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Relationships among the leaf traits in temperate forest tree species in Uttarakhand, India

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ABSTRACT

Background: The primary function of the leaf is the production of the food and interchange the gases between the atmosphere and the plant surface. Establishing the relationship among the leaf traits is essential to understand the ecosystem functioning in the forest ecosystem. Here, the present study proposes a framework for species-level relationships between the traits in the temperate forest ecosystem.

Methodology: Three morphological (leaf area, specific leaf area and leaf dry matter content), three chemical (leaf carbon, nitrogen and phosphorous content) and six physiological (chlorophyll, photosynthetic rate, stomatal conductance, intrinsic water use efficiency, transpiration rate, intercellular CO_2 concentration) leaf traits were analysed in 10 woody tree species of temperate forest using linear mixed modelling.

Results: Results showed that the leaf carbon was the only trait influencing the most to leaf area, specific leaf area and leaf dry matter content and leads to maximum variation in the functioning of the forest ecosystem.

Conclusion: The results suggested that consideration of plant traits, and especially the leaf traits, increases the ability to describe variation in the functioning of the forest ecosystem. This study indicated that leaf carbon act as the significant predictor of leaf trait variation among the different species in the temperate forest ecosystem of the Indian Himalayan region

KEYWORDS

Functional traits; Specific leaf area; Leaf nitrogen; Leaf carbon; Leaf area

INTRODUCTION

Functional traits are defined as morphological-physiological-phenological traits that influence fitness indirectly via their effects on growth, reproduction and survival of individual performance of the species (Violle et al., 2007). In this perspective, Wright et al. (2004a) defined the term 'leaf economics spectrum', which comprises of key chemical, structural and physiological properties of the leaf. Leaf economic spectrum runs from quick to slow return on investments of nutrients and dry mass in leaves, and functions individually of growth form and plant functional type (Díaz et al., 2016). Leaf traits generate variability in the ecosystem process such as interspecific variability among the species and intra-specific variability within the species (Jagodziński et al., 2016). In this study, the main focus is intraspecific variability of the traits among the various tree species.

Globally, leaf traits are associated with various ecosystem processes as well as also contribute to regulating climate (Ordoñez et al., 2009). The leaf traits are associated with each other and regulate the trade-off among functionally distinct traits (Wang et al., 2015), resulting in dynamic ecosystem processes. Leaf traits as the specific leaf area (Dwyer et al., 2014), leaf nitrogen content and leaf dry matter content (Wright et al., 2004) has been used as the indicator for plant functional strategies. Two contrasting functional strategies of leaf traits have been identified in the literature under the leaf economic spectrum (Wright et al., 2004). The first strategy explains conservation resource use approach with slower matter turnover, longer leaf life span, lower specific leaf area and leaf nitrogen content. It includes the traits that enhance nutrient conservation and increase the competitive abilities in dry and nutrient-poor surroundings (Reich, 2014). In contrast, the second strategy describes resource acquisition approach attributed to those species that utilizes resources rapidly and has a high growth rate. These species are dominant in resource-rich habitats, short-leaf life span, fast material turnover, high resource capture and fast-growth abilities and featured by high specific leaf area, photosynthetic rate and leaf nitrogen concentration (Wright et al., 2004).

Leaf economic spectrum underpinning for establishing the relationship among the species, globally people describing the significance of leaf traits in explaining variability in the ecosystem functioning (Donovan et al., 2011; Wright and Sutton-Grier, 2012; Osnas et al., 2013; Edwards et al., 2014; Asner et al., 2016). Leaf traits such as specific leaf area, leaf nutrients (nitrogen and phosphorous) and photosynthetic rate are interrelated (Liu et al., 2012; Walker et al., 2014; Dubey et al., 2017) and plays a significant role for several ecosystem processes and functioning for instance, specific leaf area is the indicator of litter decomposition of tropical plants (Bakker et al., 2010), estimates the thickness of leaf (Vile et al., 2005) and also predicts the plant growth (Liu et al., 2017) though, dry leaf matter is the predictor of net primary production (Smart et al., 2017), plant strategy (Wilson et al., 1999) and soil fertility (Hodgson et al., 2011). Mostly the studies on leaf traits have been carried out at the species level (Garnier et al., 2001; Poorter and Bongers, 2006). In comparison, a very limited understanding has been acquired about the inter-linkages of the leaf traits, particularly for the temperate forest species of the Himalayan region due to lack of limited studies.

The present study aimed to analyse the relationship between leaf area, specific leaf area, and leaf dry matter content with leaf nutrients (leaf carbon, nitrogen and phosphorous) and physiological traits (chlorophyll, photosynthetic rate, stomatal conductance, intrinsic water use efficiency, transpiration rate and intercellular CO_2 concentration) in a temperate forest ecosystem and testing the association of the leaf traits at the species level. We mainly focused on leaf area, specific leaf area and leaf dry matter content due to the wide usage of these traits across the world, low cost of acquisition and accessibility in the databases; they are easily measurable traits and give beneficial information about the species physiological and chemical association. We tested the hypothesis that among all the leaf traits selected for the study which trait is influencing the most the characteristics of leaf area, specific leaf area and leaf dry matter content as these leaf traits are the substitutions for biomass production.

1. MATERIAL AND METHODS

The study area is located in the central Himalayan region of Uttarakhand state in India. The climate is of temperate type. The soil is acidic and referred to as regosols, leptosols and dolomite (Raina and Gupta, 2009). The study was conducted in the forest stand located at 30° 28′02.6′′ N latitude; 78° 05′ 47.9′′ E longitude with an altitude of 2200 m asl. The mean annual temperature is 25ºC and the mean annual rainfall is 2150 mm. The forest types of the area is a Himalayan moist temperate forest. The vegetation is dominated by evergreen and deciduous species. Widest variety of leaf traits in the forest area was covered by the 10 dominant tree species selected for the study. The dominant evergreen trees were *Abies pindrow,* Spach Ham; *Cedrus deodara,* Loud*, Cupressus torulosa,* D. Don*, Euonymus pendulous,* Wall, *Pinus wallichiana,* Jackson*, Quercus leucotrichophora,* A. Commons*, Rhododendron arboreum,* Smith and deciduous tree species were *Aesculus indica,* Colebr*, Pyrus pashia,* Buch. Hemex D.Don, *Toona ciliata,* R tree species respectively. The shrub layer is dominated by *Rubus leucocarpus* A, *Berberis chitria* Lindl, and *Berberis lyceum* Royle. Dominant tree species were selected on the basis of importance value index and abundance of the species. During the peak vegetative season, 20 plots (10 × 10 m) were set up at random in the forest. The plot size was small as the study site is located in the hilly region and Indian scenario researchers were used such plots for ecological studies such as Sharma et al. (2011). Five individuals were selected from each plot for the evaluation of leaf traits.

From each plot, an adult of each of the most dominant woody tree species was selected for collection of data on leaf traits. Fully expanded and young leaves were collected at random from the plants with good exposure to sunlight. The leaves were placed in plastic bags and transported to the laboratory and stored at 15˚C.

1.1. Leaf trait measurements

All morphological, chemical and physiological analyses were conducted following the criteria defined by Pérez-Harguindeguy et al. (2013). Morphological traits such as leaf area was measured on five fully expanded fresh young leaves per individual and scanned by the LI-3100C (LICOR) instrument. Specific leaf area was measured as the one-sided area of the leaf divided by its oven dried weight and leaf dry matter content was calculated as the ratio between the dry and the fresh (saturated) weight of the leaf. For chemical traits measurement additional leaves were collected from each from the outer canopy for chemical analysis. The collected leaves were separated for each individual species and oven-dried (at 70˚C for 48h) and ground using a stainless steel mill. The leaf carbon and nitrogen was determined by an elemental analyser (CHNS, Euro, and EA-3000). Leaf phosphorous was analysed by using the acid digestion method. And physiological traits such as chlorophyll concentration (Chl) was estimated by measuring the absorbance of the leaf extract at 645 and 663 nm wavelengths (Arnon 1949) by using UV-VIS spectrophotometer (Thermo Scientific, Evolution 201). Photosynthesis rate, stomatal conductance, transpiration rate and intercellular CO_2 concentration were measured by the instrument LICOR-6400 XT (LICOR). It is an open design photosynthetic gas exchange system. Infrared gas analyzers (IRGAs) are attached in the sensor head that controls the conditions in the leaf chamber, and the chemical tubes used for scrubbing were CO_2 and H_2O. It comprises a variety of interchangeable leaf chambers for both coniferous and broadleaf. Before using this instrument, we have to follow the three main steps: (i) During warm up, we need to check air supply, temperature, light source, pressure, leaf fan and flow control of the instrument. (ii) After warm up, we need to check the flow zero, close the chamber, check CO_2 and H_2O, set references CO_2 and H_2O and then match the IRGAs. (iii) Measuring the leaf: we need to set light, flow at 400 µmol s^{-1}, temperature and then clamp onto leaf, set area and stomatal ratio. After this, we logged into new measurement and the information was recorded and stored in the LI-COR instrument for each parameter. Water use efficiency is the ratio between the net photosynthetic rate and the stomatal conductance.

2. DATA ANALYSIS

A principal component analysis (PCA) of nine leaf traits (three nutrients and six physiological) of 10 tree species was performed to understand the multivariate patterns present in data by evaluating the relationships among traits (Domínguez et al., 2012). The scaling problem in the data was addressed by using scaled and centred data through transforming the data as normal variants. Linear mixed models with restricted maximum likelihood (REML) estimation was used with a lme4 package of R studio software (R-3.5.1 version) (Winter, 2013). The general structure of analysis contains leaf area, specific leaf area and leaf dry matter content as the response variable, which has been modelled as a function of the fixed effect leaf traits leaf carbon content (LCC), leaf nitrogen content (LNC), leaf phosphorous content (LPC), chlorophyll content (Chl), photosynthetic rate (A), stomatal conductance (Gs), water use efficiency (WUE), transpiration rate (E) and intercellular CO_2 concentration (ICO2) with study plot as a random effect. All variables were tested for normality and log-transformed before the analysis. The per cent variation by individual fixed and random factors was also estimated. The full and null model was also determined and validated by the AIC criterion and deviance criterion (Winter, 2013).

3. RESULTS

Among the studied tree species, there was high variability in leaf traits, such as leaf area varied from 5 cm^{-2} (*Pinus wallichiana*) to 68 cm^{-2} (*Aesculus indica*), specific leaf area 23 cm g^{-1} (*Cupressus torulosa*) to 148 cm g^{-1} (*Toona ciliata*) and leaf dry matter content 0.21–0.40% (Table 2). Leaf nutrient concentration also showed great variation, for example, leaf carbon ranged between 24.11 and 61.41%, leaf nitrogen between 0.89 and 2.23% and leaf phosphorous 0.11 and 0.32%, respectively among the tree species. Likewise, physiological traits also showed the differences among the tree species such as chlorophyll content was varied from 8.77 to 23.29 mg g^{-1}, photosynthetic rate was 1.89 to 23.71 µmol CO_2 m^{-2} s^{-1}, stomatal conductance was 0.09 to 1.00 mol H_2O m^{-2} s^{-1}, water use efficiency was 30.56 to 1057.02 µ mol CO_2 mol^{-1}, transpiration rate was 0.13 to 2.17 mmol H_2O $m^{-2}s^{-1}$and intercellular CO_2 concentration 122.17 to 431.45 µ mol CO_2 mol^{-1}.

In the multivariate analysis of leaf traits by principal component analysis (PCA), the total variance explained by the leaf traits at the species level was 77%. The principal component 1 (PC1) was positively related to leaf traits Chl, A, Gs, E and ICO2 while negatively associated with LNC and LPC (Figure 1). The principal component 2 (PC2) was positively associated with leaf traits LCC, Chl, A and WUE.

The results of the linear mixed model revealed that the variation in leaf area, specific leaf area and leaf dry matter content explained by functional properties of traits. The maximum change in the leaf area was indicated by the leaf carbon (27 %) and. from study plot 50 % which was the random variable (Table 3a). Leaf area was negatively influenced by the traits such as leaf carbon, water use efficiency and intercellular CO_2 concentration whereas positively with leaf nitrogen, photosynthetic rate, stomatal conductance and transpiration rate. Comparing both the models (null model with full model), it was determined that the full model was better than null model due to its lower value for deviance and Akaike information criteria (AIC) and significant value for chi-square (p =0.00) (Table 1b).

Likewise, variation in specific leaf area and leaf dry matter content was also mostly explained by leaf carbon (27% and 26%) (Tables 4a and 5a). The random effect variation explained for specific leaf area, and leaf dry matter content lies between 9 and 11%. The traits such as leaf carbon, stomatal conductance, water use efficiency, transpiration rate and intercellular CO_2 concentration influenced the specific leaf area negatively whereas the traits such as leaf nitrogen, leaf phosphorous, chlorophyll and photosynthesis affect the specific leaf area positively. However, for leaf dry matter content the traits leaf phosphorous, chlorophyll, stomatal conductance and water use efficiency were influencing the leaf dry matter negatively.

Similarly, while assessing null model with full model for the response variable SLA and LDMC, it was determined that there were low value of AIC and deviance for both the

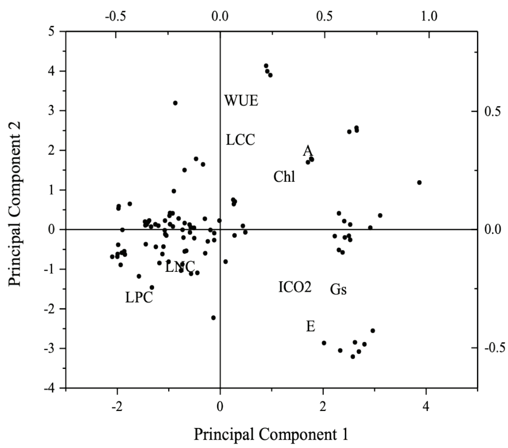

Figure 1. Bi-plot between first and second principal component of leaf traits. Leaf area (LA), Specific leaf area (SLA), Leaf dry matter content (LDMC), Leaf carbon content (LCC), Leaf nitrogen content (LNC), Leaf phosphorous content (LPC), Chlorophyll content (Chl), Photosynthesis rate (A), Stomatal conductance (Gs), Water use efficiency (WUE), and Intercellular CO_2 concentration (ICO2)

Table 1. List and description of the ten woody plant species selected for trait measurements

Species Name	Family	Leaf habit	Abundance (%)*
*Abies pindrow,*Spach Ham (AP)	Pinaceae	Evergreen	0.17
*Aesculus indica,*Colebr (AI)	Hippocastanaceae	Deciduous	0.19
*Cedrus deodara,*Loud (CD)	Pinaceae	Evergreen	0.10
*Cupressus torulosa,*D.Don (CT)	Cupressaceae	Evergreen	0.10
Euonymus pendulus Wall (EP)	Celastraceae	Evergreen	0.17
Pinus wallichiana, Jackson (PW)	Pinaceae	Evergreen	0.10
Pyrus pashia Buch.Hem ex D.Don (PP)	Rosaceae	Deciduous	0.14
Quercus leucotrichophora A.comns (QL)	Fagaceae	Evergreen	0.17
*Rhododendron arboreum,*Smith (RA)	Ericaceae	Evergreen	0.17
Toona ciliata, R. (TC)	Meliaceae	Deciduous	0.17

**Author own survey*

Table 2. Response variables leaf area, specific leaf area and leaf dry matter content of the ten species (mean ± SD)

Species	Leaf area (cm2)	Specific leaf area (cm2g-1)	Leaf dry matter content (%)
A. pindrow	20.83 ± 16.69	52.45 ± 42.14	0.31 ± 0.19
A. indica	68.37 ± 65.72	144.88 ± 124.37	0.27 ± 0.30
C. deodara	7.05 ± 4.31	49.26 ± 36.48	0.40 ± 0.11
C. torulosa	8.90 ± 3.55	23.57 ± 5.02	0.40 ± 0.15
E. pendulus	33.42 ± 14.86	136.10 ± 33.49	0.32 ± 0.10
P. wallichiana	5.00 ± 1.56	28.23 ± 38.79	0.40 ± 0.23
P. pashia	28.47 ± 22.93	64.49 ± 55.08	0.34 ± 0.35
Q. leucotrichophora	43.97 ± 16.51	119.08 ± 55.33	0.44 ± 0.12
R. arboreum	46.34 ± 16.21	80.83 ± 22.89	0.33 ± 0.16
T. ciliata	25.99 ± 20.16	148.38 ± 139.39	0.21 ± 0.16

fixed traits (SLA and LDMC) in full model, which suggested that the full model was better than the null model with significant chi-square value (p = 0.00) (Table 2b and Table 3b).

4. DISCUSSION

Temperate forest ecosystem, especially the forest of the Indian Himalayan region, is suitable as an experimental site for exploring relationships among functional traits as they are associated with the high diversity of plant species. The minor variation in the soil as well as in climatic conditions in temperate forest systems promotes the coexistence of the wide variety of trait values in different species (Tian et al., 2016). Therefore, it is imperative to understand the mechanism how plant species are associated with various traits. The LA values range from 5 cm $^{-2}$ to 68 cm $^{-2}$, which is in agreement with Singh and Negi (2018), SLA ranges between 23 cm g^{-1} and 148 cm g^{-1} and has agreement with Berner and Law (2016) and LDMC ranges between 0.21 and 0.40% as also reported by Hodgson et al. (2011). The nutrient traits and the physiological traits also showed the considerable variation among the different tree species of temperate forest in the present study.

Overall, morphological, nutrient and physiological traits showed a strong multivariate co-variation at the species level (Figure 1). The primary source of variation in plants was due mainly to different plant strategy, i.e. acquisition to conservation. SLA and LDMC were considered as the important indicators of different plant functional strategies (Wright et al., 2004; Reich, 2014). Thus, communities with a leading conservation strategy exhibited high values of leaf dry matter content and low value of specific leaf area. In contrast, communities with resource acquisition strategy showed the low value of leaf dry matter content and high value for specific leaf area.

The maximum variation percentage in the leaf area was associated with leaf carbon, and this might be due to leaf area growth. Leaf growth depends on carbon partitioned among leaf area, leaf mass, root mass, reproduction and respiration process. Similar results were reported by Niinemets et al. (2002) and Weraduwage et al. (2015). The traits such as leaf nitrogen, photosynthesis, stomatal conductance and transpira-

Table 3. Result of Restricted Estimation of Maximum Likelihood (REML) for Linear mixed model for leaf area (LA)
a. Estimate of coefficient and explained variation for parameter

Response variable	Fixed effect				Random effect		
	Parameter	Estimate	Std. Error	% variation explained	Components	Std. dev	% variation explained
LA	LCC	-26.33	83.55	26.79	Plot	13.46	50.04
	LNC	15.54	5.74	0.13			
	LPC	6.60	3.96	0.06			
	Chl	7.99	4.44	0.08			
	A	4.54	6.85	0.18			
	Gs	9.66	5.72	0.13			
	WUE	-3.00	5.24	0.11			
	E	6.91	6.17	0.15			
	ICO2	-27.00	4.50	0.08			

b. Model statistics for null and full model for LA

Model LA	df	AIC	BIC	logLik	Deviance	Chi-square		
						Value	df	P
Null Model	3	928.2	936.02	-461.10	922.2			
Full Model	12	852.9	884.16	-414.45	828.9	93.3	9	0.00

Table 4. Result of Restricted Estimation of Maximum Likelihood (REML) for Linear mixed model for specific leaf area (SLA)
a. Estimate of coefficient and explained variation for parameter

Response variable	Fixed effect				Random effect		
	Parameter	Estimate	Std. Error	% variation explained	Components	Std. dev	% variation explained
SLA	LCC	-65.27	451.93	26.82	Plot	1.74	10.81
	LNC	119.28	32.53	0.14			
	LPC	26.85	21.93	0.06			
	Chl	83.75	25.87	0.09			
	A	65.71	38.07	0.19			
	Gs	-1.93	32.66	0.14			
	WUE	-25.13	30.23	0.12			
	E	-26.41	34.93	0.16			
	ICO2	-20.26	25.13	0.08			

b. Model statistics for null and full model for SLA

Model SLA	df	AIC	BIC	logLik	Deviance	Chi-square		
						Value	df	P
Null Model	3	1216.4	1224.2	-605.21	1210.4			
Full Model	12	1178.5	1209.7	-577.24	1154.5	55.945	9	0.00

tion positively influenced the leaf area, and this may be due to having large leaf area helps better in exchanging the gases, water and nutrients from the atmosphere (Koyama and Kikuzawa, 2009); however, leaf carbon, water use efficiency and intercellular CO_2 concentration influence the leaf area negatively may due to species variation.

Specific leaf area also showed the maximum percentage variation with leaf carbon, and this might be due to specific leaf area associated with whole plant growth (Liu et al., 2017). Specific leaf area showed a positive relationship with leaf nitrogen and photosynthesis. These results were consistent with previous studies (Meziane and Shipley, 2001: Gulías et al., 2003). However, with other physiological traits such as

Table 5. Result of Restricted Estimation of Maximum Likelihood (REML) for Linear mixed model for leaf dry matter content (LDMC)
a. Estimate of coefficient and explained variation for parameter

Response variable	Fixed effect				Random effect		
	Parameter	Estimate	Std. Error	% variation explained	Components	Std. dev	% variation explained
LDMC	LCC	0.29	0.59	26.41	Plot	0.001	9.09
	LNC	0.05	0.04	0.12			
	LPC	-0.009	0.02	0.03			
	Chl	-0.10	0.03	0.07			
	A	0.04	0.04	0.12			
	Gs	-0.04	0.04	0.12			
	WUE	-0.06	0.03	0.07			
	E	0.05	0.03	0.12			
	ICO2	0.01	0.04	0.07			

b. Model statistics for null and full model for LDMC

Model LDMC	df	AIC	BIC	logLik	Deviance	Chi-square		
						Value	df	P
Null Model	3	-139.22	-131.41	72.611	-145.22			
Full Model	12	-146.41	-115.15	85.206	-170.41	25.19	9	0.00

stomatal conductance, transpiration rate, water use efficiency and intercellular CO_2, it showed a negative relationship, and it might be due to some microclimatic factors.

Leaf dry matter content also showed the maximum percentage variation with leaf carbon. It was positively associated with leaf carbon (Shipley and Vu, 2002) and this might be due to the reason that dry matter of leaves has high carbon than the green leaves. Other nutrients and physiological traits such as photosynthesis rate, transpiration rate and stomatal conductance showed the very small percentage of variation in leaf dry matter content and the reason for this that in dry leaves physiological activities are almost nil, so in the dry conditions, most of the physiological parameters doesn’t perform well.

To our knowledge, this is an important study, especially in the temperate forest ecosystem of Himalayan region to provide a direct quantification, in the field of the relative importance of leaf traits in explaining the variation in the functioning of the forest ecosystem. Such a framework has important implications for the trade-off among the leaf traits of different tree species of the forest. Our results showed that the there is significant association among the leaf traits in the temperate forest ecosystem and leaf carbon is the important indicator or predictor for bringing variation in leaf area, specific leaf area and leaf dry matter content in the temperate forest ecosystem.

5. CONCLUSION

This study is the first trait-based study, to the best of our knowledge in the Himalayan region for quantification of the significant role of leaf traits in the forest ecosystem. This study showed that at the species level, leaf area, specific leaf area and leaf dry matter content were significantly related to nutrient and physiological traits. As a response, variable leaf area, specific leaf area and leaf dry matter content were influenced considerably by leaf carbon trait. This means leaf carbon is the vital trait for predicting variation in temperate forest ecosystem of the Himalayan region.

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