

Analysis of Functional Leaf Trait Variation among the Dominant Understorey Species in the Pine Forest of Morni Hills, Panchkula, Haryana

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ABSTRACT

The functional diversity is an essential concept in the field of ecology. It refers to the relative abundance, range, and value of the functional traits present in a given community or ecosystem. Plant functional traits (leaf traits, stem traits, root traits, etc.) create a link between an ecosystem processes and plant physiology and thus offer a powerful means to study the global change on vegetation dynamics and ecosystem processes. When plant species grown in different environments, their physiological and functional traits get modified due to changes in site-specific conditions. In the present study, leaf functional traits (leaf size-LS, specific leaf area-SLA, leaf dry matter content-LDMC, leaf nitrogen content-LNC, leaf phosphorus content-LPC and leaf nitrogen to phosphorus ratio-N:P) of twelve dominant understorey species (6 shrubs and 6 herbs) were examined in the Pine forest of Morni Hills range of lower Shivaliks, Haryana, India. During the study, the maximum value of leaf size was obtained for *Murraya koenigii* and *Cynoglossum zeylanicum*, while the maximum value of LDMC was obtained for *Toxicodendron parviflorum* and *Dicliptera chinensis* among shrubs and herbs respectively. Other than this, highest value of SLA, LPC and LNC were calculated for *Parthenium hysterophorus* among shrubs and *Oxalis corniculata* among herbs. The calculated values were also found to be significantly correlated among the selected plant species. The SLA was found to be negatively correlated with, LDMC and LPC whereas positively correlated with LNC and N:P. The present study represents a step forward in the direction of functional ecology performed in the forest ecosystems of Haryana. This study is essential for predicting the patterns of community assembly as well as for describing species contributions to ecosystem processes.

Keywords: Functional diversity, Functional ecology, Vegetation dynamics, Plant functional traits, Leaf functional traits

Introduction

A group of plants irrespective of their phylogeny when found to show similarity in a given set of traits as well as their responses to environmental factors and/or their roles in ecosystems are basically said to belong to a plant functional type. On the other hand, a functional trait is defined as “the characteristic of an organism that is considered relevant to its response to the environment and/or its effects on ecosystem functioning” [1]. In contrast, Reich *et al.* [2] defined a functional trait as “any trait which impacts fitness indirectly via its effects on growth, reproduction,

and survival”. Other than this, Violle *et al.* [3] defined a trait as “any morphological, physiological or phenological feature measurable at the individual level, from cell to the whole organism level, without reference to the environment or any other level of organization”.

Plant functional traits can also be grouped as whole-plant traits (e.g., growth form, plant height), leaf traits (e.g., LS, SLA, LDMC), stem and belowground traits (e.g., bark thickness, specific root length) or regenerative traits (e.g., dispersal mode, seed mass) in terms of their useful-

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ness in a particular methodology [4]. Of these, Leaf functional trait analysis is seen to be a useful tool in the area of plant ecology as it plays a significant role in models associated with ecosystem-level processes, species co-existence, plant growth, and plasticity [5]. Leaf traits are considered quite promising to analyze the success of plant establishment and performance in the ecosystem as they are closely associated with the survival and growth of the plant [6]. As well as, their understanding can be helpful to the ecologists in predicting patterns of community assembly [7, 8] and for describing the contribution of various plant species to the ecosystem processes [3, 9]. It is also presumed that higher elevations are more stressful for plants which are primarily caused by low air temperature, the low partial pressure of CO₂, and high UV radiation, inclusive of thin soils and low nutrient availability [10].

A little attention has been conferred to the functional trait study of plants growing in forests of Haryana, India. And no such study has been reported from the Morni Hills range of Panchkula district, Haryana. In the present study, six leaf traits i.e., Leaf Size (LS), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf phosphorus content (LPC), Leaf nitrogen content (LNC) and Ratio of leaf nitrogen and phosphorus content (N:P) of 12 dominant understorey species

(6 shrubs and 6 herbs) of the Pine forest are measured to understand the functional diversity of the area.

Material and Methods

Study site

Haryana is primarily an agrarian state and comprises only 0.22% of the total forest cover of the country by occupying an area of 1602 sq. kms under forests. In Haryana, 80% of the geographical area is under agriculture and only 3.62% of the geographical area is covered by forests [11]. Morni hills lie in the North-eastern region of Haryana and are the only hills with dense forest cover in the state, hence very significant for the study.

The study site was selected as the Pine forest at an altitude of more than 1000m above mean sea level from 30°39'N to 30°45' N and 77°2'E to 77°10' E in Morni hills (Figure 1). The mean monthly temperature and rainfall varied from 15-38°C and 2.2-429.9mm respectively, as shown in Figure 2. Morni hills represent tertiary formations of Shivalik Hills [12] and form a part of the active Sub-Himalayan belt that falls in the Panchkula District, Haryana. The hills of this area are mainly composed of sandy facies and also possess an interbedded sequence of medium to coarse-grained sandstone as well as fine-grained shales.

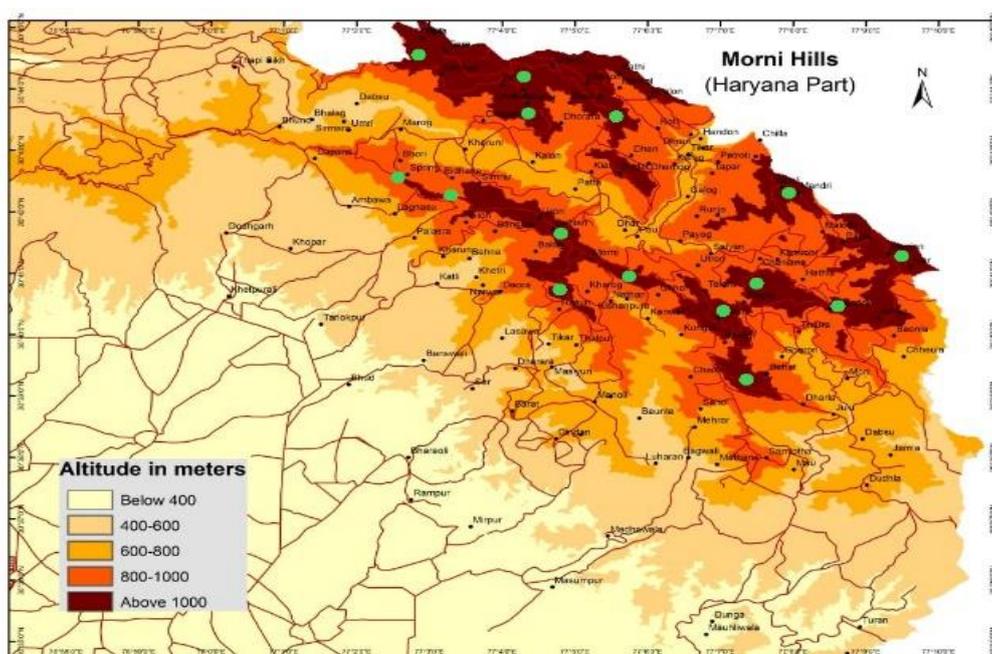


Figure 1. Map showing the location of plots studied in the Pine forest of Morni Hills, Haryana (Marked in green dots).

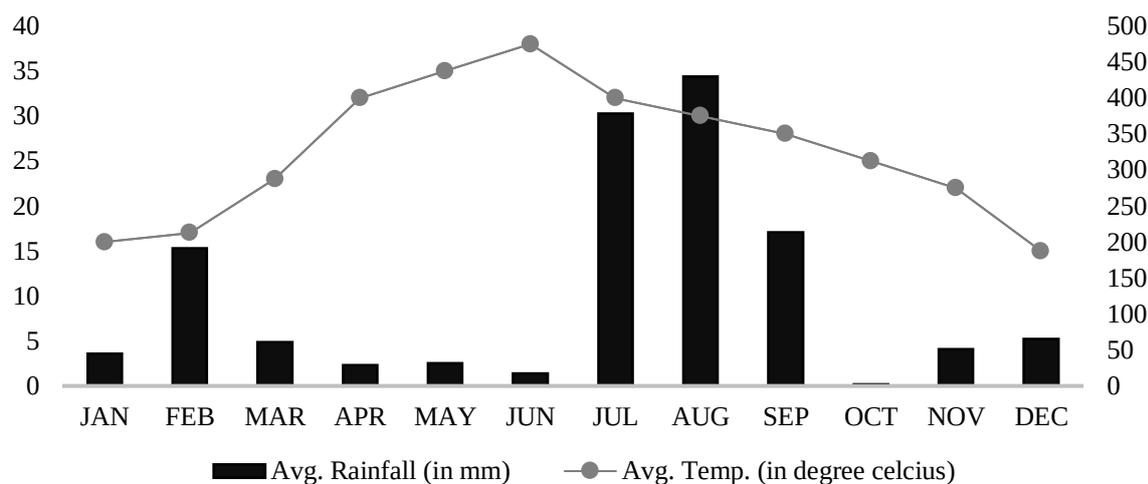


Figure 2. Climograph of the year 2019 showing monthly average temperature and rainfall of Morni Hills (Source: www.worldweatheronline.com).

Plant sampling and leaf trait analysis

The data was collected in the months of March, 2019 and October, 2019 (before monsoon and after monsoon of the year). A total of 15 plots were selected randomly in the pine forest (Figure 1) and the leaf samples were collected from each plot from the selected plant species. Fully expanded leaves without any symptoms of herbivore or pathogen attacks were taken from the adult plants. Five leaves from each plant species of shrubs and herbs were collected from each plot from the study area. Leaves were carried in sealed plastic bags to the laboratory so that they remain turgid until the measurement of leaf traits.

The fresh weight (FW) of leaves was taken and the leaf size (LS) was calculated with the help of Systronics Leaf Area Meter 211. Then, leaves were placed in the oven at 60 °C for 48 h before the measurement of leaf dry weight (DW). The SLA was calculated as the ratio of LS (mm^2)/DW (mg) and LDMC was calculated as the ratio of DW (mg)/FW (mg). For the estimation of LPC, Phosphovando molybdo yellow color method was used. While LNC was determined with the help of Kel-plus nitrogen analyzer using Kjeldal method.

Results and Discussions

Interspecific trait comparisons may have numerous possible outcomes. The plants having similar habit (maybe shrub or herb etc.) and living in the vicinity of each other may exhibit a very different set of traits. In the present study, 6 leaf traits (LS, SLA, LDMC, LNC, LPC, and

N:P) were calculated for 12 different understorey species. The selected species had significant variation in their leaf trait values (Table 1). Of which, the maximum value of LS was obtained by *Murraya koenigii* (3862.4mm^2) among shrubs and *Cynoglossum zeylanicum* (4443.1mm^2) among herbs. Leaf Size refers to the leaf foliar area exposed for photosynthesis. On the other hand, the minimum value of SLA was found to be obtained by *Toxicodendron parviflorum* ($8.56\text{mm}^2/\text{mg}$) among shrubs and *Chromolaena odorata* ($18.88\text{mm}^2/\text{mg}$) among herbs while the maximum value of SLA was observed for *Parthenium hysterophorus* ($16.82\text{mm}^2/\text{mg}$) and *Oxalis corniculata* ($37.64\text{mm}^2/\text{mg}$) among shrubs and herbs respectively.

In case of LDMC, the maximum value was calculated for *T. parviflorum* ($467.4\text{mg}/\text{g}$) among shrub species and *Dicliptera chinensis* ($347.8\text{mg}/\text{g}$) among herb species. LDMC is seen to be an indicator of plants' resource use strategy i.e., it is placed between two functional extremes in the fundamental trade-off, one is rapid assimilation and growth and the other is resourceful conservation of resources within well-protected tissues. Other than this, the highest value of LPC and LNC was recorded for *P. hysterophorus* (LPC- $2.57\text{mg}/\text{g}$, LNC- $44.13\text{mg}/\text{g}$) and *O. corniculata* (LPC- $1.79\text{mg}/\text{g}$, LNC- $54.72\text{mg}/\text{g}$) followed by others among shrubs and herbs respectively. The high leaf concentrations of N and P are highly linked with the capacity of plants for rapid growth under productive conditions and an ability to sustain yield under a limiting supply of

Table 1. Functional leaf traits of the Dominant understorey species (Shrubs and Herbs) in the Pine forest of Morni Hills, Panchkula

S. N.	Botanical name of the plants (Local name)	Name of the family	LS (mm ²)	SLA (mm ² /mg)	LDMC (mg/g)	LPC (mg/g)	LNC (mg/g)	N:P
SHRUBS								
1	<i>Carissa spinarum</i> (Jungli karonda)	Apocynaceae	447.2	8.95	414.00	1.95	21.77	11.16
2	<i>Coolebrookea oppositifolia</i> (Pansra)	Lamiaceae	3130.7	13.39	409.3	2.05	24.54	11.97
3	<i>Lantana camara</i> (Lantana)	Verbenaceae	1761.2	15.05	324.6	2.46	39.92	16.22
4	<i>Murraya koenigii</i> (Kari patta)	Rutaceae	3862.4	14.67	376.3	2.18	28.75	13.18
5	<i>Parthenium hysterophorus</i> (Gajar ghas)	Asteraceae	2119.5	16.82	225.7	2.57	44.13	17.17
6	<i>Toxicodendron parviflorum</i> (Murti)	Anacardiaceae	3332.4	8.56	467.4	1.82	19.52	10.72
HERBS								
1	<i>Bidens pilosa</i> (Kumra)	Asteraceae	718.3	28.69	189.5	1.65	42.73	25.89
2	<i>Chromolaena odorata</i> (Tivra gandha)	Asteraceae	2266.4	18.88	221.3	1.51	38.15	25.26
3	<i>Cynodon dactylon</i> (Doob)	Poaceae	52.12	17.37	233.33	1.45	36.28	25.02
4	<i>Cynoglossum zeylanicum</i> (Andhauli)	Boraginaceae	4443.1	15.04	295.1	1.42	32.21	22.68
5	<i>Dicliptera chinensis</i> (NA)	Acanthaceae	545.5	12.41	347.8	1.35	30.14	22.32
6	<i>Oxalis corniculata</i> (Khatti booti)	Oxalidaceae	380.9	37.64	150.6	1.79	54.72	36.15

Abbreviations: LS- Leaf Size, SLA-Specific Leaf Area, LDMC-Leaf Dry Matter Content, LPC- Leaf Phosphorus content, LNC- Leaf Nitrogen Content, N:P- Ratio of leaf nitrogen and phosphorus content, NA- Not Available.

nutrients. The value of N:P ranged from 10.72 to 36.15 for all of the species taken under study. The results of the present study clearly indicated the differences in the leaf trait values of the given plant species significantly.

The Pearson correlation was also analyzed for the six leaf traits calculated during the study and a histogram was prepared using R Studio (Figure 3). It showed that that LS was found to be positively correlated with two traits i.e., LDMC ($r = 0.44$) and LPC ($r = 0.21$) while negatively correlated with the other three traits i.e., SLA ($r = -$

0.39), LNC ($r = -0.41$) and N : P ($r = -0.43$). Other than this, SLA was found to be negatively correlated with LS ($r = -0.39$), LDMC ($r = -0.84$) and LPC (-0.12) while positively correlated with LNC ($r = 0.87$) and N:P ($r = 0.86$). LPC and LNC were seen to be correlated, very weakly but positively ($r = 0.086$).

Plant traits assessment is a promising approach that can overcome the limitations of the taxonomic approach [13]. Because unlike plant species that differ along with geographic location, the plant traits are universal in nature. Thus,

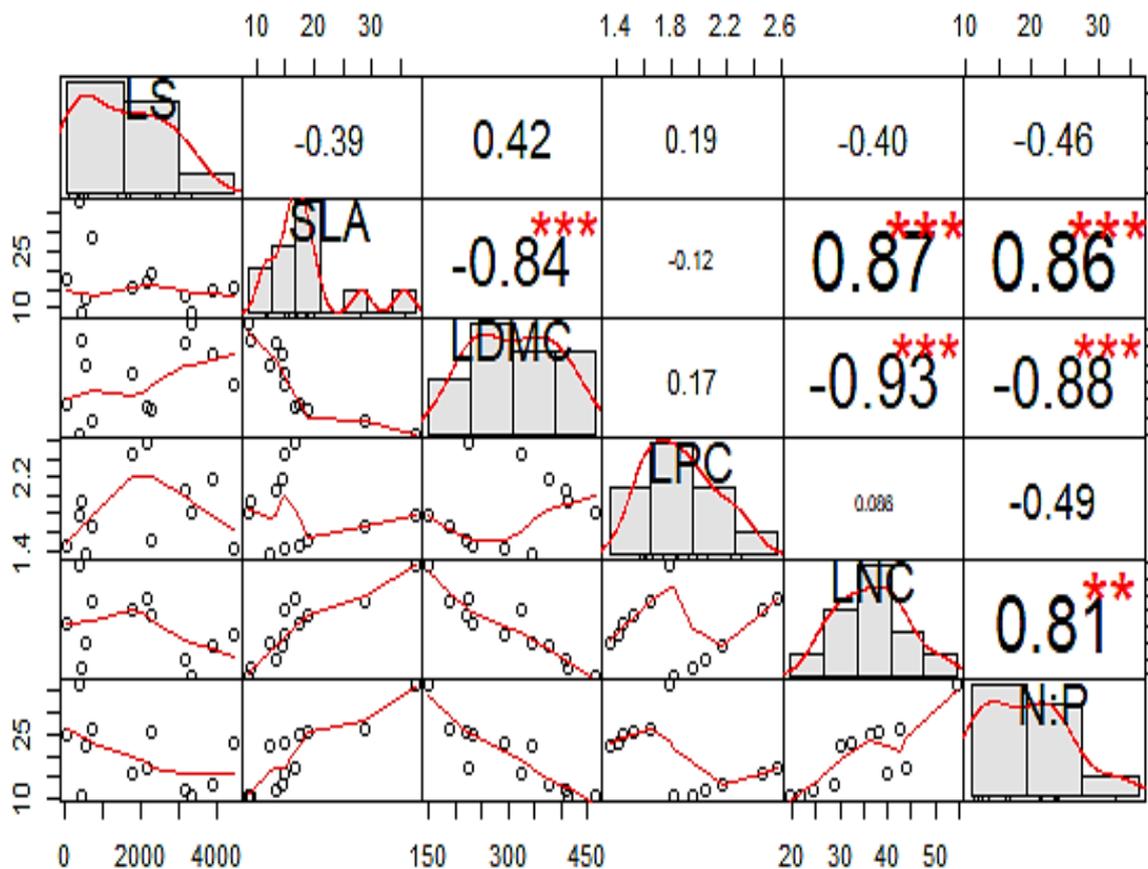


Figure 3. Relationship between the leaf traits of understorey species in the pine forest of Morni Hills, Panchkula, Haryana.

*Correlation is significant at 0.05 level.

**Correlation is significant at 0.01 level.

***Correlation is significant at 0.001 level.

the study of leaf trait variability could be helpful in predicting the effects of management and restoration studies on local as well as global scale. As the functional trait approach can be helpful in developing models showing the relationship among traits and species responses to management and restoration activities. Some studies have already investigated the use of functional plant traits in restoring and managing ecosystems [14, 15, 16, 17]. The leaf trait attributes calculated during the present study were found to be significantly correlated with each other. Our findings are also supported by the observations of Wright *et al.* [18] who reported a positive correlation of SLA with LNC and negative correlation with LDMC as well as by Salazar [19] and Bolom-Ton [20] who also found the same type of trend during their study. Other than this in the present study, SLA of understorey species was seen to be weakly but negatively correlated with

LPC, this type of correlation was recorded by Santiago and Wright [21].

The low SLA has been recommended to make a plant more efficient in its use of water by reducing water loss via leaf size other than stomata. The low value of SLA also likely to assist the plant to mitigate cell damage and thus resist wilting. Hence, we can say that plant species with lower SLA viz. *T. parviflorum* and *Carissa spinarum* among shrubs species, whereas *D. chinensis* and *Cynoglossum zeylanicum* among herbs are more efficient in comparison to other plant species with higher values of SLA. Moreover, leaves having a low value of SLA are also found to be physically robust as well as less attractive to herbivores due to their high thickness and density [22]. While species with high SLA are prone to herbivore attack due to their low thickness and high tenderness [20, 22]. Other than this, SLA and LDMC also express the re-

source use strategy of plant species [7]. The LDMC is seen to be a robust leaf attribute [23]. It has also reported to be positively correlated with leaf life span while negatively correlated with potential relative growth [4]. In the present study, the higher value of LDMC was also recorded for *T. parviflorum*, *C. spinarum* and *D.chinensis*, *C. zeylanicum*, among shrubs and herbs respectively.

On the other hand, nitrogen and phosphorus are generally considered as the main growth-limiting nutrients for plants in natural environments because they are essential in plant enzymatic activity and cell energy transfer. Phosphorus is obtained from weathering of soil whilst a large part of nitrogen is fixed from the atmosphere by plants [18]. Besides an indicator of plant nutritional status, leaf nutrient concentration has also been suggested as an alternative means to examine the nutrient availability of the soil [24, 25]. In the present study, the value of LPC for understorey species ranged from 1.35 to 2.57 mg/g which was supported by Santiago [21], because during his study the value of LPC for understorey species was found to be varied between 0.80 to 2.42 mg/g.

Apart from this, in a variety of studies SLA has been found to be associated with LNC and LPC [5, 22, 26, 27, 28]. This trend can also be observed in the present study, as the plants with higher values of SLA tend to have high LNC and LPC viz. *Parthenium hysterophorus*, *Lantana camara* among shrubs and *O. corniculata*, *Bidens pilosa* among herb species. Leaf traits have seen to be accountable to regulate the above-ground productivity, as well as the quality of grasses to some extent in an ecosystem [29]. It has been observed that SLA and LNC of the component plant species might have a substantial effect on the primary productivity and nutrient cycling of an ecosystem [30]. Other than this, LNC and LPC are also important for plant growth and development because they provide information on main attributes such as relative growth rate and gaseous exchange through leaves [31].

For optimum growth of plants, a leaf nitrogen to phosphorus mass ratio of 10 has been suggested by many workers [24, 32, 33]. Güsewell *et al.* [25] performed a review on fertilization experiments and determined that the value of N : P <10 showed N limitation while N:P >20 showed P limitation for most of the plant growth forms. In

a variety of studies, the concentrations of N and P have been found to show a strong positive correlation with each other [34, 35]. In the present study, no plant species were found to show nitrogen limitation as the value of N:P value for any of them was not recorded as >10. This suggests that the plant species under study employ efficient use of nitrogen, which enables them to keep LNC stable. While six plant species were found to have N:P ratio >20 showing phosphorus limitation. In the present study, the value of N:P ratio for shrubs was found to be less than 20 but more than 10. But for herb species, except *O. corniculata* the value of N:P ratio lied between 20 to 30 for the rest five herb species taken under study. Hence, following Güsewell [25], the plant species were found to show a certain level of phosphorus limitation. The conservative and efficient use of phosphorus can only be mediated by high or adaptable levels of presorption and high nutrient use efficiency [36].

In dry deciduous forests, the vegetation research has mainly tended to be focused on tree species and only a little attention has been given to the understorey species. However, the understorey vegetation also has ecological importance of its own; such as nutrient cycling, litter decomposition, edaphic characteristics, tree seedling regeneration *etc.* Thus, by this study an effort was made by us to understand the functional leaf attributes of some understorey species of our area.

Conclusion

Functional diversity influences various ecological processes and offers several ecosystem services but its effects on the intensity of ecological processes are controversial. Thus, to understand this more clearly, firstly functional diversity should be further studied in different ecosystems. This type of understanding may be essential for predicting patterns of community assembly as well as for describing species contributions to ecosystem processes. While such type of information is almost non-existent regarding the forests of Haryana in India. And only a few studies have been reported from the different parts of the country. Hence further studies are warranted in the field of functional ecology due to their importance in understanding and management of forest ecosystems.

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References

- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16: 646–655. doi: 10.1016/S0169-5347(01)02283-2.
- Reich PB, Wright IJ, Cavender-Bares J et al. (2003) The Evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164: 143–164. doi:10.1086/374368.
- Violle C, Navas ML, Vile D et al. (2007) Let the concept of trait be functional! *Oikos* 116: 882–892. doi: 10.1111/j.00301299.2007.15559.x.
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege H ter, Morgan HD, van der Heijden, MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380. doi:10.1071/BT02124.
- Chaturvedi RK, Raghubanshi AS, Singh JS (2011) Leaf attributes and tree growth in a tropical dry forest. *Journal of Vegetation Science* 22: 917–931. doi:10.1111/j.1654-1103.2011.01299.x
- Poorter L, Bongers F (2006) Leaf Traits Are Good Predictors of Plant Performance Across 53 Rain Forest Species. *Ecology* 87:1733–1743. doi:10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2.
- Jung V, Violle C, Mondy C et al. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140. doi:10.1111/j.1365-2745.2010.01687.x.
- Paine CET, Baraloto C, Chave J, Hérault B (2011) Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120: 720–727. doi:10.1111/j.1600-0706.2010.19110.x.
- Cornwell WK, Cornelissen JH, Amatangelo K et al. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–71. doi:10.1111/j.1461-0248.2008.01219.x.
- Körner C (2007) The use of ‘altitude’ in ecological research. *Trends in ecology and evolution*, 22(11): 569–574. doi: 10.1016/j.tree.2007.09.006.
- India state forest report (2019) Forest survey of India, Dehradun.
- Wadia DN (1961) Geology of India. Macmillan and company, London.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556. doi: 10.1046/j.13652435.2002.00664.x.
- Goodridge J (2002) The effects of native plants on non-native plant abundance in a restoration setting: differences among native species and the predictive ability of species traits. MS thesis, Oregon State University, Corvallis, OR, US.
- Gondard H, Romane F, Aronson J, Shater Z (2003) Impact of soil surface disturbances on functional group diversity after clear-cutting in Aleppo pine (*Pinus halepensis*) forests in southern France. *Forest Ecology and Management* 180: 165–174. doi:10.1016/S0378-1127(02)00597-2.
- Roberts RE, Clark DL, Wilson MV (2010) Traits, neighbours, and species performance in prairie restoration. *Applied Vegetation Science* 13: 270–279. doi:10.1111/j.1654-109X.2009.01073.x.
- Sandel B, Corbin JD, Krupa M (2011) Using plant functional traits to guide restoration: a case study in California grassland. *Ecosphere* 2: 1–6. doi:10.1890/ES10-00175.1.
- Wright IJ, Reich PB, Westoby M et al. (2004) The worldwide leaf economics spectrum. *Nature* 428: 821–827. doi:10.1038/nature02403.
- Salazar Ramon L II (2015) Leaf functional traits and forest structure of tropical dry forest species along a rainfall gradient in Florida and Puerto Rico. PhD thesis. Florida International University.
- Bolom-Ton F (2016) Factors affecting variation in forest community characteristics and leaf-litter decomposition in tropical montane forest of Chipas, Mexico: a functional ecology approach. PhD thesis. Bangor university, Mexico.
- Santiago LS, Wright SJ (2007) Leaf functional traits of tropical forest plants in relation to growth form. *Functional ecology* 21(1): 19–27. doi:10.1111/j.1365-2435.2006.01218.x
- Westoby M, Falster DS, Moles AT et al. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159. doi: 10.1146/annurev.ecolsys.33.010802.150452.
- Roche P, Diaz-Burlinson N, Gachet S (2004) Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? *Plant Ecology* 174: 37–48. doi: 10.1023/B:VEGE.0000046056.94523.57.
- Van d Driessche (1974) Prediction of mineral nutrient status of trees by foliar analysis. *The Botanical Review* 40(3): 347–394. doi:10.1007/BF02860066.
- Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243–266. doi:10.1111/j.1469-8137.2004.01192.x.
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* 23: 187–261. doi:10.1016/S0065-2504(08)60148-8.
- Wright IJ, Westoby M (2001) Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: generalisations across growth forms and growth irradiance. *Oecologia* 127: 21–29. doi:10.1007/s004420000554.

28. Gotsch SG, Geiger EL, Franco AC (2010) Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees. *Oecologia* 163: 291-301. doi: 10.1007/s00442-018-04327-3.
29. Pontes Da Silva L, Soussana JF, Louault F et al. (2007) Leaf traits affect the above-ground productivity and quality of grasses. *Functional Ecology* 21: 844-853. doi:10.1111/j.1365-2435.2007.01316.x.
30. Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30: 1-67. doi: 10.1016/S00652504(08)60016-1.
31. Garnier E, Cordonnier P, Guillem JL, Sonié L (1997) Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* 111: 490-498. doi:10.1007/s004420050262.
32. Ingestad T (1979) Nitrogen stress in birch seedlings: II. *Physiologia Plantarum* 45(1): 149-157. doi: 10.1111/j.1399-3054.1979.tb 01679.x.
33. Aerts R, Chapin FS III (1999) The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. *Advances in Ecological Research* 30: 1-67. doi: 10.1016/S0065-2504(08)60016-1.
34. Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33: 1441-1450. doi: 10.2307/2404783.
35. Thompson K, Bakker JP, Bekker RM, Hodgson JG (1997) *The soil seed banks of north west Europe: methodology, density and longevity*. Cambridge University Press, Cambridge, UK.
36. Redwine JR (2007) Leaf morphology scales multi-annual trends in nutrient cycling and leaf, flower, and fruiting phenology among species in the sub-tropical hardwood forests of the northern Florida keys. PhD thesis. Florida International University.