



*Research Paper*

**FUNCTIONAL TRAITS OF HERBS IN DRY DECIDUOUS FOREST: AN ANALYSIS**

**Dubey, Prajjwal<sup>1</sup>, A.S. Raghubanshi<sup>2</sup> and Anil K. Dwivedi<sup>3</sup>**

<sup>1</sup>CAS in Botany, Institute of Sciences, Banaras Hindu University, Varanasi- 221005,

<sup>2</sup>Institute of Environment & Sustainable Development, Banaras Hindu University, Varanasi- 221005,

<sup>3</sup>PEARL, Department of Botany, DDU Gorakhpur University, Gorakhpur- 273009, India.

**Abstract**

Vegetation research in dry deciduous forest has tended to focus on the tree component, while little attention has been paid to herbaceous plants. Herbaceous vegetation has ecological importance of, both in short term by influencing tree seedlings regeneration and in the longer term by affecting belowground processes such as decomposition, nutrient flow and build up soil nutrient. Understanding herbaceous vegetation ecology has important implication for both the conservation and production oriented forest management. Also, the productivity of herbaceous vegetation is probably comparable to that of the tree component in many forest ecosystems. Herbaceous plant functional traits influence herbivory and nutrient dynamics and provide an overview of how the leaf traits potentially provide robust predictions of species responses to biotic stress particularly herbivory and how in turn plant traits subsequently affect the ecological processes.

Key words: Dry deciduous forest, plant functional traits, decomposition, herbivory, herbs.

**INTRODUCTION**

Tropical forests cover only 7% of the Earth's land surface but harbour more than half of the world's species (Wilson 1988). On global basis, 52% of total forests are tropical and over 42% of tropical forests have been classified as dry forest (Holdridge 1967). The dry forests are more threatened and less protected than moist and wet forests (Gerhardt 1993). The dry tropical, subtropical and woodlands once covered more than half of the world's tropics (Janzen 1988), but have decreased considerably during recent past. Because of the more rigorous and less predictable environment, the dry forests are more vulnerable to stress during the successional processes (Murphy and Lugo 1986). It has been estimated that habitats such as the tropical dry forests of Central America have virtually disappeared (UNDP, UNEP, World Bank and WRI 2000).

In India, dry tropical forest accounts for 38.2% of the total forest cover (MoEF 1999). These dry tropical forests are largely threatened by lopping, burning, overgrazing and clearing for cultivation (Jha and Singh 1990). Because of these threats, since past several decades the dry deciduous forest cover in most part of the central India is being converted into dry deciduous scrub, dry savanna and dry grasslands which are progressively species poor.

A change in the species composition of plant communities in the face of disturbance is determined by the functional traits of individual species. Dry tropical forest species have evidently evolved to cope with moisture stress. Study of their functional traits can provide important clues regarding future changes in community composition due to global change if aridity is going to be altered in much of the tropics including India.

Herbaceous plant functional traits provide a general and mechanistic basis for understanding plant behavior in response to biotic stress (Vesk and Westoby 2001).

### **Herbaceous plant functional traits**

Plant functional traits are characteristics of a plant that are considered relevant to its responses to the environment and/or ecosystem functioning (Díaz and Cabido 2001). Examples of the plant functional traits are: leaf size, toughness and longevity, seed size and dispersal mode, canopy height, etc. Since long ecologists have sought for meaningful classifications of species to structure the complex diversity of life on earth (McIntyre *et al.* 1999a; Weiher *et al.* 1999). Apart from a few notable exceptions (e.g. Grime 1977), traditionally attention has focused mainly on phylogenetically oriented methodologies where species are grouped based on their common evolutionary history (Noble and Gitay 1996). As a result, ecologists often describe plant communities by species composition to reveal compositional patterns in time or space. However, the complexity and diversity of natural systems makes grouping of species essential in order to derive general principles of succession and ecosystem recovery following human impact (Keddy 1992; Grime *et al.* 1997; Westoby 1998).

Information must be interpreted and applied at larger scales because the most serious challenges to natural resource management operate at regional and global scales. However, the validity of the conclusions is restricted by phytogeographical boundaries, for the potential species pool is not the same everywhere. A central problem encountered when scaling vegetation responses to regional levels is our limited ability to quantify and interpret complex floristic responses involving a large number of individual species (Lavorel *et al.* 1997). As these problems emerged more and more in integrative ecology, interest has shifted gradually from the classical phylogenetic approach to classifying species into groups that relate directly to function based on shared biological characteristics or species traits (Lavorel *et al.* 1997; Semanova and van der Maarel 2000). The growing awareness that functional diversity, rather than species numbers per se, strongly determines ecosystem processes such as resource dynamics and biomass production (Díaz and Cabido 2001), accelerated this process. Moreover, plant functional classifications are useful to predict the dynamics of plant communities subjected to disturbances (Noble and Gitay 1996) and the higher level of abstraction in comparison with species-based analyses is essential for comparing vegetation dynamics and ecosystem processes over different biogeographical regions (Díaz and Cabido 1997).

There is a long-standing tradition in plant ecology of seeking consistent associations between plant attributes (trait-environment linkages) or plant functional types and certain environmental conditions, irrespective of the species involved (Díaz *et al.* 1998,

1999). More recently the term *plant functional type* (PFT) has been suggested with a broader connotation (Steffen *et al.* 1992; Lavorel and Garnier 2002).

Consideration of plant traits or plant functional traits (PFTs), defined as 'plant characteristics that respond to the dominant ecosystem processes' (Gitay and Noble 1997), makes it possible to seek generalities by comparing results between climatically and edaphically diverse environments. With the PFT approach it also becomes possible to consider changes taking place in communities where the flora is poorly described or where taxonomic knowledge is limited (Díaz *et al.* 2001) and, as recent research has shown, to connect changes in vegetation to changes in ecosystem functions such as productivity or flammability (Lavorel and Garnier 2002). Plant functional groupings are potentially useful communication tools for land managers, who may not necessarily relate to taxonomic units, particularly when dealing with species-rich ecosystems.

The study of interspecific variation in functional traits of plants has provided, and will continue to provide, important insights into (i) fundamental patterns and trade-offs in plant design and functioning (e.g. Poorter and Bergkotte 1992; Reich *et al.* 1992; Grime *et al.* 1997; Craine *et al.* 2001); (ii) the classification of plant species into 'functional types' or strategies (Díaz and Cabido 1997; Lavorel *et al.* 1997; Westoby 1998; Gitay *et al.* 1999; Semanova and van der Maarel 2000); (iii) the effects of (changing) species composition on ecosystem functions (e.g. Schulze *et al.* 1994; MacGillivray *et al.* 1995; Wardle *et al.* 1998; Díaz *et al.* 1999).

A strong link exists between plant ecophysiological traits and ecosystem processes (Wardle *et al.* 1998; Diaz *et al.* 2004). For example, Wardle *et al.* (1998) determined that decomposition rates of plant stems and leaf litter were negatively correlated with plant mass and growth rate but positively correlated with stem nitrogen content. Evergreen leaves have often been associated with nutrient-poor soil (Goldberg 1982; Givnish 1987; Grubb 1985) and large seeds with low resource levels (Westoby *et al.* 1992). Life history characteristics interact with disturbance to generate much of the pattern of species distribution in a community. Traits related to dispersal ability have been of particular interest because they are thought to influence species' response to increasingly prevalent human disturbances (Peterken and Game 1984; Whitney and Foster 1988). Global climate change and terrestrial ecosystems (GCTE) research has contributed to the development of plant functional classifications to describe response to climate and atmospheric changes. These classifications recognize that species can be grouped according to similarity of response which in turn, can be related to biological similarities. Likewise, it is proposed that vegetation response to disturbance can be described using a limited set of biological traits of the component species, and that functional classifications for response to different disturbance types can be derived. Previous attempts at these classifications have repeatedly built functional groups that reflect broad life forms. Therefore, a hierarchical approach may be useful to identify relevant traits (morphological, regeneration and disturbance specific) within life forms (Lavorel *et al.* 1997). This approach can be applied to the selection of relevant traits used in the construction of functional classifications for response to different disturbances.

Understanding of the grazing impact in herbaceous vegetation is of critical importance both for the understanding plant response and for management decisions. Recent attempts to explain the great variability in ecosystem response to grazing (Milchunas and Lauenroth 1993) have also focused on the role of plant functional traits. The general hypothesis states that the sensitivity of plant communities to grazing depends on the frequency and strength of adaptations helping plants avoid or tolerate herbivory

(van der Meijden *et al.* 1988; Díaz *et al.* 1992; Lavorel *et al.* 1999; McIntyre *et al.* 1999b; Díaz *et al.* 2001; McIntyre and Lavorel 2001; Vesk and Westoby 2001). This hypothesis predicts that grazing impacts will be smaller in systems where grazing-resistance traits are well developed and common among plant species than in systems where such traits are poorly developed or rare.

Although previous studies have identified certain key traits such as life form, plant stature, seed size and leaf toughness (Milchunas and Lauenroth 1993; Díaz *et al.* 2001; McIntyre and Lavorel 2001; Westoby *et al.* 2002), cross-system generalizations appear elusive (Vesk and Westoby 2001; Vesk *et al.* 2004). Competition for light will select for traits such as taller growth forms with larger leaves and faster growth (Keddy 1989; Gaudet and Keddy 1995), but should make plants more vulnerable to grazing (Noy-Meir *et al.* 1989; McIntyre *et al.* 1995; Sammul *et al.* 2000; Díaz *et al.* 2001). On the other hand, adaptations to aridity such as shorter plants, small leaves, basal meristems and annual life cycle, should increase tolerance to, or avoidance of, grazing ('convergent selection') (Coughenour 1985; Milchunas *et al.* 1988). Therefore, moderate or small changes in the composition of plant communities in response to grazing are expected in semi-arid rangelands with lower productivity in which plant growth is usually limited by soil resources.

Information regarding PFTs of Indian forest species is almost non-existent. In one study of phenotypic traits by Sagar and Singh (2003), trees of dry tropical forest were tried to be classified using a limited set of 'soft traits'. Specific leaf area (SLA), leaf nitrogen, leaf phosphorus, photosynthetic rate ( $A_{mass}$ ) and stomatal conductance are important functional traits, playing key role in plant functioning. Leaf traits are good predictors of plant performance as they are closely associated with growth and survival of the plant (Poorter and Bongers 2006). SLA is a potential predictive tool for the grazing responses; grazing resistant species are reported to be shorter in height and have smaller, more tender leaves, with higher SLA than grazing-susceptible species (Díaz *et al.* 2001). SLA represents the light-intercepting area of a leaf per unit dry mass, related to net assimilation rate (Reich *et al.* 1992; Reich *et al.* 1991) and besides being easy to measure, is a strong correlate of photosynthetic capacity and potential relative growth rate and inversely related to the degree of physical defense of a leaf (Reich *et al.* 1991; Reich *et al.* 1997; Wright and Westoby 2002; Cornelissen *et al.* 2003). At the ecosystem level, SLA (or related leaf traits) and leaf nitrogen content (LNC) of component species may have a significant impact on primary productivity and nutrient cycling (Reich *et al.* 1992; Cornelissen *et al.* 1999; Aerts and Chapin 2000). SLA and LNC 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). Leaf nitrogen (N) is integral to the proteins of photosynthetic machinery, especially Rubisco. Leaf phosphorus (P) is found in nucleic acids, lipid membranes and bioenergetics molecules such as ATP. Phosphorus is derived from weathering of soil minerals in a site, in contrast to nitrogen, much of which may be fixed from the atmosphere by plants (Wright *et al.* 2004). Above ground productivity and quality of grasses is partly controlled by leaf traits and especially by the leaf lamina N content per unit fresh matter (Pontes *et al.* 2007).

### **Role of Water Availability**

Nutrient supply limits growth rates in tropical dry forests (Hedin *et al.*, 2009) and may determine spatial variation in growth of individual species in these forests (Swaine *et al.*, 1987). Variation in soil water availability determines intra- and inter-annual patterns of growth within seasonal forests (Baker *et al.*, 2003a). However, the role of

soil water in determining spatial variation in stand-level growth rates is unclear. In a semi-deciduous forest in Ghana, the growth rates of pioneers associated with high-rainfall with less fertile soils were substantially lower than those abundant in low-rainfall forests with more fertile soils (Baker *et al.*, 2003a). These results indicate that associations of species with particular environmental conditions are useful indicators of maximum growth rate (Baker *et al.*, 2003a).

The total amount of rainfall sets limits to distribution of forests in the tropics (Holdridge, 1967; Walter, 1979; White, 1983; Woodward, 1987; Portillo-Quintero & Sánchez-Azofeifa, 2010). Spatial and temporal variation in soil water availability acts as a limiting factor for overall rates and temporal patterns of growth (Baker *et al.*, 2003b). Forests experiencing strongly seasonal climates are specially sensitive to soil water availability. In a dry forest in Mexico (mean annual rainfall 707mm) the annual increment of two deciduous species measured over 10 years correlated with rainfall during the mid wet-season (Bullock, 1997). Whigham *et al.* (1990) reported that over a five-year period the annual production of leaf litter correlated positively with annual rainfall and that the mean basal area increment correlated positively with total rainfall during the previous two years. Santiago *et al.* (2004) studied coordinated change in leaf functional traits that affect productivity and nutrient cycling in relation to seasonality in lowland tropical forests. Availability of soil water also controls the timing of growth within seasonal forests. For example, an evergreen species, *Exostema caribaeum*, in dry forest in Puerto Rico (mean annual rainfall 929 mm) recorded maximum daily rates of photosynthesis five times higher during the wet season as compared to the dry season (Lugo *et al.*, 1978). Fluctuations in the girth of *Millettia thonningii* trees, in parallel with monthly rainfall, were about ten times greater than the underlying annual increment. In seasonal forest species, the pattern of cambial activity determined by measuring either the width of the band of differentiating xylem which stains for cellulose (Amobi, 1973), or the width of unligified xylem (Lowe, 1968), also demonstrated the role of increased soil water availability in the initiation of growth (Borchert, 1999). The timing and amount of growth in forest with substantially high mean annual rainfall is also influenced by soil water availability. For example, using tree ring chronologies of seven species in a semi-deciduous forest in Venezuela (mean annual rainfall 1700 mm), Worbes (1999) reported positive correlations between annual rainfall and mean annual growth rates. Devall *et al.* (1995) also found that annual rainfall correlated with variation in tree ring width in seasonal forest in Panama.

Irrigation for ameliorating the seasonal drought over five dry seasons in a semi-deciduous forest in Panama (mean annual rainfall 2600 mm) showed increased fine-root production and leaf longevity, and also influenced phenology. Community-level fine-root production during the dry season, measured by using in-growth cylinders with root-free soil, was five times greater in irrigated plots than in control plots (Cavelier *et al.*, 1999). Leaf fall in irrigated plots was delayed for two out of nine tree species (Wright and Cornejo 1990). In addition, three shrub species retained about 20% more newly flushed leaves, over the first two years in the irrigated plots compared to non-irrigated plots (Mulkey *et al.*, 1993). In contrast, irrigation did not affect community level leaf-litter production (Cavelier *et al.* 1999), and stem diameter growth of shrubs (Wright & Cornejo, 1990).

Variation in topographic positions influences soil water availability at small spatial scales, in both evergreen and semi-deciduous tropical forests (Becker *et al.*, 1988; Daws *et al.*, 2002; Green & Newbery, 2002; Baker *et al.*, 2002, 2003a; Cielo-Filho *et al.*, 2007; Comita & Engelbrecht, 2009). However, the effect of this variation on tree growth has

rarely been studied. According to Becker *et al.* (1988), during the dry season in a semi-deciduous forest in Panama, pre-dawn water potentials of the shrub *Psychotria horizontalis* and of saplings of the tree *Trichilia tuberculata*, were half as low in slope compared to plateau positions, indicating the influence of topographic variation in soil water availability. Borchert (1999) reports that in the seasonally dry forest in Costa Rica, species such as *Astronium graveolens*, occurring in moist localities, maintain cambial activity into the dry season and are leafless only for a short period, whereas in deciduous species occurring in drier sites, girth increment ceases during the dry season. Noy-Meir (1973) hypothesized that exploitation of spatially and/or temporally distinct zones of soil moisture by plants allows different life-forms to coexist in environments where water availability controls the ecosystem structure. A simple two-layer conceptual model of soil and plant interactions has been proposed by Walter (1979). The two life-forms (shrubs and grasses) can coexist at a site because their differing rooting patterns coincide with the vertical separation of soil water resources. However, the conceptual expansion of the two-layer/two life-form model to a three-layer/three life-form model and beyond may be more appropriate for more complex tropical dry forest communities.

### **Functional Traits important for the Adaptation to Moisture Stress**

Processes of the vegetation such as regeneration, growth and mortality determine drought tolerance capacity of a tree species. In arid regions, decrease in grass cover is accompanied by increase in shrub cover and bare ground, and increase in water losses through evaporation and deep drainage and reduction in transpiration (Aguiar *et al.*, 1996). Most of the reduction in transpiration is due to the individual effects of the PFTs. Shrubs transpire less water per unit of biomass than grasses. Because the production per mm of water transpired is also lower in shrubs than in grasses, it is estimated that a 43% reduction in above ground net primary production (ANPP) can occur in steppe along the grazing intensity gradient (Aguiar *et al.* 1996). According to Aguiar *et al.* (1996), transpiration per unit of biomass and production per unit of water transpired are key attributes for defining PFTs in arid and semi-arid regions.

### **Application of herbaceous plant functional traits**

Herbaceous plant functional traits provide useful input to various ecological models where vegetation responses to biotic and abiotic influences are predicted. Leaf traits such as SLA and LNC could be used as easily assessable predictive tools of litter decomposability without requiring any detailed knowledge of individual species taxonomy and biology (Fortunel *et al.* 2009). Photosynthetic characteristics and stomatal behaviour of plant species help to predict carbon and water fluxes at the leaf, plant, ecosystem and biome levels (Schulze *et al.* 1994).

### **Grouping of herbaceous species in different functional types**

An important approach for assessing the complex responses of the plant communities sensitive to the accelerated climate changes and increasing intensity of land use is to identify plant functional types (PFTs) and characterize the functional response of each type to a suite of environmental conditions (Breshears and Barnes 1999). Few investigations thus far have developed the characterization schemes that group species into types relating to the ecosystem-function role they perform. Most “functional” classification schemes have had as their goal predicting patterns in species distribution rather than predicting the effect of diversity on the provision or maintenance of ecosystem function. In this sense, these schemes are more correctly labeled plant-ecology-strategy schemes (Westoby 1998) than plant-function-type (PFTs). The best known schemes for plant adaption to the environment is the triangular model of Grime

1979), which is based on three general response strategies (competitiveness, weediness, and survival).

Westoby (1998) has proposed an explicit three-dimensional PFT, using three particular measurable plant attributes (specific leaf area, canopy height, and seed size) that allow any plant species to be easily and exactly placed in the classification schemes. Box (1981) introduced schemes for predicting the presence of 90 different PFTs, based on an environmental envelope comprised of eight bioclimatic indices. Similarly, Leishman and Westoby (1992) determined 43 plant attributes for some three hundred species from the semiarid mulga woodlands of western New South Wales in Australia. They used 8 vegetative, 9 life-history, 15 phenology, and 11 seed-biology attributes, and concluded that three hundred species fell into five groups that were related with respect to growth characteristics, reflecting adaptations of plants to their environments. The reproductive attributes (to do with seed size and dispersal) were unrelated to these five groups. Raunkiaer (1934) classified plants into four life-form classes: annual grasses, annual forbs, perennial grasses and perennial forbs.

#### CONCLUSION:

Information regarding PFTs of Indian forest species is almost non-existent. In one study of phenotypic traits by Sagar and Singh (2003), trees of dry tropical forest were tried to be classified using a limited set of 'soft traits'. Further study is warranted in this regard as a logical pre-requisite for build-up of response models of forest herb species native to India.

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