, nk=not known. SSD (stem specific density); N_{mass} (mass-based nitrogen concentration); P_{mass} (mass-based phosphorus concentration); C_{mass} (mass-based carbon concentration); Na_{mass} (mass-based sodium concentration); K_{mass} (mass-based potassium concentration); Ca_{mass} (mass-based calcium concentration).

Table 3. List of root traits of tree species in tropical deciduous forests

Species/Forest	Mean Value	Range	±1SE	References
		N_{mass} (%)		
Deciduous forest of India	0.9 (n=25)	nk	0.1	Singh and Singh 1991
Dry forest of Brazil	1.2 (n=3)	0.8 to 1.5	0.3	Geßler <i>et al.</i> 2005
		P_{mass} (%)		
Deciduous forest of India	0.06 (n=25)	nk	0.02	Singh and Singh 1991
		C_{mass} (%)		
Dry forest of Brazil	42.7 (n=3)	39.7 to 47.4	0.61	Geßler <i>et al.</i> 2005
		Na_{mass} (%)		
Deciduous forest of India	0.09 (n=25)	nk	0.02	Singh and Singh 1991
		K_{mass} (%)		
Deciduous forest of India	0.31 (n=25)	nk	0.06	Singh and Singh 1991
		Ca_{mass} (%)		
Deciduous forest of India	0.56 (n=25)	nk	0.13	Singh and Singh 1991

n=number of species, nk=not known. N_{mass} (mass-based nitrogen concentration); P_{mass} (mass-based phosphorus concentration); C_{mass} (mass-based carbon concentration); Na_{mass} (mass-based sodium concentration); K_{mass} (mass-based potassium concentration); Ca_{mass} (mass-based calcium concentration).

lower LMA, LL and LSC_{max} compared to the tree species of other biomes. SLA and LNC relates positively to LL and, in combination, accurately predicts the maximum photosynthetic rate across the species (Reich *et al.* 1997). Therefore, a trait set of high SLA, LNC and N_{mass} is expected to lead to high light saturated photosynthetic rates. Observations in four lowland Panamanian forests also indicate that nitrogen content per unit mass and light- and CO_2 -saturated photosynthetic rate per unit mass of upper canopy leaves decreases with annual precipitation, while leaf thickness increases and SLA decreases (Santiago *et al.* 2004). Similarly, relatively high g_c (205–680 $\text{mmol m}^{-2} \text{s}^{-1}$), together with relatively short LL (6–8 mo) and LSC_{max} (19–54 $\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) are expected to confer a selective advantage in seasonally dry environments. Because g_c plays an important role in plant–atmosphere water exchange by relating positively to the rate of photosynthesis, high g_c may be essential in the deciduous species with short LL to optimally utilize resources in a limited duration of favourable soil moisture. Markesteijn *et al.* (2010) have also reviewed literature to show that tolerance to water stress by plants is codetermined by a suite of FTs such

as high cavitation resistance, strong stomatal control or the maintenance of tissue turgor pressure at low leaf water potentials. Other studies also support these observations. For example, Li *et al.* (2009) studied adaptation responses to different water conditions and the drought tolerance of *Sophora davidii* seedlings in a greenhouse experiment and found that water stress decreased leaf relative water content, SLA, leaf area ratio and WUE, whereas it increased the biomass allocation to roots, which resulted in a higher root: stem mass ratio under drought.

4. Plant functional types

It is being increasingly realized that, in order to understand the interaction of plants and ecosystem processes and their potential response to global environmental changes, groups of species with shared characteristics, known as plant functional types (PFTs), need to be identified. Groupings of plant species on the basis of FTs can yield information on the relative contribution of each PFT to total ecosystem plant biomass (Hoorens *et al.* 2010). Inter-specific variation in FTs can help in the

Table 4. List of reproductive traits of tree species in tropical deciduous forests

Species/Forest	Mean Value	Range	±1SE	References
		Fruit no. per tree		
Dry forest of Costa Rica	271 (n=7)	4 to 1182	219	Rockwood 1973
		Fruit wt. (g)		
Dry forest of Costa Rica	108 (n=7)	1.3 to 385	88.2	Rockwood 1973
		Seed wt. (mg)		
Deciduous forest of Mexico	184 (n=22)	0.66 to 1622	116	Huante <i>et al.</i> 1995
Deciduous forest of India	316 (n=37)	0.10 to 2224	84.6	Khurana <i>et al.</i> 2006
Deciduous forest of India	1229 (n=99)	1.0 to 20000	670	Murali 1997
		Seed viability (days)		
Deciduous forest of India	256 (n=99)	5 to 720	38.1	Murali 1997
		Period for seed germination (days)		
Deciduous forest of India	16.9 (n=98)	8 to 45	1.4	Murali 1997

n=number of species.

classification of plant species into PFTs (Von Willert *et al.* 1990, 1992; Díaz and Cabido 1997; Lavorel *et al.* 1997; Westoby 1998; Gitay *et al.* 1999; Semenova and van der Maarel 2000; Powers and Tiffin 2010). These groupings of plant species on the basis of common biological parameters reduce a wide diversity of species to small number of functional groups, which enables the identification of general principles for the functioning of organisms which can be used for making predictions (Duru *et al.* 2009). The identification of tree PFTs through either deductive or inductive approaches (Gitay and Noble 1997) is primarily limited by our restricted knowledge of plant physiological attributes. This is particularly true for TDFs. Because the extent and intensity of seasonal drought in TDF may vary with geographical location, there can be a mosaic of different PFTs showing varying adaptations to seasonal drought (Borchert 2000). With the development of modern ecophysiological techniques, the definition of plant PFTs has shifted from primarily morphological classifications (e.g. Raunkiaer 1907; Box 1981) to function based groupings (e.g. Díaz and Cabido 1997; Lavorel *et al.* 1997; Reich *et al.* 1998; Walker *et al.* 1999; Pausas and Lavorel 2003; Suding *et al.* 2008). Nevertheless, growth-form categories continue to attract attention. Dubey *et al.* (2011) grouped TDF herbs into annual grasses, perennial grasses, annual forbs and perennial forbs, and studied the intra-

seasonal variation in their leaf traits. The seasonal pattern in leaf traits, in general, was an early season peak in SLA, LNC and LPC, and a midseason peak in stomatal conductance and A_{mass} , which was associated with increase in soil moisture. Annual forbs generally exhibited highest leaf trait values and the perennial grasses the lowest.

Several PFTs, based on leaf phenology and wood density, have been recognized in the dry forests of Costa Rica by Borchert (1994), ranging from deciduous hardwood and water-storing light wood trees in dry upland forest to evergreen light soft-wood trees confined to moist lowland sites. Since plant growth rate integrates several traits underlying trade-offs among resource acquisition strategies, defence against natural enemies and allocation to reproduction, Baker *et al.* (2003a) classified plant species of the semi-deciduous forest of Ghana into dry forest pioneers and wet forest pioneers on the basis of variations in their growth rates under different soil moisture conditions. Saldaña-Acosta *et al.* (2008) classified 33 tree species of Mexican cloud forest into two functional groups on the basis of SLA, height at maturity, wood density and seed mass.

Sagar and Singh (2003) categorized trees of Indian TDF on the basis of leaf size, leaf texture, deciduousness and bark texture and found that both the percent of species and importance values were larger for medium or low deciduous

categories than for highly deciduous trait, representing a trade-off between water loss and the period of dry matter synthesis. The tree vegetation was characterized by the preponderance of and domination by species having a combination of small leaf size (below 201 cm² leaf area), medium leaf texture, rough bark texture and medium deciduousness (2–3 mo deciduous). However, habitats could not be discriminated, either by the proportion of species belonging to different trait categories or by the cumulative importance value of the trait categories. Thus, although a few attempts have been made to characterize and classify dry deciduous forest trees into plant PFTs, there is no universally acceptable suite of traits that can be used to predict the response of the dry forest ecosystem to environmental changes.

5. Research needs with particular reference to TDF

The information on plant functional traits and their capacity to predict changes in environment and species composition, with particular reference to TDFs, is incomplete and fragmentary. The demand for detailed studies on plant FTs of TDF persists for the effective restoration of the forest ecosystem and predicting the effects of climate change. There is a need to develop a comprehensive list of ecologically significant functional traits, and to determine the coordination among them and the relationships between the traits and habitat conditions of the dry tropical forest biome. For this a well-authenticated database is needed, which could then help in grouping species into PFTs and in developing predictive models that could explain species distributions and productivity, and effect of changes in environment such as disturbance regime and climate.

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