Forest Ecology and Management 482 (2021) 118740

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest

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ARTICLE INFO

Keywords:
Tropical dry forest
Soil moisture content
Functional guilds
Drought avoidance
Drought resistance
Drought tolerance

ABSTRACT

This study evaluates drought survival mechanisms of tropical dry forest (TDF) trees based on their functional traits (FTs). We addressed the following questions: (i) What are the dominant functional guilds (FGs) of tree species across a soil water availability gradient in TDF? (ii) What are the important FTs influencing tree species assemblage in different FGs? (iii) What is the functional composition of different FGs in the study sites, and how are they influencing biomass accumulation capacity (BAC) across the soil water availability gradient?

We selected 12 FTs associated with plant water use strategies, viz., canopy cover intensity (CC), wood specific gravity (WSG), saturated stem water content (QWsat), leaf size or leaf area (LA), specific leaf area (SLA), relative water content (RWC), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum saturated stomatal conductance (Gs_{max}), maximum saturated photosynthetic rate (A_{max}), and intrinsic water use efficiency (WUEi). By using these FTs, we classified 47 tree species by HCPC (hierarchical clustering on principal components) into three FGs, viz, drought avoiding (DAFG), drought resistant (DRFG), and drought tolerant (DTFG). For species grouping, QWsat was the most significant for DAFG, impacts of A_{max}, LPC, Gs_{max} and LNC were significant for DRFG, while LDMC and CC were significant for DTFG. Across the five forest fragments, along a soil moisture content (SMC) gradient, the three FGs exhibited significant differences in species richness, stem density, aboveground biomass, and biomass accumulation capacity (BAC). We observed increasing dominance of DAFG towards drier sites, while the abundance of DRFG and DTFG was higher towards moister sites. Among the three FGs, DTFG showed highest biomass and BAC in our study region. Strategies of DAFG were more associated with savanna habitats, while DRFG and DTFG exhibited strategies important for TDFs. Our findings could help forest managers in restoration and conservation of TDFs.

1. Introduction

The success of plant species to establish in a water availability gradient, and ability to adapt future changes in the availability of water, often depends on their life history strategies, however we have limited understanding of how plants utilize these strategies for establishment and growth in habitats with variable water availability (Anderson et al., 2012). Alterations in environmental drivers could have a dramatic impact on the drought survival strategies of trees, leading to shift in species composition of water-limited tropical dry forest (TDF) ecosystems (Sullivan et al., 2020). The TDFs contain a high diversity of tree species, exhibiting wide variations in drought deciduousness and drought survival strategies (Poorter and Markesteijn, 2008; Chaturvedi et al., 2011a; Santiago et al., 2017). The drought survival strategies in

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Abbreviations: A_{max}, maximum saturated photosynthetic rate; BA, basal area; BAC, biomass accumulation capacity; BAC_{BA}, rate of change in biomass per unit basal area; BAC_{SA}, rate of change in biomass per unit stand area; CC, canopy cover intensity; DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild; FG, functional guild; FT, functional trait; Gs_{max}, maximum saturated stomatal conductance; HCPC, hierarchical clustering on principal components; LA, leaf size or leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; QWsat, saturated stem water content; RWC, relative water content; SA, stand area; SLA, specific leaf area; SMC, soil moisture content; TDF, tropical dry forest; WSG, wood specific gravity; WUEi, intrinsic water use efficiency.

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https://doi.org/10.1016/j.foreco.2020.118740
Received 5 June 2020; Received in revised form 17 October 2020; Accepted 25 October 2020

trees vary from drought avoidance to drought tolerance, involving several mechanisms by which trees respond and survive drought (Levitt, 1980). These drought survival strategies are strongly influenced by environmental drivers, such as, resource availability, and the related mechanisms such as decomposition and nutrient fluxes across the ecological gradients (Chaturvedi et al., 2011a; Mason et al., 2013). Through several decades, changes in climatic conditions have led to a decline in annual rainfall, while it has increased the length of dry season and rainfall variability in the tropical region (IPCC, 2014). Consequently, the increasing drought and rainfall variability could have significant impact on the structure and function of tree communities in tropical ecosystems (Sullivan et al., 2020), therefore, a proper understanding of the drought adaptive mechanisms in trees is essential for predicting their responses to future changes in climatic conditions.

Tropical trees have been reported to exhibit three adaptive strategies for survival against drought (Poorter and Markesteijn, 2008): (i) drought avoidance, by suspending their physiological functions, and remaining dormant during the drought period, (ii) drought resistance, by continuing their physiological functions, even during drought period with the help of strategies to reduce water loss, and (iii) drought tolerance, by their capacity to maintain physiological functions at the minimum cell water content. These three mechanisms are strongly linked with functional traits (FTs) of the tree species. The drought avoiding trees survive drought by avoiding low water potential through strong stomatal control, limiting transpiration and by restricting photosynthesis. On the other hand, the traits linked with osmotic regulation and the capacity to withstand minimum leaf water potential is important for the survival of drought resistant and drought tolerant trees (Poorter and Markesteijn, 2008). In TDFs, the important adaptations for drought avoiding trees include leaf shedding (Hoffman et al., 2011), deep root system (Johnson et al., 2016), and re-sprouting capacity (Bond and Midgley, 2003). These adaptive mechanisms may also be utilized by drought resistant and drought tolerant trees, up to some extent, nevertheless, they have additional mechanisms which resist xylem cavitation, allowing them to function even during the drought period.

Drought avoidance, resistance and tolerance in TDF species have been observed to be co-ordinated by a set of FTs particularly associated with high cavitation resistance, strong stomatal control, or traits which maintain high turgor pressure during drought, when leaf water potential is low (Markesteijn et al., 2010). According to Markesteijn et al. (2011), and Pineda-García et al. (2013), the tree species in TDFs exhibit wide variation in wood specific gravity (WSG), which is an important drought survival strategy for the co-existing species. WSG is defined as the density of wood relative to the density of water, and is expressed in g cm^{-3}. Generally, trees with low WSG maintain higher saturated stem water content (QWsat) during drought, as compared to the trees with high WSG, however, in such situations, trees with low WSG are also prone to hydraulic failure (Markesteijn et al., 2011). Consequently, trees in TDFs maintain their QWsat up to a level that minimizes hydraulic failure and avoids dieback and death due to drought (Urli et al., 2013). As a result, the species exhibiting low WSG survive drought through drought avoidance strategy, whereas species with high WSG, survive drought through drought resistance and tolerance strategies (Pineda-García et al., 2013; Wolfe and Kursar, 2015).

TDF species exhibit substantial variations in timing, extent and rate of deciduousness (i.e., leaf shedding during dry period), which is determined by their capacity to tolerate drought (Borchert, 1994; Williams et al., 2008). According to Poorter and Markesteijn (2008), deciduousness is positively related to specific leaf area (SLA), and negatively related to leaf dry matter content (LDMC). Leaf relative water content (RWC) is an important indicator of the physiological adaptation and gives information about the water status of plants (Chaturvedi et al., 2013), while photosynthesis and stomatal conductance exhibit significant response to drought stress (Golldack et al., 2011). Under mild to moderate drought, leaf photosynthesis has been observed to decline by stomatal limitation, while under severe drought, non-stomatal conditions are responsible for reduction in photosynthesis (Misson et al., 2010), leading to decrease in productivity of the plant species.

In TDFs, the ability of plants to tolerate water stress and their capacity to access water during drought period determines their success in occupying different niches with respect to soil water availability (Engelbrecht and Kursar, 2003). According to Méndez-Alonzo et al. (2013), variations in water availability in TDF promotes considerable divergence in leaf phenology and xylem traits, where evergreen and semi-deciduous species, containing low WSG can be more common at moist sites, while a combination of high-deciduous species having low WSG, plus tardily deciduous species with high WSG, might be more frequent at drier sites. TDF species growing at different drought conditions also differ in their survival strategies for avoiding or tolerating long drought periods (Chaturvedi, 2010). The species exhibiting acquisitive strategy are highly deciduous, fast growing, show high SLA, low LDMC and have low WSG, conferring rapid water transport and storage (Poorter et al., 2019), however they are also at the risk of cavitation and mortality due to drought. These species avoid drought period, and take advantage of the short, but favourable wet season by maximising growth rate during this period. However, for the species exhibiting conservative strategy, studies generally indicate that they are slow growing, drought tolerant species, have longer leaf life-span, lower leaf area, SLA, leaf nitrogen and phosphorus contents, and lower rate of photosynthesis, which helps them to minimize water loss (Markesteijn et al., 2011, Méndez-Alonzo et al., 2012; Poorter et al., 2019).Although, the species with low WSG, exhibiting rapid water transport, and at the risk of cavitation, may escape the risk of hydraulic failure during the drought period, if they have strong root system for acquiring underground water from greater depths, lower leaf area for minimizing transpiration, and greater efficiency of utilizing stem water reserves (Poorter and Markesteijn, 2008; Pérez-Ramos et al., 2013; Pineda-García et al., 2013). Thus, most probably the coordinated action of traits and processes can mitigate the impact of drought on survival and growth of trees in TDFs (Meinzer et al., 2010).

Environmental conditions influence tree species via their functional strategies, which also change across habitats, therefore prediction of community assembly is a challenging task and remains poorly studied (see Dubuis et al. 2020). Climatic changes are expected to alter timing and intensity of drought period, which might significantly impact the drought tolerance mechanisms of TDF trees. Therefore, it is important to understand the composition of drought survival strategies and resilience capacity of tree species in these forests. To improve our understanding of the survival strategies of tree species distributed in a drought gradient and for predicting their performance in different drought conditions, we categorized the tree species into different groups (functional guilds, FGs). We addressed questions: (i) What are the dominant FGs of tree species across a soil water availability gradient in TDF? (ii) What are the important FTs influencing tree species assemblage in different FGs? (iii) What is the functional composition of different FGs in the study sites, and how are they influencing biomass accumulation capacity (BAC) across the soil water availability gradient? Since, FGs are derived on the basis of relationships of FTs with environmental gradients, we expect that the classification of tree species into FGs will help in understanding the changes in species composition and function in response to future changes in environmental conditions. We hypothesize that for a tree species, a key trait associated with certain drought adaptive strategy will determine its adaptation to specific soil water availability gradient. The trees exhibiting different adaptive strategies will show distinct adaptations for a FT to the soil water availability gradient and their assemblage may result into different FGs associated with different ecological strategies.

2. Materials and methods

2.1. Study sites

We selected five forest fragments or study sites in Vindhyan highlands (21°29′ – 25°11′ N; 78°15′ – 84°15′ E), situated in Sonebhadra district of Uttar Pradesh, India (see GPS locations of study sites in Table S1). These sites cover around 40 km radius, and the distance between two nearest forest fragments was around 5 km. The size of the largest fragment was 2555 ha, while that of the smallest fragment was 637 ha. The altitude for these sites ranges from 279 to 357 m asl. The selected sites contain naturally established old-growth forests. Anthropogenic disturbance in the forest region was minimum and removal of large logs was prohibited. The idea behind the site selection was to get maximum variations in soil moisture content (SMC), and to cover maximum possible tree species diversity of the region. The area experiences tropical monsoon climate. We collected monthly climatic and weather data for 12 year period, starting from January 2008 to December 2019 from the website, www.worldweatheronline.com. The data includes minimum, average and maximum temperatures, rainfall, and relative humidity. The average temperature during this period ranged from 10.5 °C, in January to 42.5 °C, in May. The average annual rainfall was 662.3 mm, with minimum rainfall of 2.69 mm in November to a maximum of 208.7 mm in July. The study region experienced >80% of the total annual rainfall only during three months (July-September), and the remaining 20% in the other nine months. Similar to rainfall, relative humidity in the study region also was higher (>70%), during July-September period. Minimum and maximum relative humidity during this period was 22.0% in April, and 76.4% in August. More detailed description of the study region is given in Chaturvedi (2010).

2.2. Sampling design

We randomly established nine rectangular plots (100 m × 50 m) at each of the five forest fragments. The distance from the forest edge for each plot was maintained at least at one km. Plots were randomly selected to reduce bias caused by within site differences in soil conditions. The idea was to separate the plots at the maximum possible distance at each site, keeping the minimum distance of at least 300 m between the two nearest plots in each forest fragment. Thus, we established a total of 45 plots for the present study. We counted the stems and measured their diameter at breast height (DBH) for all tree species inside each plot using a measuring tape, and identified all individuals $\geq$ 10 cm DBH for further measurements. In each plot, growth measurements were recorded for two years, starting from September 2010 to August 2012. Increases in girth for all individuals were measured annually with the help of metal dendrometer bands fitted at 1.37 m height for each species (Chaturvedi et al., 2011b, 2017). We also measured height increments for each selected individual inside each plot with the help of a 15 m graduated measuring pole for individuals up to 15 m height (one person holding the pole, a second acting as ‘‘spotter'' to assess the mark on the pole which reached the level of the top of the crown), while for the taller individuals trigonometric method was applied. Composite surface (0–30 cm) soil samples were collected at five random locations from each plot, but only once in September 2010, for the physico-chemical analysis. These samples were analysed for texture (Sheldrick and Wang, 1993), organic carbon (Walkley and Black, 1934), total nitrogen (Bremner and Mulvaney, 1982) and total phosphorus (Olsen and Sommers, 1982) contents. To get the actual organic carbon content, values obtained by Walkley and Black method were multiplied by a correction factor (1.95) given by Krishan et al. (2009) for similar soils of central India. The correction factor is based on the relationship between Walkley and Black estimate and that from oxidative combustion-infrared analysis method using total organic carbon analyser. Soil bulk density at each site was determined by the core method (Krzic et al., 2000). For the foliage cover intensity (canopy cover intensity, CC), and wood and leaf trait measurements, we marked at least five individuals, $\geq$ 10 cm DBH, for each tree species coming inside the rectangular plot. For some species, whose individuals were less than five inside the plot, we marked the remaining individuals outside the plot boundary. Sampling for most of these measurements were done in September 2010, however, few rare species which were not sampled in the year 2010, were covered in 2011. Soil moisture content (SMC) at a depth of 10 cm was measured every month for two years, starting from September 2010 to August 2012, by a theta probe instrument (type ML 1, Delta-T Devices, Cambridge, UK), as percentage by volume under the canopy, at four sides of the main trunk, at a distance of one meter from each marked individual tree species.

2.3. Data collection

2.3.1. Tree foliage cover intensity/canopy cover intensity (CC)

The tree CC was recorded for all marked individuals of each species, monthly for two years, starting from September 2010 to August 2012. For this observation, we tagged 20 to 50 terminal twigs on the four sides of each marked individual. We recorded the date of leaf budding or leaf flushing, leaf shedding (including the time of yellowing, browning, partial or total leaf shedding) for each marked individual, at each plot, at each forest fragment. During these observations we also recorded the proportion of leaves in the canopy under a particular phenophase or phenological event. For estimation of the intensity of phenological event (viz., CC), we followed Fournier (1974), and quantified the phenophases for each individual from zero to four (Fournier intensity index). Among these five indices, zero represents absence of phenophase, one indicates the intensity of phenophase between 1 and 25%, two between 26 and 50%, three between 51 and 75%, and four between 76 and 100%. We calculated the intensity of phenophases for foliage cover, for each species at each forest fragment by the formula: ($\sum$Fournier intensity/4N) × 100, where $\sum$Fournier intensity is the sum of Fournier intensity for all individuals of a species, and N is the number of individuals of the species.

2.3.2. Functional traits (FTs)

We selected 12 FTs associated with plant water use strategies, including one structural trait, viz., CC, two wood traits, viz., wood specific gravity (WSG) and saturated stem water content (QWsat), and nine leaf traits, viz., leaf size or leaf area (LA), specific leaf area (SLA), relative water content (RWC), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum saturated stomatal conductance (Gs_{max}), maximum saturated photosynthetic rate (A_{max}), and intrinsic water use efficiency (WUEi).

WSG was measured for five individuals, for each woody species inside each plot, at the five forest fragments, following protocol given in Chaturvedi et al. (2010). The individuals selected for the measurement of WSG were different from those which were marked for the measurement of tree growth, and samples were collected from the trees outside the plots. We took wood samples from the main trunk at the height of 1.4 m, up to the radial depth, with the help of stem borer. The wood samples were sealed in plastic bags separately and brought to the laboratory. The volumes of fresh wood samples, after removing bark were estimated by water displacement method, and the wood samples were dried in oven at 80 °C till constant weight. The values of WSG were expressed as g cm^{-3}. For determining the amount of saturated stem water content (QWsat, %), we collected stem samples > 3 cm diameter, from the same five individuals which were selected for WSG measurement for each species. The volume and dry weight of the stem samples were estimated after removing outer bark, by following the same method which was applied during the measurement of WSG, however, before measuring volume, stem samples were soaked in water overnight. The formula for obtaining QWsat was, according to Borchert (1994), : [(stem water saturated weight – stem dry weight)/stem dry weight] × 100.

Leaf traits were measured on the same tree stems which were marked for the study of phenology. While, we measured LA, SLA, LDMC, A_{max}, Gs_{max}, and WUEi, according to Pérez-Harguindeguy et al. (2013), RWC was measured according to Tanentzap et al. (2015). For the measurement of LA, SLA, LDMC and RWC, ten fully expanded, mature, and sun facing leaves were collected from each marked individual of each woody species. Fresh leaf weights for all leaves were recorded just after collection, at the field site, by portable electronic weighing balance. After weighing, leaves were wrapped in moist paper for rehydration, sealed in separate plastic bags, and were brought to laboratory. All measurements were done within 24 h of bringing the samples to laboratory. All rehydrated fresh leaves were weighed on electronic balance and scanned on a table scanner, and their dimensions were determined with the help of Image-J programme (Abramoff et al. 2004). After LA measurements, all leaf samples were dried in separate paper bags in oven at 70 °C till constant weight. SLA was calculated as the ratio of LA (cm^2) and dry weight (g), while LDMC was measured as the ratio of dry weight (g) and rehydrated fresh mass (g), multiplied by 100, and expressed as % rehydrated fresh weight. RWC was determined as [(Fresh weight – Dry weight) ÷ (Rehydrated weight – Dry weight)] × 100, and expressed as % saturated leaf. For measurement of A_{max} ($\mu mol\ m^{-2}\ s^{-1}$) and Gs_{max} ($mol\ m^{-2}\ s^{-1}$), we sampled three twigs from each marked tree species, at mid-canopy height, having full sun exposure for at least part of the day, with healthy and fully expanded leaves. Measurements were done immediately after collecting the samples using an LC Pro Console Photosynthesis meter (model EN11 ODB, ADC Bioscientific Ltd., UK) between 09:30 h and 12:30 h (solar noon). The WUEi was determined as the ratio of A_{max} and Gs_{max}, and expressed as $\mu mol\ mol^{-1}$.

2.4. Statistical analysis

Species composition or relative ecological importance of the woody species at each forest fragment was expressed by the importance value index (IVI) (Curtis and McIntosh, 1951). Relative IVI for each species was calculated as the average of the values for relative basal area, relative density, and relative frequency. Stem biomass was obtained by using the equation given by King et al. (2006); stem biomass = 0.5× (π/4) × WSG×$(DBH)^2$ × H, where, 0.5 is the form factor, defined as the ratio of stem volume to the volume of a cylinder with the height (H, m), and diameter at breast height (DBH, cm) of the tree. We validated the estimates from this equation against those obtained by using species-specific as well as multi-specific allometric equations relating destructively measured tree biomass and the CBH, for TDF tree species, as well as actually measured biomass of harvested trees (Chaturvedi et al., 2010). We also compared the estimates of stem biomass of two dominant species obtained by CBH-based equation and observed that the estimate from the WSG-based equation was closer to the directly measured biomass ($R^2 = 0.97$, $P < 0.001$), as compared to the CBH-based equation ($R^2 = 0.83$, $P < 0.001$). We calculated biomass per unit stem basal area (BA), as well as per unit stand area (SA). The biomass accumulation capacity (BAC) for each tree species was calculated as the rate of change in biomass per unit BA (BAC_{BA}) and per unit stand area (BAC_{SA}).

The statistical analyses were done in R version 3.6.2 (R Development Core Team, 2018). We used likelihood ratio tests (LRTs) for testing interactions and main effects. We also used Wald tests for evaluating the parameter estimates. We used var() function in R for calculating inter-species and intra-species variances in the FTs, while wilk shapiro test was used to check normality of the measured data. On the basis of normality test, the data exhibiting non-normal distribution (viz., tree biomass, $BAC_{BA,}$ $BAC_{SA,}$ QWsat, LA and RWC) were log-transformed before statistical analysis. Further, we compared all data (viz., SMC, CC, WSG, QWsat, LA, SLA, RWC, LDMC, LNC, LPC, Gs_{max}, A_{max}, and WUEi), in the form of response variables, with a linear mixed-effects model (nlme::lme, Pinheiro et al., 2016), where we defined site and plot as fixed effects, and species as random effect. We used an autoregressive moving average model for accounting temporal autocorrelation. This model structure was required to appropriately account for the temporal autocorrelation caused by repeated measurements of SMC, biomass and BAC for the same individuals of each tree species. Pearson's correlation coefficient was calculated on average values of SMC, CC, wood traits, and leaf traits for each species across the study sites by using "Hmisc" (Harrell, 2017) and "xtable" (Dahl, 2016) package.

We observed species groupings as FGs, by using CC, wood traits and leaf traits data for each species through PCA, hierarchical clustering, and partitioning clustering particularly through k-means method by HCPC (hierarchical clustering on principal components). According to Kassambara (2017), HCPC is a robust tool for multivariate data analysis, where it allows three techniques (viz., hierarchical clustering, k-means partitioning, and PCA) in combination for extracting information from the data and summarising results in a best possible format. The HCPC basically uses Euclidean distances for defining distance between individuals, while the hierarchical tree is constructed by Ward's agglomeration method (Husson et al. 2010; Husson et al. 2011). According to Husson et al. (2010), the categories of cluster variables are represented by the categories of the categorical variables. The HCPC generates a list of FTs in ascending order of *P*-value, which shows the order of impact of the categorical variables. HCPC also develops V-test values which are reported to be associated with the *P*-values (Husson et al. 2011). Moreover, the order of over represented positive V-test values exhibit categories of categorical variables according to their influence on the cluster variables (Husson et al. 2011). Our analysis, was based on the average value of SMC, CC, wood traits, and leaf traits for all individuals of each species across the nine plots, and the five forest fragments. We showed the clusters of tree species in the form of PCA biplot. The clustering of tree species was based on the shared set of FTs. Initially we classified the total tree species into two FGs [viz., drought avoiding FG (DAFG), and drought tolerant FG (DTFG)], however we noticed that the majority of species were clustered in DTFG, therefore by using the same method, we extracted another species cluster from DTFG, and based on their shared FTs, termed the cluster as drought resistant FG (DRFG). For this analysis, we used the R package "FactoMineR" and "factoextra" (Kassambara & Mundt 2016). We used functions prcomp() and PCA(), "FactoMineR" package for PCA analysis.

The differences among FGs were computed by Tukey HSD tests for SMC, species richness, stem density, biomass, BAC, CC, wood and leaf traits. Tukey HSD test was also performed for observing differences in soil properties among the five forest fragments. The Tukey HSD tests were done by using "multcomp" package (Hothorn et al., 2008). For plotting boxplots, we also used "ggplot2" package (Wickham, 2009).

Through step-wise regression, we identified best predictors of BAC for each of the classified FGs in the forest region. For predicting BAC_{BA}, and BAC_{SA} (response variables), we used CC, wood traits and leaf traits (explanatory variables) for each tree species, across each plot in the five forest fragments. We calculated community weighted mean for CC, wood traits and leaf traits following Lavorel et al. (2008) for each plot, at each forest fragment, and through step-wise regression, we identified best predictors of BAC_{SA} for the three FGs. Further, we also included soil properties in each plot ($n = 45$), as predictors, along with the community weighted mean of CC, wood traits and leaf traits for identifying best predictors for the BAC_{SA} in the forest region. The idea was to assess the accountability of FTs and soil properties for BAC in the forest. For step-wise regression, we used the R package "tidyverse" (Wickham et al. 2019), "caret" (Kuhn et al. 2016), and "leaps" (Lumley & Miller 2009). We used the stepAIC() function in "MASS" package (Venables et al., 2010), for choosing the best model by AIC (Burnham and Anderson, 2012). The multicollinearity between predictor variables in the regression models was checked with generalized variation inflation factor (GVIF) by using vif() function in "car" package (Fox, 2018).

3. Results

3.1. Soil and vegetation properties

Table 1 shows the average values of soil physico-chemical properties at the five forest fragments in TDF, arranged in decreasing SMC or increasing dryness. We observed significantly greater clay content (12.1%), organic C (2.25%), total N (0.16%), and total P (0.06%) at the most moist site, while these soil parameters were significantly lower (clay, 3.00%; organic C, 1.40%; total N, 0.12%; total P, 0.02%) at the most dry site (Table 1). Conversely, the sand content was significantly higher at the most dry site (70.2%), whereas it was significantly lower at the most moist site (Table 1). We observed highest silt content, and bulk density at the sites with intermediate SMC. Across the five forest fragments, the total number of woody species having DBH ≥ 10 cm was 47, ranging from 13 to 35 species per forest fragment (Table S1). These species belong to 24 families, where the highest number of species was recorded for the family Fabaceae (10 species), followed by Rubiaceae (4 species), Anacardiaceae (3 species), Combretaceae (3 species), Apocynaceae (2 species), Meliaceae (2 species), Oleaceae (2 species), Phyllanthaceae (2 species), Rhamnaceae (2 species), Rutaceae (2 species), and Salicaceae (2 species). The other 13 families registered, only one species, for each family (Table S1). We found ten species, common to all nine forest fragments, while 19 species were rare and their presence was recorded only at one of the five forest fragments. The density of stems ≥ 10 cm DBH across the fragments ranged from 188 to 537 per ha. On the basis of relative importance value index (IVI), we observed distinct tree communities in each of the five forest fragments. These tree communities in decreasing SMC gradient were: (1) *Shorea robusta-Buchanania cochinchinensis*, (2) *Tectona grandis-Shorea robusta*, (3) *Shorea robusta-Soymida febrifuga*, (4) *Buchanania cochinchinensis-Shorea robusta*, and (5) *Acacia catechu-Lagerstroemia parviflora*. Among the five forest fragments, *Shorea robusta-Buchanania cochinchinensis* community represented most moist study site, whereas *Acacia catechu-Lagerstroemia parviflora* community represented the most dry study site. We found *Shorea robusta* and *Buchanania cochinchinensis* as the two dominant trees in two forest fragments, however, *Shorea robusta* was most abundant at the comparatively moist forest fragment, while *Buchanania cochinchinensis* was the most abundant at the comparatively dry forest fragment (Table S1). The average value of SMC measured across the woody species, monthly for two years was 9.35% and ranged from 3.14%, for *Nyctanthes arbor-tristis* to 12.96% for *Albizia odoratissima* (Table S2). Between site and between plot diffences for SMC were statistically significant (Table 2). We also observed significant differences between sites for the tree biomass, $BAC_{BA,}$ and BAC_{SA} (Table 2).

Table 1
Summary of soil physico-chemical properties for the five forest fragments located in Vindhyan highlands. Values in parentheses are standard errors.

Parameter	Site 1	Site 2	Site 3	Site 4	Site 5
SMC (%)	16.1 (±0.71)^{a}	15.2 (±0.39)^{a}	11.3 (±0.68)^{b}	10.1 (±0.35)^{b}	7.78 (±0.62)^{c}
Clay (%)	12.1 (±0.21)^{a}	10.6 (±0.68)^{b}	7.08 (±0.50)^{c}	4.83 (±0.25)^{d}	3.00 (±0.31)^{e}
Silt (%)	27.2 (±0.50)^{a}	22.9 (±0.77)^{b}	32.1 (±0.81)^{b}	26.2 (±0.36)^{b}	28.8 (±0.70)^{c}
Sand (%)	60.7 (±0.35)^{a}	66.5 (±0.33)^{a}	60.8 (±0.57)^{b}	69.0 (±0.35)^{c}	70.2 (±0.49)^{c}
Organic C (%)	2.25 (±0.08)^{a}	2.18 (±0.13)^{a}	1.56 (±0.03)^{b}	1.55 (±0.03)^{b}	1.40 (±0.03)^{b}
Total N (%)	0.16 (±0.01)^{a}	0.15 (±0.01)^{a}	0.13 (±0.01)^{b}	0.13 (±0.01)^{b}	0.12 (±0.01)^{b}
Total P (%)	0.06 (±0.01)^{a}	0.05 (±0.01)^{a}	0.03 (±0.01)^{b}	0.02 (±0.00)^{b}	0.02 (±0.00)^{b}
BD (g cm^{-3})	1.36 (±0.01)^{a}	1.39 (±0.01)^{ab}	1.38 (±0.02)^{ab}	1.38 (±0.02)^{ab}	1.32 (±0.02)^{b}

^{a,b,c,d,e}Values affixed with different letters in a row are significantly different from each other at $P < 0.05$ (Tukey HSD test).

Table 2
Summary of ANOVA associated with linear mixed-effects model for soil moisture content (SMC), tree biomass, biomass accumulation capacity per unit basal area (BAC_{BA}), biomass accumulation capacity per unit stand area (BAC_{SA}), tree canopy cover intensity (CC), wood specific gravity (WSG), saturated stem water content (QWsat), leaf size or leaf area (LA), specific leaf area (SLA), relative water content (RWC), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum saturated stomatal conductance (Gs_{max}), maximum saturated photosynthetic rate (A_{max}), and intrinsic water use efficiency (WUEi) as response variables, with site and plot defined as fixed effects, and species as random effect. Number of observations = 573; Number of groups = 47; $^{ns}P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Factor	**SMC (*F* value)**	**Biomass (*F* value)**	**BAC_{BA} (*F* value)**	**BAC_{SA} (*F* value)**
Site	575.8***	12.17***	35.33***	47.68***
Plot	5.186***	3.269*	1.121 ns	1.334 ns
Site × Plot	0.490 ns	0.693 ns	1.723**	0.635 ns
Factor	**CC (*F* value)**	**WSG (*F* value)**	**QWsat (*F* value)**	**LA (*F* value)**
Site	414.4***	141.3***	171.2***	41.14***
Plot	0.782 ns	12.76***	0.379 ns	7.068***
Site × Plot	0.404 ns	2.545***	0.783 ns	0.998 ns
Factor	**SLA (*F* value)**	**RWC (*F* value)**	**LDMC (*F* value)**	**LNC (*F* value)**
Site	256.0***	60.64***	179.1***	205.5***
Plot	11.89***	4.448***	14.99***	25.28***
Site × Plot	4.530***	1.177 ns	2.110***	3.465***
Factor	**LPC (*F* value)**	**Gs_{max} (*F* value)**	**A_{max} (*F* value)**	**WUEi (*F* value)**
Site	296.4***	335.2***	363.9***	236.3***
PLot	13.38***	13.66***	16.55***	8.592***
Site × Plot	2.421***	2.859***	2.961***	3.529***

3.2. Functional traits (FTs)

Across the five study sites, ANOVA indicated significant differences for canopy cover intensity (CC), wood traits and leaf traits (Table 2). These FTs also exhibited significant differences between plots at the five study sites, except for CC and QWsat, where between plot differences were statistically not significant (Table 2). The site × plot, two-way interactions were significantly different for WSG, SLA, LDMC, LNC, LPC, Gs_{max}, A_{max} and WUEi (Table 2).

We observed the interspecific variance, greater for LA, QWsat and SLA, whereas lower for LPC, WSG and Gs_{max} (Table S3). Similarly, the intraspecific variance was also recorded higher for LA, QWsat and SLA for majority of the species (Table S3). The greatest intraspecific variances for LA, QWsat and SLA were respectively recorded for *Adina cordifolia*, *Lannea coromandelica*, and *Lagerstroemia parviflora*, while, the lowest variances for LA, QWsat and SLA were observed for *Carissa spinarum*, *Casearia elliptica*, and *Tectona grandis*, respectively (Table S3). The maximum LA was recorded for *Tectona grandis* (970 cm^2) at the second site, along decreasing SMC gradient, however the minimum value was observed for *Carissa spinarum* (7.41 cm^2), also at the same study site. Greatest QWsat and SLA were recorded for *Lannea coromandelica* (205.6%) and *Lagerstroemia parviflora* (178.5 cm^2 g^{-1}), respectively, at the most moist site, whereas the lowest values of QWsat and SLA were recorded for *Shorea robusta* (32.5%) and *Butea monosperma* (65.0 $cm^2 g^{-1}$), respectively, at the drier sites. Across the tree species, LPC and Gs_{max} were highest for *Holarrhena pubescens* (0.38%) and *Anogeissus latifolia* (0.61 mol $m^{-2}s^{-1}$), respectively, at the most moist site, while we recorded lowest LPC as well as lowest Gs_{max} for *Nyctanthes arbor-tristis* (LPC, 0.14%; Gs_{max}, 0.16 mol $m^{-2}s^{-1}$), at the most dry site. We observed highest WSG for *Shorea robusta* (0.77 g cm^{-3}), at the most dry site, whereas lowest WSG for *Boswellia serrata* (0.41 g cm^{-3}), at the second most moist site. Among other traits, CC was highest for *Shorea robusta* (90.2%) at the second most moist site, whereas the value of CC was lowest for *Boswellia serrata* (35.0%) at the most dry site. We found greatest RWC for *Holarrhena pubescens* (99.72%), and lowest LDMC for *Anogeissus latifolia* (30.8%), both at the most moist site, whereas RWC was detected lowest and LDMC was observed highest for *Butea monosperma* (RWC, 76.1%; LDMC, 38.5%) at the second-most dry site. Maximum LNC was recorded for *Terminalia tomentosa* (2.94%) at the second-most moist site, whereas the value of LNC was observed minimum for *Ziziphus nummularia* (1.20%), at the second-most dry site. For A_{max}, we recorded both maximum (*Holarrhena pubescens*, 18.6 μmol m^{-2}s^{-1}) as well as minimum (*Ceriscoides turgida*, 5.82 μmol m^{-2}s^{-1}) values at the most moist site. Similarly, for WUEi, both greatest (*Nyctanthes arbor-tristis*, 67.2 μmol mol^{-1}) as well as lowest (*Buchanania cochinchinensis*, 30.1 μmol mol^{-1}) values were observed at the most dry site.

Results of Pearson's correlation exhibited significant positive relationship of SMC with SLA, RWC, LNC, LPC, Gs_{max}, and A_{max}, however the association of SMC was significantly negative with LDMC and WUEi (Table 3). CC exhibited significantly positive correlations with WSG and RWC, while the relationship of CC with QWsat was significantly negative. The association of WSG was significantly positive, also with SLA, whereas WSG exhibited significantly negative correlation with QWsat (Table 3). Although, QWsat and LDMC did not show significant correlation with each other, both these traits exhibited significantly positive correlation with WUEi. While, the association of QWsat was statistically not significant with other leaf traits, LDMC exhibited significantly negative correlation with RWC, LNC, LPC, Gs_{max}, and A_{max}. Moreover, among the other leaf traits, LA showed significantly positive association with LDMC, whereas the relationship of LA was significantly negative with RWC and LNC. The correlation between SLA and RWC was significantly positive, and both these traits also exhibited significantly positive relationship with LNC, LPC, Gs_{max}, and A_{max}. Similarly, we observed significantly positive correlation between LNC and LPC, while both these traits also exhibited significantly positive association with Gs_{max} and A_{max}. The relationship of Gs_{max} and A_{max} was significantly positive, and the correlation of WUEi was significantly negative with LPC and Gs_{max} (Table 3).

From the above results, between sites and between species differences among FTs are hard to predict precisely, and their linkage with plant-site water relations across the SMC gradient is also difficult to establish, therefore, we needed some other approach to better understand the species response across the SMC gradient.

3.3. Functional guilds (FGs)

3.3.1. PCA and HCPC analyses

3.3.1.1. Total species. The PCA biplot (Fig. S1) explained the variability among the 47 tree species on the basis of their FTs. The eigenvalues of the first two PCA axes were 4.37 and 2.19, respectively. The individual variance explained by the first two PCA axes were 36.4% and 18.3%, while the two axes together accounted for 54.7% of the total multivariate variation during PCA. The first PCA axis exhibited stronger associations with LPC (r = 0.878), Gs_{max} (r = 0.845), and A_{max} (r = 0.812), while the second PCA axis indicated stronger correlations with QWsat (r = -0.853), CC (r = 0.776) and WSG (r = 0.742). The HCPC separated total 47 tree species into two separate clusters as shown in Fig. S1. Description of quantitative variables of HCPC, including V-test indicated that the species in cluster 1 exhibit significant positive influence for WUEi, LDMC and LA (Table S4). However, in cluster 2, the species were observed to have significant positive influence of Gs_{max}, A_{max}, LPC, RWC, LNC and SLA (Table S4). The FTs describing species in cluster 1 are important features of drought avoiding species, while those describing species in cluster 2 are important features of drought tolerant species, therefore woody species in cluster 1 and 2, respectively were considered as the two FGs, as drought avoiding functional guild (DAFG) (8 species), and drought tolerant functional guild (DTFG) (39 species).

We observed significant variation in average SMC ($F_{1,115} = 10.5, P < 0.01$) between the two FGs. Across the two FGs, tree species also exhibited significant differences for average CC ($F_{1,115} = 25.4$, $P < 0.001$), QWsat ($F_{1,115} = 39.2$, $P < 0.001$), LA ($F_{1,115} = 11.0$, $P < 0.01$), SLA ($F_{1,115} = 27.3$, $P < 0.001$), Gs_{max} ($F_{1,115} = 42.8$, $P < 0.001$), A_{max} ($F_{1,115} = 13.4$, $P < 0.001$), and WUEi ($F_{1,115} = 43.6$, $P < 0.001$).

3.3.1.2. Drought avoiding species. Variability among the eight drought avoiding tree species on the basis of their FTs is shown in Fig. S2 as PCA biplot. The eigenvalue of the first two PCA axes were 4.62 and 2.77, respectively. The individual variance explained by the first two PCA axes were 38.5% and 23.0%, while the two axes together accounted for 61.5% of the total multivariate variation during PCA. The first PCA axis exhibited stronger associations with LPC (r = 0.841), LDMC (r = -0.811) and LNC (r = 0.799), while the second PCA axis indicated stronger correlations with SLA (r = 0.819), LA (r = -0.800) and WUEi (r = 0.712). The HCPC for the eight tree species in drought avoiding category, separated these species into two separate clusters as shown in Fig. S2. Cluster 1 contained two tree species and the cluster 2 contained the other six tree species. The quantitative description of HCPC variables and V-test showed that for both clusters, the drought avoiding species exhibited significant influence only for QWsat (Table S5). Therefore, we considered all eight species in a single FG, as drought avoiding functional guild (DAFG).

3.3.1.2.1. Drought tolerant species. Fig. S3 shows a PCA biplot explaining variability among the 39 drought tolerant tree species on the basis of their FTs. The eigenvalues of the first two PCA axes were 3.44 and 2.29, respectively. The individual variance explained by the first two PCA axes were 28.7% and 19.1%, while the two axes together accounted for 47.8% of the total multivariate variation during PCA. The first PCA axis exhibited stronger associations with A_{max} (r = 0.835), LPC

Table 3

Pearson's correlation coefficients between average soil moisture content (SMC), tree canopy cover intensity (CC), wood specific gravity (WSG), saturated stem water content (QWsat), leaf size or leaf area (LA), Specific leaf area (SLA), relative water content (RWC), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum saturated stomatal conductance (Gs_{max}), maximum saturated photosynthetic rate (A_{max}), and intrinsic water use efficiency (WUEi), across the five forest fragments. n = 47, $^{ns}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	SMC	CC	WSG	QWsat	LA	SLA	RWC	LDMC	LNC	LPC	Gs_{max}	A_{max}
CC	0.10 ns											
WSG	0.19 ns	0.35*										
QWsat	−0.23 ns	−0.65***	−0.50***									
LA	0.01 ns	−0.24 ns	0.02 ns	0.07 ns								
SLA	0.31*	0.12 ns	0.37*	−0.07 ns	−0.22 ns							
RWC	0.29*	0.29*	0.13 ns	−0.02 ns	−0.41**	0.49***						
LDMC	−0.39**	−0.05 ns	0.24 ns	−0.21 ns	0.33*	−0.15 ns	−0.38**					
LNC	0.43**	0.01 ns	0.09 ns	0.07 ns	−0.27*	0.37*	0.32*	−0.55***				
LPC	0.47***	0.02 ns	−0.01 ns	−0.04 ns	−0.25 ns	0.37*	0.49***	−0.64***	0.64***			
Gs_{max}	0.65***	0.12 ns	0.04 ns	−0.11 ns	−0.14 ns	0.31*	0.41**	−0.50***	0.42**	0.73***		
A_{max}	0.50***	0.06 ns	0.09 ns	0.06 ns	−0.24 ns	0.52***	0.46**	−0.41**	0.53***	0.68***	0.79***	
WUEi	−0.55***	−0.18 ns	−0.01 ns	0.29*	−0.05 ns	0.05 ns	−0.16 ns	0.40**	−0.22 ns	−0.50***	−0.72***	−0.20 ns

($r = 0.813$) and Gs_{max} ($r = 0.777$), while the second PCA axis indicated stronger correlations with WSG ($r = 0.720$), RWC ($r = 0.665$) and QWsat ($r = -0.663$). The HCPC separated 39 drought tolerant tree species into two distinct clusters as shown in Fig. S3. According to the quantitative description of HCPC variables and V-test results, the tree species in cluster 1 exhibited significant positive influence for LDMC and CC (Table S6), whereas cluster 2 showed positive impact of A_{max}, LPC, Gs_{max} and LNC. On the basis of FTs in the two clusters, the 39 drought tolerant tree species were categorized, respectively into two FGs, as (i) drought resistant functional guild (DRFG) (13 species), and (ii) drought tolerant functional guild (DTFG) (26 species).

Based on the above results, we classified 47 tree species into three FGs, as (i) DAFG (8 species), (ii) DRFG (13 species), and (iii) DTFG (26 species), as shown in the PCA biplot (Fig. 1). The statistical features of the PCA biplot in Fig. 1 are same as described for Fig. S1.

3.3.2. Characteristic features

3.3.2.1. Functional traits (FTs). Across the five study sites, significant difference among FGs was observed for CC (RSE = 8.894, $F_{4,44} = 10.49$, Adj $R^2 = 0.292$, $P < 0.001$), which exhibited highest value for DTFG, as compared to other FGs (Fig. 2). Among wood traits, QWsat exhibited significant difference among the three FGs (RSE = 39.78, $F_{2,44} = 3.969$, Adj $R^2 = 0.114$, $P < 0.05$), whereas the difference among FGs for WSG was not significant (RSE = 0.068, $F_{2,44} = 0.628$, Adj $R^2 = -0.016$, $P > 0.05$). Among the three FGs, QWsat was highest and widely distributed for the DAFG (38.3% for *Acacia catechu* at the most dry site to 205.6% for *Lannea coromandelica* at the most moist site) (Fig. 2). Among the leaf traits, LA (RSE = 227.5, $F_{2,44} = 2.077$, Adj $R^2 = 0.045$, $P > 0.05$) did not exhibit significant difference among the FGs, however this trait was much variable among the tree species in DAFG (25.8 cm^2 for *Ceriscoides turgida* at the most moist site to 859.9 cm^2 for *Butea monosperma* at the second most dry site) (Fig. 2). Other leaf traits also showed significant differences across the three FGs (Fig. 2), viz., SLA (RSE = 24.67, $F_{2,44} = 5.001$, Adj $R^2 = 0.148$, $P < 0.05$), RWC (RSE = 4.291, $F_{2,44} = 8.499$, Adj $R^2 = 0.246$, $P < 0.001$), LDMC (RSE = 1.222, $F_{2,44} = 9.300$, Adj $R^2 = 0.265$, $P < 0.001$), LNC (RSE = 0.262, $F_{2,44} = 8.893$, Adj $R^2 = 0.256$, $P < 0.001$), LPC (RSE = 0.029, $F_{2,44} = 16.61$, Adj $R^2 = 0.404$, $P < 0.001$), Gs_{max} (RSE = 0.052, $F_{2,44} = 31.50$, Adj $R^2 = 0.570$, $P < 0.001$), A_{max} (RSE = 1.539, $F_{2,44} = 21.12$, Adj $R^2 = 0.467$, $P < 0.001$), and WUEi (RSE = 5.584, $F_{2,44} = 9.132$, Adj $R^2 = 0.261$, $P < 0.001$). Among the three FGs, DAFG exhibited significantly lower SLA, RWC, LNC, LPC, Gs_{max} and A_{max}, however, this FG showed highest WUEi as compared to the other two FGs. We also found that the DRFG exhibited higher SLA, RWC, LNC, LPC, Gs_{max}, and A_{max}, as compared to the other two FGs (Fig. 2).

3.3.2.2. Soil moisture content (SMC) and vegetation structure. Across the study five sites, the results of Tukey's HSD test indicated significant differences among the three FGs in their preferences for SMC (RSE = 1.504, $F_{2,44} = 4.163$, Adj $R^2 = 0.121$, $P < 0.05$) (Fig. 3). Generally, DAFG recorded significantly lowest SMC, as compared to other FGs. However, SMC between DRFG and DTFG were not significantly different (Fig. 3). Among the three FGs, although, we observed greater differences in species richness, the stem density (RSE = 128.1, $F_{2,44} = 0.071$, Adj $R^2 = -0.042$, $P > 0.05$), aboveground biomass (RSE = 3.342, $F_{2,44} = 0.019$, Adj $R^2 = -0.045$, $P > 0.05$), BAC_{BA} (RSE = 0.028, $F_{2,44} = 0.519$, Adj $R^2 = -0.021$, $P > 0.05$), and BAC_{SA} (RSE = 75.94, $F_{2,44} = 1.163$, Adj $R^2 = 0.007$, $P > 0.05$) were not significantly different (Fig. 3). Between species variation in stem density (DAFG, 1–52 stems ha^{-1}; DRFG, 1–54 stems ha^{-1}; DTFG, 1–92 stems ha^{-1}), biomass (DAFG, 118–17356 kg ha^{-1}; DRFG, 154–19714 kg ha^{-1}; DTFG, 78–9253 kg ha^{-1}), BAC_{BA} (DAFG, 0–0.13 kg cm^{-2} yr^{-1}; DRFG, 0–0.13 kg cm^{-2} yr^{-1}; DTFG, 0–0.12 kg cm^{-2} yr^{-1}), and BAC_{SA} (DAFG, 2.52–1785 kg ha^{-1} yr^{-1}; DRFG, 10.8–616 kg ha^{-1} yr^{-1}; DTFG, 0.98–327 kg ha^{-1} yr^{-1}) was very high in each FG.

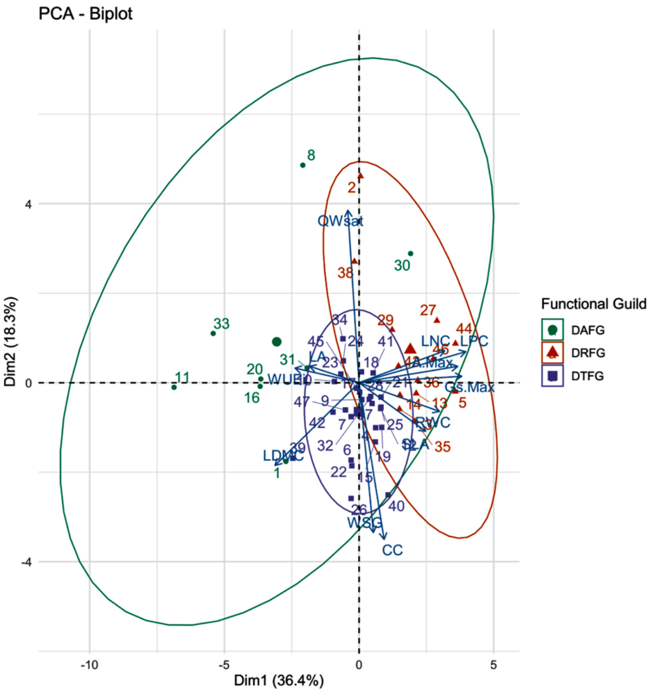

Fig. 1. Ordination of the 47 tree species of tropical dry forest along first and second PCA axes into three functional guilds (viz., DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild), resulting from PCA of their canopy cover intensity (CC), wood traits and leaf traits. WSG, wood specific gravity; QWsat, stem water storage capacity; LA, leaf area; SLA, specific leaf area; RWC, relative water content; LDMC, leaf dry matter content; Gs.Max, maximum saturated stomatal conductance; A.Max, maximum saturated photosynthesis; WUEi, intrinsic water use efficiency. 1, *Acacia catechu*; 2, *Adina cordifolia*; 3, *Aegle marmelos*; 4, *Albizia odoratissima*; 5, *Anogeissus latifolia*; 6, *Azadirachta indica*; 7, *Bauhinia racemosa*; 8, *Boswellia serrata*; 9, *Bridelia retusa*; 10, *Buchanania cochinchinensis*; 11, *Butea monosperma*; 12, *Carissa spinarum*; 13, *Casearia elliptica*; 14, *Cassia fistula*; 15, *Cassine glauca*; 16, *Ceriscoides turgida*; 17, *Chloroxylon swietenia*; 18, *Cordia myxa*; 19, *Dalbergia latifolia*; 20, *Desmodium oojeinense*; 21, *Diospyros melanoxylon*; 22, *Eugenia jambolana*; 23, *Flacourtia indica*; 24, *Gardenia latifolia*; 25, *Grewia serrulata*; 26, *Hardwickia binata*; 27, *Holarrhena pubescens*; 28, *Holoptelea integrifolia*; 29, *Lagerstroemia parviflora*; 30, *Lannea coromandelica*; 31, *Madhuca latifolia*; 32, *Mitragyna parvifolia*; 33, *Nyctanthes arbor-tristis*; 34, *Phyllanthus emblica*; 35, *Pterocarpus marsupium*; 36, *Schleichera oleosa*; 37, *Schrebera swietenioides*; 38, *Semecarpus anacardium*; 39, *Senna siamea*; 40, *Shorea robusta*; 41, *Soymida febrifuga*; 42, *Tectona grandis*; 43, *Terminalia chebula*; 44, *Terminalia tomentosa*; 45, *Uvaria tomentosa*; 46, *Ziziphus glaberrima*; 47, *Ziziphus nummularia*.

Although, the DTFG accounted for maximum number of tree species, the number of rare species, which were present at only one forest fragment, was also found highest for the DTFG (10 species), as compared to DRFG (5 species) and DAFG (4 species). The dominant family on the basis of species number, for the DAFG (3 species) and DTFG (5 species) was Fabaceae, whereas the dominant family for DRFG was Combrataceae (3 species). On the basis of stem density, Fabaceae registered greater dominance for DAFG (63.4%). While, for the other two FGs, Fabaceae accounted for fewer individuals (viz., DRFG, 3.3%; DTFG, 9.2%), compared to other families in their group. On the basis of stem density, the dominant family for DRFG was Combretaceae (56.6%), whereas for DTFG, the dominant family was Dipterocarpaceae (26.1%). Among the tree species, maximum stem density was recorded for *Shorea robusta*, a drought tolerant species, at the most moist site (92 stems ha^{-1}), while highest biomass was observed for *Adina cordifolia*, a drought resistant species, also at the most moist site (19.7 ton ha^{-1}). Here, it is interesting to note that, *Adina cordifolia* was not a very common species, and was recorded at only two forest fragments (average

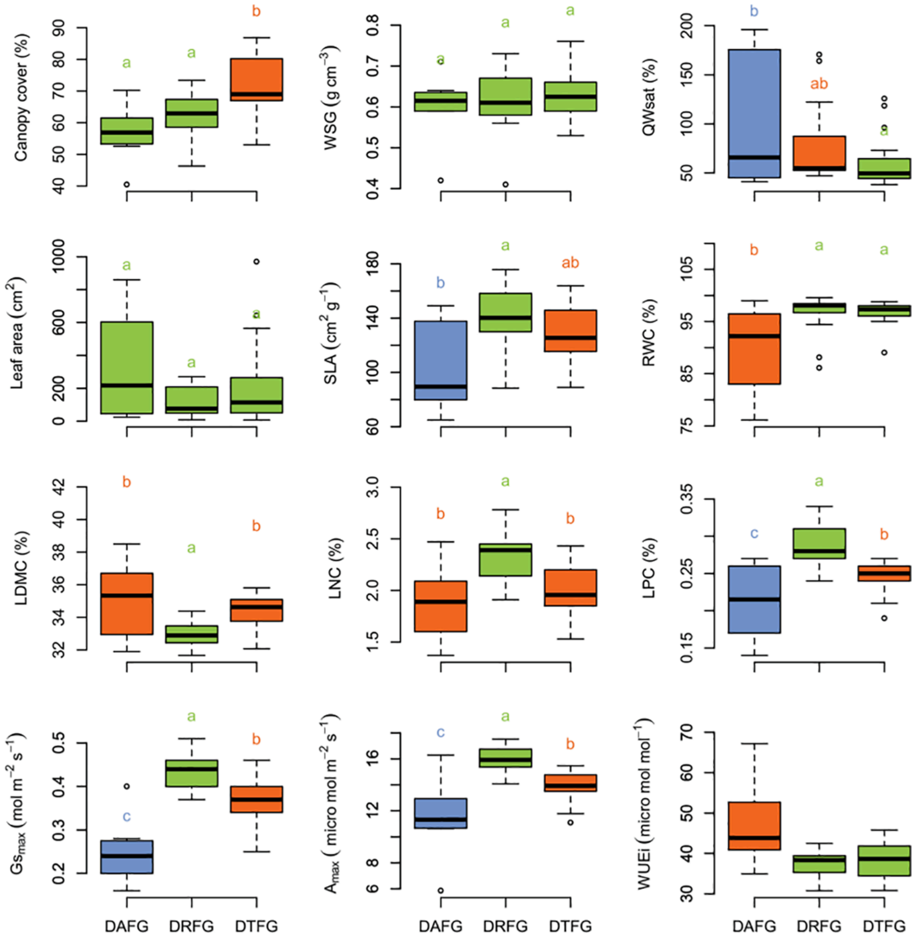

Fig. 2. Boxplot showing distribution of canopy cover intensity (CC), wood traits, and leaf traits, for tree species in the three functional guilds in tropical dry forest. DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild; WSG, wood specific gravity; QWsat, saturated stem water content; LA, leaf size or leaf area; SLA, specific leaf area; RWC, relative water content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; Gs_{max}, maximum saturated stomatal conductance; A_{max}, maximum saturated photosynthetic rate; WUEi, intrinsic water use efficiency. Different letters and colours indicate significant differences (Tukey's HSD test, $P < 0.01$) between functional guilds.

stem density = 46 ha^{-1}). Although, *Adina cordifolia* registered lower stem density (17 stems ha^{-1}), compared to *Shorea robusta* (92 stems ha^{-1}), at the same site, we found greater biomass for *Adina cordifolia* due to the presence of large size individuals, with DBH reaching up to 50 cm. The highest BAC_{BA} was observed for *Lannea coromandelica*, a drought avoiding tree, at the most moist site (0.13 kg cm^{-2} yr^{-1}), whereas greatest BAC_{SA} was accounted for *Acacia catechu*, also a drought avoiding tree, at the most moist site (410 kg ha^{-1} yr^{-1}).

Fig. 4 shows results for SMC, species richness and stem density in the three FGs, at five study sites, separately. Generally, for all five study sites, SMC was significantly highest for DRFG, while it was lowest for DAFG. We found that the differences for SMC among the three FGs were significant for all study sites, except the most moist site, where the DRFG and DTFG showed similar SMC. For all five study sites, species richness was highest for DTFG, and lowest for DAFG, except the two sites at the drier end, where the species richness was not significantly different between DAFG and DRFG at the site four, while the differences between the species richness for DRFG and DTFG were not significant for the site five, which was the most dry site (Fig. 4). We observed remarkable decline in the species richness for the three FGs while moving from the most moist site towards the most dry study site. The average species richness across the nine plots for the DAFG, DRFG, and DTFG at the most moist site were 3, 6 and 10 species, respectively, whereas, for the most dry site, the average species richness for the DAFG, DRFG, and DTFG were 2, 3 and 3 species, respectively. Here, we found that the DRFG and DTFG exhibited considerable decline in species richness, due to increasing dryness, as compared to the DAFG. Stem density of trees in the three FGs, at the five study sites also exhibited similar trend as observed for species richness, however differences among the three FGs were not significant for the fifth study site (RSE = 2.672, $F_{2,24} = 0.394$, Adj R^2 = -0.049, $P > 0.05$) (Fig. 4). Among the five study sites, the average stem density, per species for the three FGs was recorded highest at the most moist site (DAFG, 8 stems ha^{-1}; DRFG, 18 stems ha^{-1}; DTFG, 34 stems ha^{-1}), whereas the average stem density, per species was lowest at the most dry site (DAFG, 7 stems ha^{-1}; DRFG, 8 stems ha^{-1}; DTFG, 6 stems ha^{-1}). Similar to species richness, the stem density also exhibited considerable decline due to increasing dryness, for DRFG and DTFG, while the decline in stem density for DAFG was negligible.

3.3.2.3. Biomass accumulation capacity (BAC). Although, the tree biomass, across the five study sites did not exhibit significant difference among the three FGs (see Fig. 2), we found significantly different tree biomass among the three FGs, at three study sites at intermediate SMC levels (Fig. 5). At these three sites, the biomass for DTFG was highest, whereas, the biomass of DAFG was lowest. The most moist and the most dry study sites did not show significant difference for tree biomass among the three FGs (Fig. 5). Similar to species richness and stem density, the above ground biomass also exhibited considerable decline while moving from the most moist study site towards the most dry site. At the most moist site, the average biomass per species for DAFG, DRFG, and DTFG were, 20.1 ± 2.9 ton ha^{-1}, 30.3 ± 1.4 ton ha^{-1}, and 24.6 ± 0.6 ton ha^{-1}, respectively, whereas, the average biomass per species for the three FGs at the most dry site were 4.0 ± 1.1 ton ha^{-1}, 4.2 ± 0.6 ton ha^{-1}, and 5.5 ± 1.0 ton ha^{-1}, respectively. Here, it is important to note that for biomass, the DAFG also exhibited considerable decline, which may be due to the presence of large size trees at the moist site as compared to the dry site. When we compare the stand biomass among the three FGs, with their BAC_{BA} and BAC_{SA}, we found some interesting results. For the most moist study site, although biomass among the three FGs were not significantly different (RSE = 24800, $F_{2,24} = 0.383$, Adj R^2

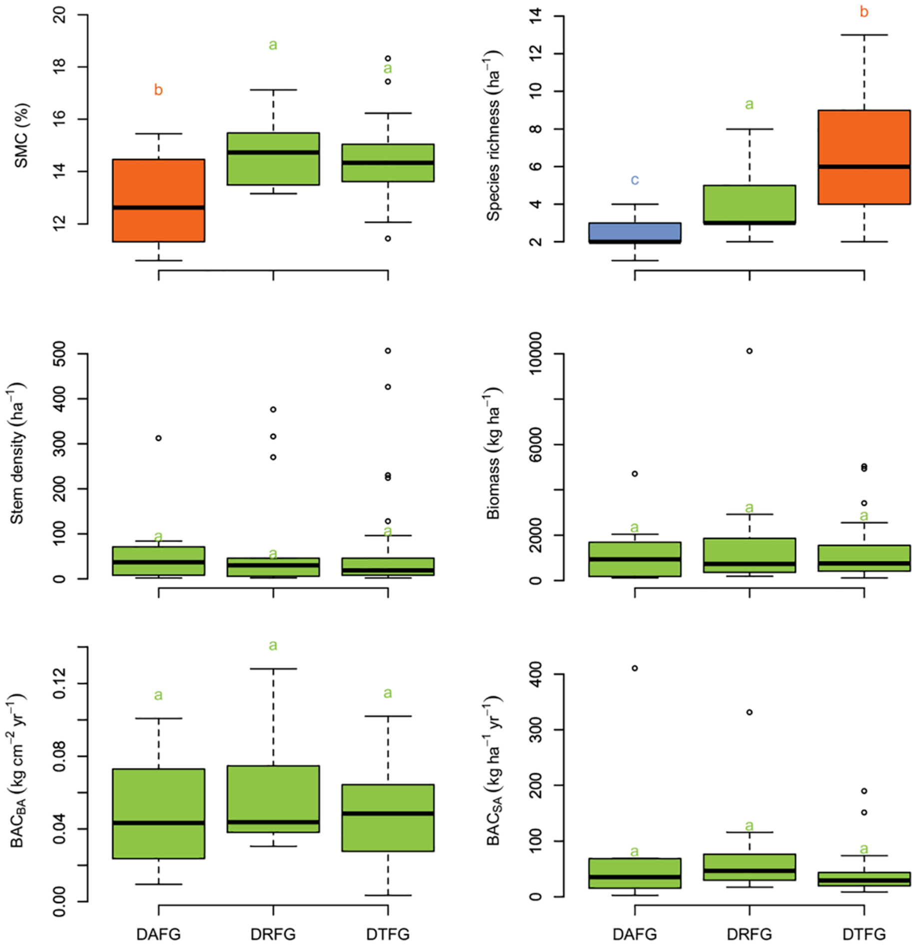

Fig. 3. Boxplot showing distribution of soil moisture content (SMC), species richness, stem density, aboveground tree biomass, biomass accumulation per unit stem basal area (BAC$_{BA}$), and biomass accumulation per unit stand area (BAC$_{SA}$), for tree species in the three functional guilds in tropical dry forest. DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild. Different letters and colours indicate significant differences (Tukey's HSD test, $P <$ 0.01) between functional guilds.

= -0.050, $P > 0.05$), the three FGs exhibited significant difference for the BAC$_{BA}$ (RSE = 0.023, $F_{2,24} = 7.781$, Adj $R^2 = 0.343$, $P < 0.01$) and BAC$_{SA}$ (RSE = 610.1, $F_{2,24} = 8.536$, Adj $R^2 = 0.367$, $P < 0.01$) (Fig. 5). The study site one (i.e., most moist site), exhibited highest average BAC$_{BA}$ (0.09 kg cm^{-2} yr^{-1}), as well as BAC$_{SA}$ (1.99 ton ha^{-1} yr^{-1}) for DAFG, as compared to the other two FGs. The site two registered significantly highest average biomass (14.1 ton ha^{-1}) (RSE = 2660, $F_{2,24} = 44.85$, Adj $R^2 = 0.771$, $P < 0.001$), as well as BAC$_{SA}$ (0.62 ton ha^{-1} yr^{-1}) (RSE = 140.0, $F_{2,24} = 17.72$, Adj $R^2 = 0.563$, $P < 0.001$) for the DTFG, whereas lowest for the DAFG (0.22 ton ha^{-1} yr^{-1}). Conversely, the BAC$_{BA}$ was accounted significantly highest (RSE = 0.012, $F_{2,24} = 31.50$, Adj $R^2 = 0.701$, $P < 0.001$) for the DAFG (0.09 kg cm^{-2} yr^{-1}), whereas the lowest value was recorded for the DTFG (0.05 kg cm^{-2} yr^{-1}). For study sites, three and four, significantly lowest tree biomass as well as BAC$_{SA}$ was observed for DAFG, whereas, the highest biomass and the BAC$_{SA}$ was recorded for DTFG (Fig. 5). Moreover, the three FGs did not exhibit any significant difference for BAC$_{BA}$ for study sites, three and four. For the study site five, which is the most dry site, we did not find significant difference among the three FGs for the tree biomass (DAFG, 4.0 ton ha^{-1}; DRFG, 4.2 ton ha^{-1}; DTFG, 5.5 ton ha^{-1}), BAC$_{BA}$ (DAFG, 0.03 kg cm^2 yr^{-1}; DRFG, 0.02 kg cm^2 yr^{-1}; DTFG, 0.02 kg cm^2 yr^{-1}), and the BAC$_{SA}$ (DAFG, 70.6 kg ha^{-1} yr^{-1}; DRFG, 57.9 kg ha^{-1} yr^{-1}; DTFG, 49.6 kg ha^{-1} yr^{-1}) (Fig. 5).

3.3.2.4. Influence of functional traits (FTs) on biomass accumulation capacity (BAC) of functional guilds (FGs). Table 4 summarizes the results of step-wise regressions relating FTs with BAC$_{BA}$ and BAC$_{SA}$ for the three FGs. We found that the BAC$_{BA}$ in DAFG was significantly influenced by Gs$_{max}$ and LA, and the model accounted for 60% variance in the BAC$_{BA}$. For DRFG, the significant impact on BAC$_{BA}$ was recorded for WSG and RWC, and the model accounted for 27% variance in the BAC$_{BA}$. For DTFG, we observed significant influence of SLA and A$_{max}$ on BAC$_{BA}$ (Table 4). The combined influence of SLA and A$_{max}$ registered 23% variance in the BAC$_{BA}$. For DAFG, we found that the FTs were explaining about 60% variance in the BAC$_{BA}$, whereas for DRFG and DAFG, <30% variance in BAC$_{BA}$ was explained by FTs. This suggests the importance of other environmental factors in modulating the growth of trees in our TDF region.

According to the step-wise regression result for DAFG, the maximum variance for BAC$_{SA}$ (57%) was explained by the model containing LPC, QWsat and RWC as predictors (Table 4). Interestingly, for DAFG, the FTs explaining maximum variance for the BAC$_{BA}$ were Gs$_{max}$ and LA, whereas for for DRFG, the highest variance in BAC$_{SA}$ (37%) was also accounted for LA and Gs$_{max}$ (Table 4). For the DTFG, the FTs explaining maximum variance in BAC$_{SA}$ were A$_{max}$, WSG, LA and SLA, and the model accounted for 49% variance in the BAC$_{SA}$. According to the above results, FTs were more efficient in predicting BAC$_{SA}$ as compared to the BAC$_{BA}$, for DRFG and DTFGs, however for DAFG we did not observe any significant difference (Table 4).

We also analyzed the community weighted mean of FTs for the BAC$_{SA}$ for the three FGs (Table 5). For DAFG, the step-wise regression generated model involving LPC, LDMC and QWsat, which explained 61% variance in the BAC$_{SA}$. For DRFG, the model exhibited only LA as the predictor variable, which explained 14% variance in the BAC$_{SA}$. While, for DTFG, the model showed SLA, LDMC, A$_{max}$, and WSG as the predictor variables, which exhibited 54% variance in the BAC$_{SA}$ (Table 5).

Although, the above results exhibited significant influence of FTs in explaining BAC for the three FGs, these FTs were able to account only

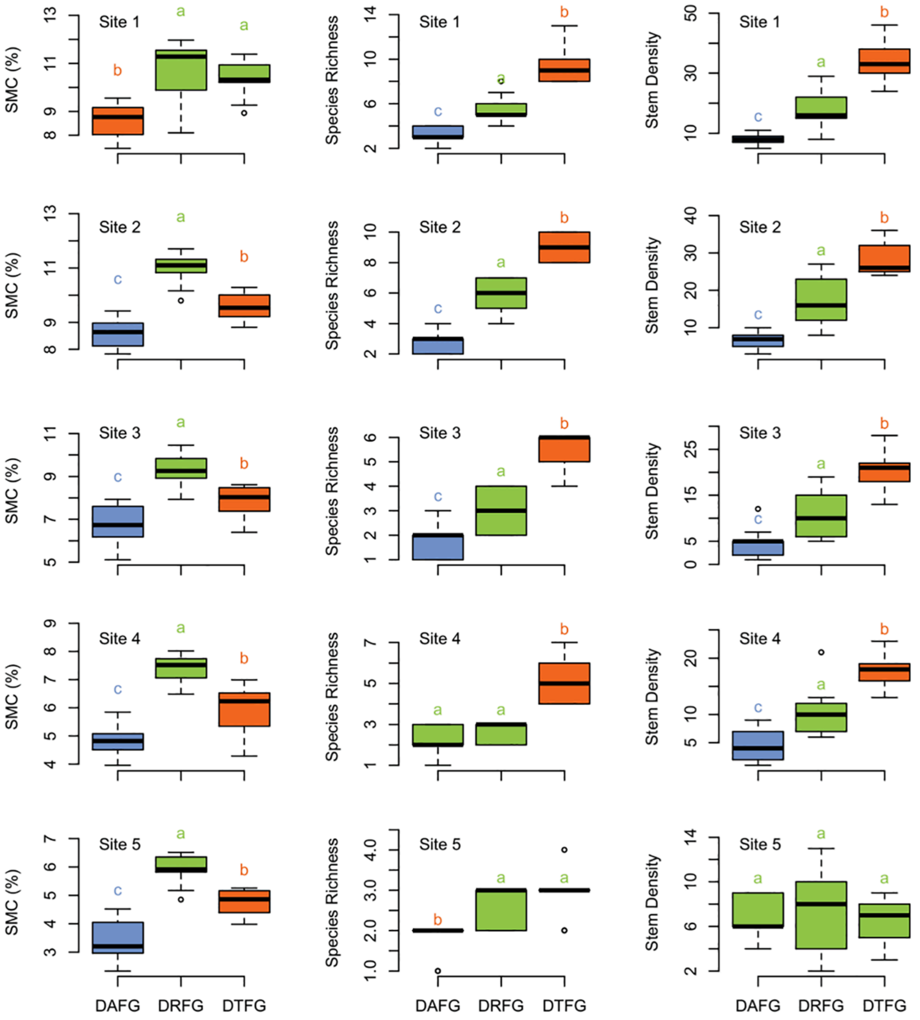

Fig. 4. Boxplot showing distribution of soil moisture content (SMC) under tree canopy, tree species richness, and stem density per hectare, for tree species in the three functional guilds across the five forest fragments in tropical dry forest. Sites 1 to 5 are in decreasing SMC gradient. DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild. Different letters and colours indicate significant differences (Tukey's HSD test, $P < 0.01$) between functional guilds. Since the between sites differences in SMC, species richness, and stem density are very high, we have shown different scales for Y-axis, for the five study sites.

upto 61% variance, which indicates that the impact of other environmental factors are also important in modulating BAC in TDFs. Therefore, along with community weighted mean of FTs, we also observed the accountability of soil physico-chemical properties for influencing BAC_{SA}, across 45 plots, in the forest fragments (Table 5). Interestingly, in this analysis the most accurate model exhibited LPC, LA, A_{max}, soil total N, and CC as the predictor variables, which explained 90% variance in BAC_{SA} in the forest region (Table 5).

4. Discussion

4.1. Functional traits (FTs)

The climatic data and soil properties showed that our study sites are subjected to extreme weather conditions, and contained nutrient poor soils, therefore the tree species exhibited substantial variations in their FTs, as survival strategy in extreme and harsh environment. Several studies have reported that the variations in FTs significantly influence species distributions (Roderick et al., 2000; Prior et al., 2003; Kraft and Ackerly, 2010; Messier et al., 2010), as well as ecosystem processes (Díaz et al., 2004; Suding et al., 2005). We observed significant between sites variations for CC, LDMC, LNC, LPC, Gs_{max}, A_{max}, and WUEi, while the between species differences were significant for WSG, SLA, RWC, LNC, LPC and A_{max}. We recorded greatest inter-specific as well as intra-specific variances across the species for LA, QWsat and SLA. We also observed that the species, which exhibited greatest intraspecific variance for LA, QWsat, and SLA, were quite abundant, and were recorded at all the five forest fragments, whereas the species showing least variation in LA, QWsat and SLA exhibited less abundance and were located at fewer sites (Table S1). Our findings have been supported by other studies, particularly involving LA and SLA, where they have reported lower plasticity in LA and SLA for more specialized species (Laurans et al., 2012), whereas greater intraspecific variations in LA and SLA for species exhibiting broader distribution across the plant communities (Sides et al., 2014). Consistent with our study, earlier investigations have also reported high variation of QWsat among tropical trees, and have shown strong link of QWsat with soil–plant water systems (e.g., Borchert, 1994). According to Borchert (1994), the evaporating water from mesophyll cells produces negative water potential giving rise to gradients for water conductance through soil–plant systems. Landsberg and Waring (2016), emphasized that the water potential gradients actually act as the driving force for movement of water through the system, which indicates that water status in plants is determined by the relations between rate of stomatal conductance and the rate of soil water uptake, and the movement of water through soil–plant systems. This proves that the stem hydraulic conductance substantially influences movement of water from soil to leaves and determines the maximum conductance under favourable conditions (i.e., during monsoon season), however under unfavourable condition (i.e., during hot dry pre monsoon season), it affects plant response to declining leaf water potential and increasing vapour pressure deficit.

The interspecific variability in FTs has been considered as the basis of species coexistence in the natural ecosystem (McGill et al., 2006; Weiher et al., 2011; Shipley et al., 2016), however, recent empirical studies have

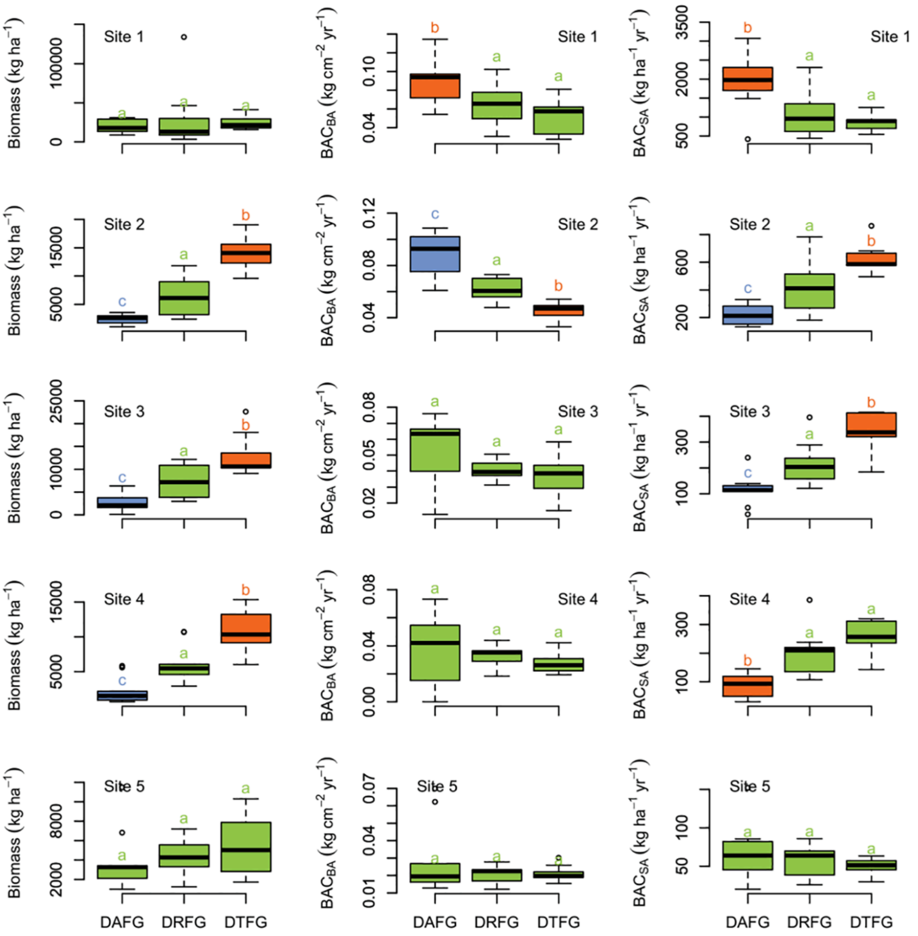

Fig. 5. Boxplot showing distribution of tree biomass per hectare, biomass accumulation per unit stem basal area (BAC$_{BA}$), and biomass accumulation per unit stand area (BAC$_{SA}$), for tree species in the three functional guilds, across the five forest fragments in tropical dry forest. Sites 1 to 5 are in decreasing soil moisture content (SMC) gradient. DAFG, drought avoiding functional guild; DRFG, drought resistant functional guild; DTFG, drought tolerant functional guild. Different letters and colours indicate significant differences (Tukey's HSD test, $P < 0.01$) between functional guilds. Since the between sites differences in biomass per hectare, BAC$_{BA}$, and BAC$_{SA}$ are very high, we have shown different scales for Y-axis, for the five study sites.

Table 4

Summary of step-wise regressions relating tree biomass accumulation per unit basal area (kg cm^{-2} yr^{-1}), and biomass accumulation per unit stand area (kg ha^{-1} yr^{-1}) for the three functional guilds, with tree canopy cover intensity (CC), wood traits and leaf traits. WSG, wood specific gravity; QWsat, saturated stem water content; LA, leaf size or leaf area; SLA, specific leaf area; RWC, relative water content; LPC, leaf phosphorus content; Gs$_{max}$, maximum saturated stomatal conductance; A$_{max}$, maximum saturated photosynthetic rate. For full list of models, see Table S7.

Group	ANOVA	Variable	Estimate	Std. Error	*t*-value	*P*
Biomass accumulation per unit stem basal area						
Drought avoiding	RSE = 0.033, df = 18, Adj. R^2 = 0.556, R^2 = 0.600, F = 13.501, P < 0.001, AIC = 32.86	Intercept	−0.008	0.021	−0.393	0.699
		Gs$_{max}$	0.308	0.068	4.533	0.000
		LA	−0.000	0.000	−2.625	0.017
Drought resistant	RSE = 0.032, df = 29, Adj. R^2 = 0.225, R^2 = 0.273, F = 5.641, P < 0.01, AIC = 78.21	Intercept	−0.070	0.096	−0.729	0.471
		WSG	−0.247	0.076	−3.260	0.003
		RWC	0.003	0.001	2.439	0.021
Drought tolerant	RSE = 0.056, df = 63, Adj. R^2 = 0.210, R^2 = 0.234, F = 9.615, P < 0.001, AIC = 80.18	Intercept	−0.095	0.035	−2.699	0.009
		SLA	0.000	0.000	2.739	0.008
		A$_{max}$	0.006	0.003	2.364	0.021
Biomass accumulation per unit stand area						
Drought avoiding	RSE = 12.82, df = 17, Adj. R^2 = 0.492, R^2 = 0.569, F = 7.468, P < 0.01, AIC = 37.38	Intercept	−7.813	3.447	−2.266	0.037
		LPC	15.23	4.661	3.268	0.005
		QWsat	−0.013	0.004	−3.474	0.003
		RWC	0.104	0.040	2.576	0.020
Drought resistant	RSE = 224905, df = 29, Adj. R^2 = 0.330, R^2 = 0.374, F = 8.649, P < 0.01, AIC = 66.28	Intercept	−308.8	120.0	−2.572	0.015
		LA	0.627	0.176	3.559	0.001
		Gs$_{max}$	708.2	259.7	2.727	0.011
Drought tolerant	RSE = 93446, df = 61, Adj. R^2 = 0.456, R^2 = 0.489, F = 14.60, P < 0.001, AIC = 42.18	Intercept	−389.4	68.58	−5.677	0.000
		A$_{max}$	21.10	3.938	5.358	0.000
		WSG	358.3	81.71	4.385	0.000
		LA	0.090	0.029	3.039	0.003
		SLA	0.266	0.266	−2.949	0.005

also highlighted the importance of intraspecific variability in traits for community trait assemblage at finer scales (Auger and Shipley, 2013; Siefert et al., 2015; Hausch et al., 2018; He et al., 2018). It has been reported that the high intraspecific trait variability increases the probability of a species to pass through environmental filters (Violle et al., 2012), whereas, the low trait variability exhibits high level of habitat

Table 5
Summary of step-wise regressions relating tree biomass accumulation per unit stand area (kg ha^{-1} yr^{-1}) for the three functional guilds, with community weighted mean of tree canopy cover intensity (CC), wood traits and leaf traits. For the general model for the tropical dry forest, the predictor variables also include soil physico-chemical properties, along with community weighted mean of tree canopy cover intensity (CC), wood traits and leaf traits. WSG, wood specific gravity; QWsat, saturated stem water content; LA, leaf size or leaf area; SLA, specific leaf area; RWC, relative water content; LDMC, leaf dry matter content; LPC, leaf phosphorus content; Gs$_{max}$, maximum saturated stomatal conductance; A$_{max}$, maximum saturated photosynthetic rate. For full list of models, see Table S8.

Group	ANOVA	Variable	Estimate	Std. Error	*t*-value	*P*
Drought avoiding	RSE = 11.47, df = 17, Adj. R^2 = 0.546, R^2 = 0.614, F = 9.010, P < 0.01, AIC = 31.51	Intercept	22.54	4.496	5.014	0.000
		LPC	3.995	0.848	4.709	0.000
		LDMC	−2.552	0.688	−3.708	0.002
		QWsat	−0.920	0.316	−2.914	0.010
Drought resistant	RSE = 310667, df = 30, Adj. R^2 = 0.106, R^2 = 0.135, F = 4.673, P < 0.05, AIC = 98.28	Intercept	−39.22	57.79	−0.679	0.503
		LA	21.44	9.919	2.162	0.039
Drought tolerant	RSE = 84595, df = 61, Adj. R^2 = 0.507, R^2 = 0.537, F = 17.72, P < 0.001, AIC = 39.64	Intercept	667.1	267.6	2.493	0.015
		SLA	14.91	34.19	0.436	0.664
		LDMC	−311.0	62.92	−4.942	0.000
		A$_{max}$	174.4	44.59	3.912	0.000
		WSG	143.9	56.07	2.567	0.013
Tropical dry forest	RSE = 8.643E7, df = 39, Adj. R^2 = 0.889, R^2 = 0.902, F = 71.744, P < 0.001, AIC = 12.85	Intercept	−1850.9	443.3	−4.175	0.000
		LPC	1168.5	179.5	6.509	0.000
		LA	−0.1500	0.034	−4.391	0.000
		A$_{max}$	−21.138	4.367	−4.841	0.000
		Soil total N	8742.6	3496	2.501	0.017
		CC	1.1780	0.557	2.116	0.041

specialization for the species, and provides relative fitness advantage within the selected habitat (Sultan, 2000; Caley and Munday, 2003). This suggests that the intra-specific trait variability can potentially exhibit the community response to environmental conditions. However, Jackson et al. (2013) argued that it is not necessary that the intra-specific trait variability, also contributes to the ecological processes in a particular habitat. According to Chacón-Madrigal et al. (2018), it is difficult to predict species distribution or range of spread on the basis of local variability of FTs. Their study on 17 congeneric pairs of one narrow site specific, and one widely distributed species, emphasized that the successive local adaptations during range expansion could be the reason for the greater trait variability in the widely distributed species. Therefore, the trait variability could be an effect, and not the cause of wider species distribution.

The tree canopy has been known to modify the micro-climatic conditions, particularly wind speed, relative humidity, incoming solar radiation, and terrestrial radiation (Frey et al., 2016; Davis et al., 2019). Therefore, the changing canopy structure has significant impact on the ecosystem processes at our study sites. We recorded significantly greater CC for the species present at the comparatively moist sites, compared to the comparatively dry sites. Leaf traits reflect the trade-off between resource acquisition and conservation in an ecosystem. Similarly, across the moisture and fertility gradient, we recorded significantly greater LNC, LPC, Gs$_{max}$, and A$_{max}$ for the species present at the comparatively moist and fertile sites, while LDMC and WUEi were higher for the species present at the comparatively dry and nutrient poor sites. Our findings are in conformity with several other studies across the globe, where LNC, LPC, SLA, and A$_{max}$ have been reported to increase, whereas, LDMC tends to decrease with increasing soil resources (Reich et al., 1999; Díaz et al., 2004; Wright et al., 2004; Vitousek et al., 2010). Species exhibiting high LDMC have been considered to be associated with the environment exhibiting low water availability, nutrient deficiency, and light limitation (Reich, 2014). Stomatal conductance has been reported to be influenced by leaf water potential, plant hormone concentration, light flux intensity, vapour pressure deficit, and SMC (Sperry et al., 2017). However, WUEi is mainly controlled by vapour pressure deficit, atmospheric CO_2 concentration, and SMC, while it is regulated by stomatal conductance (Tarin et al., 2020). According to Prentice et al. (2014) and Sperry et al. (2017), WUEi is determined by the magnitude of A$_{max}$ and Gs$_{max}$, which is governed by the dynamic co-ordination among the traits influencing A$_{max}$ and Gs$_{max}$, and the adjustment of these traits to environmental conditions. Guerrieri et al. (2019) emphasized that trees experiencing more xeric conditions reduce Gs$_{max}$ for minimizing water loss, while Gs$_{max}$ remains high for trees which do not experience water stress, leading to increase in A$_{max}$, which maintains high growth in moist habitats.

We did not find significant between sites differences across the tree species for WSG, QWsat, LA, SLA, and RWC; among these traits, between species differences were significant for WSG, SLA and RWC, whereas the differences were not significant for QWsat and LA. These observations suggest that the average values of these traits across species are not much different for the trees growing in a moisture gradient. The importance of these traits at the comparatively dry sites might relate to the strategy for success against drought stress (Chaturvedi et al., 2011a), while at the comparatively moist sites, these traits are important for providing competitive superiority (Kunstler et al., 2016). For instance, greater WSG at drier habitat is likely a strategy against drought (O`Brien et al., 2017), whereas at moister habitat, trees are generally taller and higher WSG is essential for supporting higher tension in the xylem vessels (Pratt et al., 2007). The tree species at drier habitats get a short favourable growth period of ample soil water availability, therefore these species need to have greater SLA and RWC for acquiring limited resources efficiently, in short time (Chaturvedi et al., 2011a). Whereas, greater SLA and RWC for the tree species at moister habitats is linked to better survival, recruitment, and productivity in the more competitive environment (Evans, 1989; van der Werf et al., 1993; Grime, 2001). Generally, SLA and WSG have been reported to be negatively correlated (Laughlin et al., 2017), however, in a shaded environment, plant may exhibit greater SLA, as well as higher WSG (Plavcová and Hacke, 2012; Russo and Kitajima, 2016).

Most of the FTs in our study exhibited significant variations across sites and species, while they were also significantly correlated across species, which suggests substantial coordination between these variables. According to Meinzer et al. (2008), the stem and leaf hydraulic conductance exhibit remarkable variations, however we have little knowledge about the set of FTs facilitating the dynamics of water relations in different species, which also determines their assemblage along a water availability gradient. Recently, in a long-term study to elucidate species response to extreme drought in a TDF located in Costa Rica, Powers et al. (2020) observed significant correlation of hydraulic traits with tree mortality, while other morphological or leaf traits did not show any significant influence. In our study, the between species differences of FTs, and their associations were not able to sufficiently predict the comprehensive response of tree species to variations in water availability, therefore we grouped species having similar characteristic features and observed their cumulative response.

4.2. Functional guilds (FGs)

4.2.1. Drought avoiding functional guild (DAFG) vs drought tolerant functional guild (DTFG)

Initially, on the basis of FTs, total tree species of the study region were separated into two FGs (viz., DAFG and DTFG), where majority of the species (83%) belonged to DTFG, as compared to the DAFG (17%). For this grouping, PCA axes exhibited stronger associations with QWsat, CC, LPC, Gs_{max}, and A_{max}, whereas the V-test indicated significant influence of WUEi, LDMC and LA for the DAFG, and Gs_{max}, A_{max}, LPC, RWC, LNC and SLA for the DTFG. Across the two FGs, significant differences were recorded for CC, QWsat, LA, SLA, Gs_{max}, A_{max}, and WUEi. The DTFG exhibited higher average CC (69%), compared to the DAFG (55%), which suggests that the species in DTFG were able to attain canopy or foliage for a longer time period as compared to the drought avoiding species. While, on the other hand, the DAFG showed significantly higher average values for QWsat (124%), LA (274 cm^2), and WUEi (47.0 $\mu mol\ mol^{-1}$), compared to that of DTFG (QWsat, 65.4%; LA, 182 cm^2; WUEi, 38.0 $\mu mol\ mol^{-1}$). For other traits, SLA (131 $cm^2\ g^{-1}$), Gs_{max} (0.39 $mol\ m^{-2}\ s^{-1}$), and A_{max} (14.6 $\mu mol\ m^{-2}\ s^{-1}$) were significantly greater for the DTFG, compared to the DAFG (SLA, 117 $cm^2\ g^{-1}$; Gs_{max}, 0.27 $mol\ m^{-2}\ s^{-1}$; A_{max}, 12.5 $\mu mol\ m^{-2}\ s^{-1}$). Similar to our observations, Feeley et al. (2011), and Fauset et al. (2012), also reported less dense wood with high QWsat for the drought avoiding trees, compared to the drought tolerant trees in tropical forests. The denser wood provides greater embolic resistance to drought tolerant species, compared to the drought avoiding trees which are susceptible to xylem embolism. Due to higher QWsat, the drought avoiding species maintain large reservoir of stored water, and highly conductive xylem, which quickly replaces water lost through transpiration, and reduces decline in leaf water potential (Borchert and Pockman, 2005). However, this leads to decline in conductance early in water stress, compared to drought tolerant species, which exhibit more anisohydric stomatal behavior, and maintain gas exchange even under drier conditions (Klein, 2014). For the drought avoiding trees, LA has been reported lower, and WUEi greater, as compared to the drought tolerant trees (Zhang et al., 2012). Reduction in LA is an important plant strategy for decreasing water loss through leaves (Markesteijn and Poorter, 2009). Delzon et al. (2004), and Gotsch et al. (2010), emphasized that the species growing at drier habitat invest more on the sapwood area, while less on LA and height, thereby lowering photosynthesis and reducing productivity, which is the strategy for minimizing water loss. This is commonly observed for drought avoiding trees growing at drought conditions, however in our study, the average LA for DAFG was greater compared to the DTFG. The greater LA observed in our study could be due to the presence of large compound leaves for most of the drought avoiding tree species (Table S9), although the size of leaflets was very small. For instance, LA for a compound leaf of *Boswellia serrata* was 494 cm^2, whereas the size of one leaflet was not >2.0 cm^2. Compared to simple leaves, compound leaves have been reported to allow better exchange of air over the leaf surface, which improves the efficiency of heat transfer at higher temperatures (Gurevitch, 1990). Also, besides having larger total area, compound leaves provide all advantages of small leaves, and lesser resources are required for the production and maintenance , compared to the simple leaves, therefore compound leaves are more suitable for the resource limited habitats (Xu et al., 2009).

Generally, SLA is associated with LA for capturing sun light per unit biomass, which is also linked with Gs_{max} and A_{max}. In contrast, we found significantly lower SLA, Gs_{max}, and A_{max} for the DAFG, which registered higher LA, compared to the DTFG. Consistent with our results, the empirical studies by Wright et al. (2007), and Xu et al. (2009) have emphasized that the relationships of LA with SLA vary for different species and community types. Xu et al. (2009) argued that the lower SLA for trees at water limited habitats could be due to highly lignified and thick leaf lamina, which is an adaptation for reducing water loss. For the DAFG, the strategy for minimizing water loss is also linked with reduction in Gs_{max}, A_{max}, as well as productivity, at the water limited habitats.

The lower CC for DAFG as compared to DTFG indicates that the drought avoiding species remain leafless for longer period, while the drought tolerant species exhibit longer leaf life-span. Similar to our study, the differences in leaf life span among differently deciduous woody species, reported in other studies, have been considered to be mainly controlled by hydraulic architecture (Borchert, 1994; Brodribb et al., 2002). Particularly, during the dry season, when soil water availability is low, the hydraulic architecture of drought tolerant trees allows them to withstand a higher xylem pressure gradient which is necessary to maintain the transport of water to the canopy leaves (Choat et al., 2005). We observed significantly positive correlation of CC with WSG, and significantly negative association with QWsat. This suggests that the drought tolerant species exhibiting higher CC have denser wood and lower stem water content, while denser wood is also related to the resistance to cavitation under conditions of drought (Chave et al., 2009), and therefore, drought tolerant species are highly efficient in transporting water to canopy leaves during the dry season (Markesteijn and Poorter, 2009). On the basis of our results, we can argue that the drought tolerant species in our study region are more efficient in water transport, which could be a probable reason for their greater abundance in the region, as compared to the drought avoiding species.

The results of our study indicated that the drought avoiding species in our study region exhibit greater QWsat, and WUEi. These features have been commonly observed for pioneer species, for instance, Nogueira et al. (2004) reported higher water potential and WUEi for pioneer species during Brazilian reforestation. The pioneer species are hydraulically more efficient and are able to comply the increased demand of water for photosynthesis during the favourable wet period, however their xylem vessels are less protected in drought period, and often experience cavitation (Markesteijn et al., 2011). Therefore, these species mainly follow resource gain or acquisitive strategy, which allows for short term high resource gain during the limited wet period, at the cost of long term of inactive phase during the long dry period (Markesteijn et al., 2011). This indicates that pioneer species also exhibit greater SLA and A_{max}, however, in our study, we observed significantly lower SLA and A_{max} for the drought avoiding species. Therefore, the drought avoiding trees in our study region with greater WUEi, and lower SLA and A_{max} are exhibiting FTs more like savanna trees, and resemble less with the FTs for forest trees (see Hoffmann et al., 2005).

In our study, the most abundant drought avoiding species, which were found at two or more forest fragments, were *Acacia catechu*, *Boswellia serrata*, *Madhuca latifolia* and *Lannea coromandelica*. Although, these trees species are highly deciduous, and commonly found in new colonizing vegetation, they also exhibit many other unique characteristics which are generally found in plants adapted to savanna vegetation. For instance, most of the drought avoiding species in in our study have been reported to prefer open canopy, dry habitats, where soils are sandy or rocky (Table S9). The tolerance to drought, frost and fire for the drought avoiding species have also been observed higher compared to the trees classified in other groups, although the drought avoiding trees classified in this study remain leaf less, and suspend their growth for greater part of the dry season (Chaturvedi et al., 2011a). In our earlier study (Chaturvedi, 2010), we have reported greater bark thickness, presence of epicormic buds, and greater resprouting capacity for these tree species, which emphasizes that these species are fire adapted. Mostly, the seed dispersal agents for the drought avoidant species are animals, which suggest that the browsing and grazing animals have an important role in their life cycle. Although, some species are highly browsed by domestic cattle and wild animals (e.g. *Acacia catechu* and *Desmodium oojeinense*), others have developed browsing resistant traits, such as thorns (*Ceriscoides turgida*), and resins or alkaloids (*Lannea coromandelica* and *Nyctanthes arbor-tristis*).

4.2.1.1. Drought resistant functional guild (DRFG) vs drought tolerant functional guild (DTFG). We classified the 39 drought tolerant tree species, from the first classification, again into two groups, i.e., DRFG and DTFG, for better understanding of the drought tolerance strategies for these tree species in our study region. We observed the dominance of DRFG and DTFG, in terms of species richness and stem density, and found that these FGs are more abundant at our study sites, as compared to the DAFG. The average SMC for the tree species in DRFG and DTFG were significantly greater compared to the SMC for drought avoiding species, which indicates that, the drought resistant and drought tolerant species preferred moist habitats in the forest region. The two FGs significantly differed for CC, QWsat, SLA, LDMC, LNC, LPC, Gs_{max}, and A_{max}. The average QWsat, SLA, LNC, LPC, Gs_{max}, and A_{max} were greater for DRFG, whereas, CC and LDMC were higher for the DTFG. Even, when compared among the three FGs, the DRFG exhibited highest average SLA, LNC, LPC, Gs_{max}, and A_{max}, whereas the DTFG showed highest CC, compared to the other two FGs. Most of the tree species in DRFG and DTFG have simple leaves, and they mostly prefer fertile and moist habitats (Table S9). The resistance for drought, frost and fire has also been reported lower for DRFG and DTFG. This indicates that most of the trees in DRFG and DTFG, do not have sufficient adaptive strategies of savanna vegetation. However, both FGs exhibit sufficient characteristics of TDFs. The DRFG in our study exhibited greater QWsat, SLA, LNC, LPC, Gs_{max}, and A_{max}, therefore these species are more efficient to act as pioneer species in the TDF. According to Lo Gullo and Salleo (1988), the drought resistant species adopt the 'water spending' strategy for avoiding water stress. These species undergo rapid changes in water potential, and extract water from soil rapidly for compensating the water loss. Among the tree species in DRFG, for instance, *Holarrhena antidysenterica* and *Terminalia tomentosa* are well known pioneer species, and occur abundantly in our study region. Moreover, these two species have also been reported as the highly productive tree species of the study region (Chaturvedi, 2010). Another species, *Pterocarpus marsupium*, although, a moderate light demander can also be used for revegetating degraded land and for improving soil (Troup, 1921).

We found a trade-off between drought avoidance/resistance and drought tolerance strategies, where the DTFG exhibited significantly greater CC, compared to the other two FGs. The DTFG in our study also exhibited significantly higher LDMC, as compared to DRFG. The higher LDMC provides higher mechanical strength to leaves in hot sunny environment, and makes them resistant against herbivory and wind (Pérez-Harguindeguy et al., 2013). For DTFG, higher LDMC indicates that the leaves of these species contain tough and persistent tissues, which allow them to function longer, even during the water limited conditions. The DTFG in our study, generally prefer moist and fertile soil, and occur with many companion species growing together. Therefore, these species experience more competition for light and resources, as compared to trees in other two FGs. Earlier studies (e.g., Smith and Huston, 1989; Niinemets and Valladares, 2006) have reported a trade-off between the ability of species to tolerate shade and drought, where the drought tolerant species invest more on roots for capturing belowground water, while the shade tolerant species invest more on leaves for capturing light. Consistent with these reports, we also observed greater CC and LA for the trees in DTFG, compared to other two FGs. In fact, the tree species exhibiting greatest LA (i.e., *Tectona grandis*) also belonged to the DTFG. As discussed earlier, the physiological drought tolerance during low water conditions is based on the physiological traits associated with resistance to xylem embolism, such as WSG (Markesteijn and Poorter, 2009). According to Woodcock (2000), WSG of trees in old-growth forests is greater than the newly vegetated forests. Although, higher WSG provides greater mechanical strength and supports large sized trees with wider crowns, it minimizes maintenance respiration by reducing trunk surface area, compared to trees with lower WSG (Fournier et al., 2013). In our study, the DTFG exhibited higher WSG, compared to trees in other two FGs, in fact, DTFG also contained *Hardwickia binata*, which registers highest WSG among all trees of the Indian sub-continent (Troup, 1921). Some other species showing greater WSG in the DTFG include *Albizia odoratissima*, *Dalbergia latifolia*, *Shorea robusta*, and *Tectona grandis*. These trees can attain height upto 30 m, and are among the most important timber species of the TDF (Troup, 1921).

4.2.1.2. Structure of functional guilds (FGs) in the study region. Across the five study sites, we did not find significant differences between FGs for stem density, and aboveground biomass, however we observed large interspecific variations, for both these parameters in each FG. Moreover, when we evaluated species richness, stem density, and aboveground biomass, separately for the five study sites, the differences were significant for most of the study sites, except for the most dry site. Also, we observed considerable decline in species richness, stem density, and biomass for DRFG and DTFG, while moving from moist to dry study sites. It was interesting to note that, while moving towards drier sites, although, there was decline in species richness, stem density, and biomass for DRFG and DTFG, these vegetation parameters were still higher for DRFG and DTFG compared to the DAFG, even at the most dry site. In another related study, Bartlett et al. (2019) evaluated the shift in plant hydraulic strategies along a spectrum from drought avoidance strategy to drought tolerance strategy, and reported that the drought induced shift increased the competitive ability of the drought tolerant strategy as compared to the drought avoiding strategy. Therefore, the drought resistant and drought tolerant trees in our study are competitively more adapted to the habitat conditions, exhibiting their dominance at the most competitive environment, i.e., at the most moist site, as well as, at the most dry site.

Our study showed remarkable variations in the composition of FGs across the five study sites in a SMC gradient. In terms of species richness and stem density, DAFG was significantly low towards the moist sites, whereas, while moving towards the drier sites, the DRFG and DTFG exhibited considerable decline in their species richness and stem density, resulting into increment in the composition of DAFG, although the DAFG did not show any significant decline in species richness and stem density, while moving from the moist sites towards the relatively dry sites. These changes in the composition of FGs could have remarkable impact on the functioning of ecosystems. Murphy and Lugo (1986) reported dominance of drought avoiding species in the most dry forests, while Fauset et al. (2012), and Clark et al. (2016) emphasized increasing relative abundance of drought avoiding species with declining SMC in several forests. Bartlett et al. (2019) also suggested that the shift in the continuum from drought avoiding to drought tolerant strategies could significantly influence the functioning of ecosystems, and could show considerable impact on biomass carbon accumulation, gas exchange and hydrology of the habitat.

4.2.1.3. Biomass accumulation capacity (BAC) of functional guilds (FGs) in the study region. Across the five study sites, generally we found significantly greater biomass for DRFG and DTFG, as compared to the DAFG, except for the most moist and the most dry site. The influence of higher biomass for the DRFG and DTFG, is also clearly visible in their BAC, where the BAC_{SA} of DRFG and DTFG showed significantly greater values, compared to the DAFG. Our results are supported by an earlier study by Prado-Junior et al. (2016) in TDFs of Brazil. Their study showed that the initial stand biomass is the most important predictor of biomass recruitment, growth and mortality. They also emphasized that the high growth and BAC in Brazilian dry forest is associated with the dominance of drought tolerant or conservative species, which exhibit high WSG which enables these species to function even during the drought period.

Surprisingly, for our most moist site, although the biomass for the three FGs was not significantly different, the BAC for the DAFG was significantly highest. This discrepancy in biomass and BAC could be justified by the presence of large sized drought avoiding trees at the moist sites, which increased their biomass proportion, and thus, the BAC, as well. Our justification could be supported by several other studies which suggested that the species with low tissue construction cost will exhibit greater BAC, in favourable physical environment (Muller-Landau, 2004; Poorter et al., 2008; Chave et al., 2009; Paine et al., 2015). Moreover, according to Poorter et al. (2009), when the drought avoiding plants are fully exposed to sunlight, and they have same access to water as other co-occurring species, the drought avoiding species increase their competitive ability and grow faster.

The 'plant economic spectrum' (Reich, 2014) hypothesis predicts that leaf and wood traits (including root traits) are related to resource acquisition and transport, and exhibit correlation across all vascular plant species (Markesteijn et al., 2011; Reich et al., 2008). The leaf and wood traits reflect the tissue construction cost in the form of leaf size and wood volume, and therefore, show strong association with growth and BAC (Reich et al., 1998; Westoby et al., 2002; Chave et al., 2009; Gibert et al., 2016). However, recently, various empirical studies have reported that the correlations between FTs and growth are not always consistent (Wright et al., 2010; Paine et al., 2015; Gibert et al., 2016). In our study we observed significant impact of FTs on BAC of TDF trees categorized in the three FGs.

We observed that the variance in BAC_{BA} for the DAFG was majorly explained by Gs_{max} and LA. These traits are involved in the most important drought survival strategy for the drought avoiding species, i.e., stomatal closure and leaf shedding. Trees in this FG minimize water loss, also by reducing leaf surface area. Regarding the BAC_{SA}, the model selected LPC, QWsat and RWC as the more significant predictor variables, for DAFG. Studies have shown that these traits have strong link with habitat conditions, as plants derive phosphorus mainly from weathering of primary minerals (Belnap, 2011), while stem and leaf water potential have been observed to be strongly affected by soil water availability, as well as climatic conditions (Suter et al., 2019). For DRFG, we observed that the predictor FTs explaining maximum variance for BAC_{BA} were WSG and RWC, while LA and Gs_{max} were accounting major variance for BAC_{SA}. For DTFG, the predictor FTs for explaining greater variance for BAC_{BA} were SLA and A_{max}, while for accounting maximum variance for BAC_{SA}, important FTs were A_{max}, WSG, LA and SLA. For these two FGs, we observe much similarity in the set of traits for explaining variance in the BAC_{BA} and BAC_{SA}.which suggests that the strategies for biomass accumulation for trees in both FGs are very similar. Generally, the trees in these two FGs are found to occur together as companion species (Troup, 1921), and compete for the same resources. However, the most striking difference between the two FGs is the presence of RWC and Gs_{max} in the models for DRFG, which indicates that the drought resistant trees maintain higher leaf water potential, and show greater stomatal control, compared to the drought tolerant trees. Since, DRFG exhibit lower CC, compared to DTFG, they need use these FTs as a strategy for increasing photosynthesis during the limited favourable conditions. Moreover, among the three FGs, significantly highest SLA, LNC, LPC, Gs_{max} and A_{max} for DRFG, clearly shows their acquisitive resource use strategy, while significantly greatest CC for DTFG emphasize their conservative resource use strategy.

The community weighted mean traits value has been considered to better reflect the local optimum trait strategy in response to habitat conditions (Wright et al., 2004; Sonnier et al., 2010). When we analysed the influence of community weighted mean of FTs on BAC_{SA}, the results were much similar, as we found for the absolute values of FTs. However, inclusion of LDMC as an additional trait explaining variance in BAC_{SA} for DAFG and DTFG increased the predictive power of the model. Moreover, LDMC was not significantly influencing BAC_{SA} for DRFG. LDMC provides mechanical strength to leaves, and protects leaves from wind and herbivores. Greater LDMC is also associated with water limited, light limited, and nutrient limited environment. We observed higher LDMC for DAFG as well as DTFG, as compared to DRFG. The greater LDMC for the DAFG could be an adaptation against water stress, nutrient limitation, and herbivory, whereas higher LDMC for the DTFG might be an adaptation for supporting large leaves in the light limited environment, and also for increasing leaf life-span.

Through step-wise regression analyses, we found that the maximum percentage of variance in BAC_{SA}, explained, only by FTs was 61% for DAFG, 37% for DRFG, and 54% for DTFG. Further, when we added soil physico-chemical properties, also as predictor variables, together with FTs, we found that the proportion of variance in the model increased to 90%. This indicates that the soil properties play an important role in the productivity of TDFs. The most significant variables in the final model were LPC, LA, A_{max}, total soil N, and CC. Among these variables, LPC alone explained 69% variance in the BAC_{SA}, while all variables together explained 90% variance in the final model. The presence of soil N and LPC in the final model suggests the significance of N and P in the TDF productivity. Several previous studies (e.g., Bejarano-Castillo et al., 2015; Campo, 2016) have also indicated the importance of N and P in tropical forests productivity and nutrient cycling. They also emphasized that in near future, these soil elements could become more limited, although, still we have little knowledge about the controlling mechanisms of N and P on the productivity of TDFs.

5. Conclusions

We reported that the tree species experiencing drought conditions, maintained their physiological functions by three strategies, i.e., drought avoidance, drought resistance, and drought tolerance. We found that the drought avoiding species tend to avoid drought period by shedding their leaves at the start of dry period, while drought tolerant as well as drought resistant species had ability to tolerate water stress to greater extent, and they are able to sustain foliage for longer period. The tree species in our study region appear to be arranged on a continuum between the two strategies of resource exploitation (viz., acquisitive and conservative strategies), which also explains the continuous variation in FTs across the study sites in a gradient of soil moisture stress. Our study showed the dominance of DTFG in the study region in terms of greater species richness, stand biomass, as well as BAC. The important FTs for greater productivity and storage of biomass for DTFG were A_{max}, WSG, LA and SLA, whereas LDMC was responsible for greater LA and CC for DTFG. Along with FTs, we found significant contribution of N and P for the BAC of TDF trees in our study region, however, still we have limited information about the dynamic interactions between environmental factors and tree physiological attributes modulating species distribution and BAC in TDF ecosystems.

CRediT authorship contribution statement

R.K. Chaturvedi: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Anshuman Tripathi:** Conceptualization, Validation, Investigation, Data curation, Writing - original draft. **A.S. Raghubanshi:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition. **J.S. Singh:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

None.

Acknowledgements

R.K.C. thanks Council of Scientific and Industrial Research, India (award no. 09/13(452)/2012–EMR–I) and National Natural Science Foundation of China (NSFC), Chinese Academy of Science, China (award No. 31750110466) for financial support. Authors thank the two anonymous reviewers for their constructive comments for improving the standard of manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118740.

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