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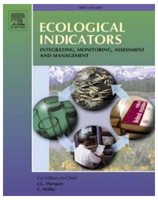

Quantifying leaf-trait co-variation and strategies for ecosystem functioning of *Quercus leucotrichophora* (Ban Oak) forest in Himalaya

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ABSTRACT

Leaf functional traits determine a plant's survival and growth. Variation in leaf traits control the functioning of forest ecosystem. The study examines the variation in 18 leaf traits (4 morphological, 6 physiological, 6 biochemical, and 2 stoichiometry) of 3 dominant evergreen broadleaved tree species (*Quercus leucotrichophora*, *Rhododendron arboreum*, and *Myrica esculenta*) of Ban Oak forests (BOF) of Garhwal Himalaya. The aim of the study is to understand the resource utilization plant strategy of major tree species of BOF and determining the impact of seasonality and elevation on leaf traits. Leaf traits data were collected during three seasons (winter, summer and monsoon) within two altitudes (1400–1700 amsl and 1701–1980 amsl) for two years (2019–2021). Thirty-six individuals from each of the three major tree species were selected for measurement on leaf traits for the three seasons of two years. Results showed that specific leaf area, leaf mass per area, photosynthesis rate, stomatal conductance, intercellular CO_2, transpiration rate, leaf phosphorus, potassium concentration, and photosynthetic nitrogen use efficiency were higher during monsoon season. However, intrinsic water use efficiency and leaf nitrogen concentration were higher during summer season, and leaf dry matter content, water use efficiency, and leaf C/N were higher in winter season. Structural Equation Modelling (SEM) was used to established the relationship between plant strategies, i.e. resource capture and defense (RCD), gas exchange (GE), photosynthetic and resource utilization (PRU), and nutrient cycle and limitation strategy (NCL). Among the morphological, physiological, biochemical and stoichiometry traits, specific leaf area, transpiration rate, leaf nitrogen concentration, and leaf C/N ratio, were having positive relationship with RCD, GE, PRU and NCL, respectively. Result demonstrates that all the three major species of BOF had resource conservative strategies. *Q. leucotrichophora* was major species for forest functioning, whereas *M. esculenta* had higher resource uptake efficiency. Overall, leaf traits were varied with different species and seasonal changes facilitate an adaptive role in a plant's survival under the existing microclimatic condition. The findings of the study provides insight into changes in leaf traits and the plant strategies at the temperate forests of the Himalayas and provide inputs for projection of future changes in leaf attributes and the environment's adaptation at Himalaya and regional level.

1. Introduction

Plant functional traits are physical, structural and functional features associated with survival, growth and development of plant and influence the functioning of forest ecosystem (Garnier et al., 2015; Violle et al., 2007). Leaf traits are the key parameters to making it possible for plants to responds to environment conditions and influence species adaptation and distribution (Díaz et al., 2007). However, leaf traits strategy also assist to understand the forest functioning (energy flux, nutrient dynamics, and organic mass storage) (Cai et al., 2020). Variation in leaf traits serve to identify species life history strategies (Reichstein et al., 2014), parameterizing dynamic vegetation models, and explaining species taxonomy (Díaz et al., 2007). However, the information on interaction of leaf traits with environment is lacking especially in temperate forests of the Himalayan region (Rawat et al., 2022).

Leaf traits are predictors of plant performance and serve as efficient indicators of plant resource-use strategies. Such as, morphological traits i.e. leaf area (LA) determines construction of canopy architecture, whole plant leaf energy, water balancing, and light interception, and specific leaf area (SLA) measures the trade-off between resource capture and

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conservation plant strategies, and illustrates how photosynthetic ability affects the forest productivity (Qin and Shangguan, 2019). Leaf mass per area (LMA) meaures resource allocation strategies (Smart et al., 2017). Physiological traits i.e. photosynthetic rate (A), transpiration (E), and stomatal conductance (Gs) regulate CO_2 and H_2O exchange (Renninger et al., 2015). Leaf traits are also influenced by elevation and microclimate (Li et al., 2021). For instance, edaphic factors influence the growth and development of species (Saha et al., 2018) and topographic and biotic factors influence the species composition and structure (Negi and Mukherjee, 2020).Overall, variation in leaf traits determine the plant species functioning and, as a result, determine overall functioning of the forest ecosystem (Homeier et al., 2021).

Studies had been conducted in various forest ecosystems i.e., tropical dry forests (Chaturvedi, 2013), subtropical forests (Kooyman et al., 2010), and temperate forests (Rawat et al., 2021) with aiming to predict the linkages between plant functional traits and ecosystem functioning. However, evaluations of the linkages between plant functional trait (PFT) and ecosystem functioning are limited to a few services or processes and also at local or regional scale (Rawat et al., 2022). The Himalayan mountain ecosystem, particularly the temperate forests is considered to be susceptible to climate change (Pandey et al., 2022).

Banj Oak forest (BOF) is one of the vital dominant climax plant communities in moist temperate forests of Western Himalayas, and is intricately linked with agro-ecosystems and life support system of the inhabitant's peoples of Central Himalayan (Dobriyal et al., 2016). The BOF forest tree species provides enormous ecosystem services such as *Quercus leucotrichophora* A. Camus species support soil and water conservation, a good source of fodder and fuel, and key forest forming species in moist temperate forest (Singh and Rawat, 2010). *Rhododendron arboreum* Smith flower juice is used for medicinal and ornamental purposes, whereas *Myrica esculenta* Buch. -Ham. ex. D. Don species fruit has medicinal and economic importance to local people (Sharma et al., 2019). However, development activities (tourism, dam construction and road building) led to excessive pressure on Himalayan forests leading to forest degradation, and ultimately disturbing the intricate relationship with the livelihood of the local population (Chakraborty et al., 2018). Therefore, management of ecosystem services is critical for the deprived and poor Himalayan human communities in the absence of specific information supporting the forest functioning. Besides, understanding the vulnerability, adaptability, and functionality of temperate species in the context of changing conditions is also inadequate as trait differentiation has not been evaluated (Rawat et al., 2022). The solution to the problem lies with an evaluation of linkages between leaf traits and the functioning of the forests at individual and community levels.

2. Theoretical setting: A priori model

Establishment of the intricate relationship between physiological, morphological, and chemical traits is used to evaluate species functioning. In the present evaluation, four different plant strategies were defined to understand the functioning of banj oak forest. Resource capture and defense (RCD), gas exchange (GE), photosynthetic and resource utilization (PRU) and nutrient cycling and limitation (NCL) strategy are considered as latent strategies of BOF. RCD is defined as a mechanism controlled by morphological traits (LA, SLA, and LDMC) and explains the species distribution (survival ability in an environment) at an individual level and growth form at the community level (Dong et al., 2020). GE is a process of physiological traits (A, Gs, Ci, E, and WUE) and explain the nutrient availability to the plant and affects the plant's performance and fitness (Boretti and Florentine, 2019). PRU is the strategy of biochemical traits (LCC, LNC, LPC, LKC, and PNUE) and defines the plant's ability to survive and directly attests that they produce secondary and primary metabolites that are directly involved in the growth and development of the plant (Yang et al., 2018). Moreover, nutrient concentrations and distribution in tree species influence biomass productivity (Son et al., 2004) and stoichiometry traits (C/N, N/P, and C/P) that are responsible for forest productivity and nutrient balancing (Fernández-Martínez et al., 2017) and therefore RCD and NCL was considered to be related with each other. SLA, is an indicator of resources use in plant, explains a plant's ability to capture light and function and influence the net primary productivity however LA and LDMC measures plant growth and carbon assimilation rate (Qin and Shangguan, 2019) hence RCD was considered to relate with GE. Moreover, SLA is also positively correlated with plant growth rate and signifies the rate of return on investment for a light-intercepting leaf (Kooyman et al., 2010). However, A is positively related with E, Gs (Luong and Loik, 2022), and Ci (Sharma et al., 2018) for the maintaining of leaf temperature, carbon flux, and photosynthetic tradeoff. Moreover, A is positively linked with LNC and SLA (Li et al., 2021) and therefore, it was considered that GE is linked with PRU. RCD positively influences GE (Meziane and Shipley, 2001) and NCL (Xing et al., 2021). Hence, it was concluded that gas exchange is mainly influenced by the species-specific physical character, whereas nutrient cycling is influenced by the structure tissue of morphological traits (Wu et al., 2018). Moreover, metabolic activity of the plant is determined by the leaf traits functioning i.e., plant growth and productivity (Yang et al., 2019).

Therefore, a lack of understanding of leaf traits variability and their interaction with season and elevation in Himalayan region may restrict the policy makers for developing an effective forest management plans for the sustainability of ecosystem and also flow of ecosystem services. Therefore, the following research questions were considered in the present study (i) how the various leaf traits of major temperate species are responded to forest functioning under seasonal change?. (ii) How forests functioning controlled by various leaf strategy?. The study hypothesizes that temperate forest species respond to seasonal changes. Specifically, the objectives of the study were (i) to understand the different resource utilization strategies of the major species, and (ii) to establish the relationship among morphological, physiological, biochemical and stoichiometric traits of the major tree species. The analysis will facilitate broadening the understanding of the functionality of the species of temperate forests and also support the scientific management of forests for the intended purpose.

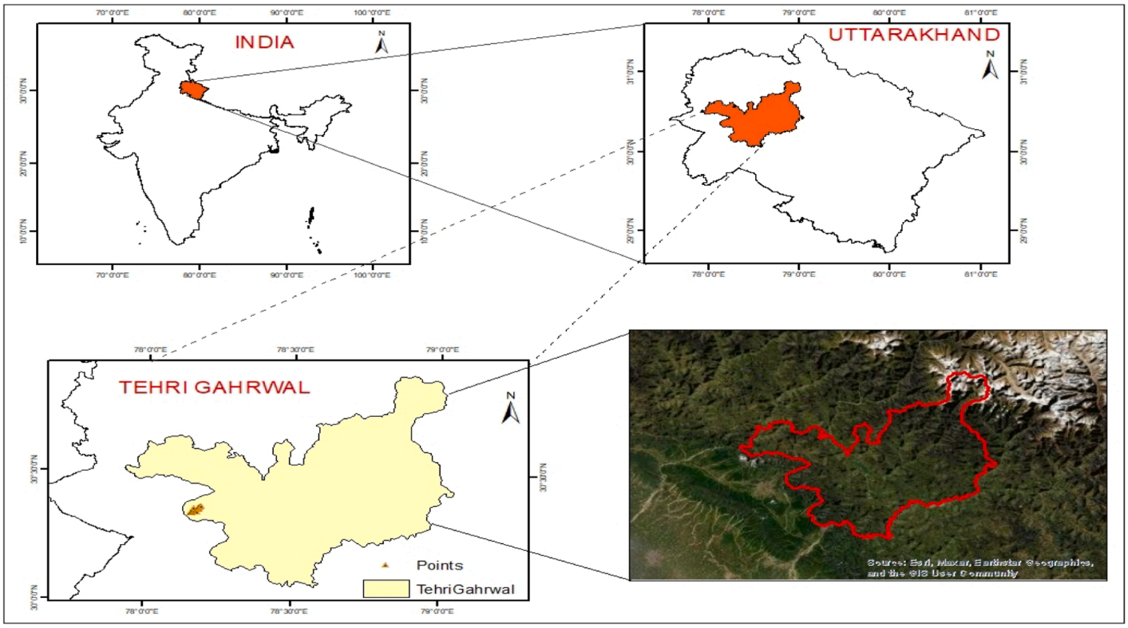
3. Methodology

3.1. Study site

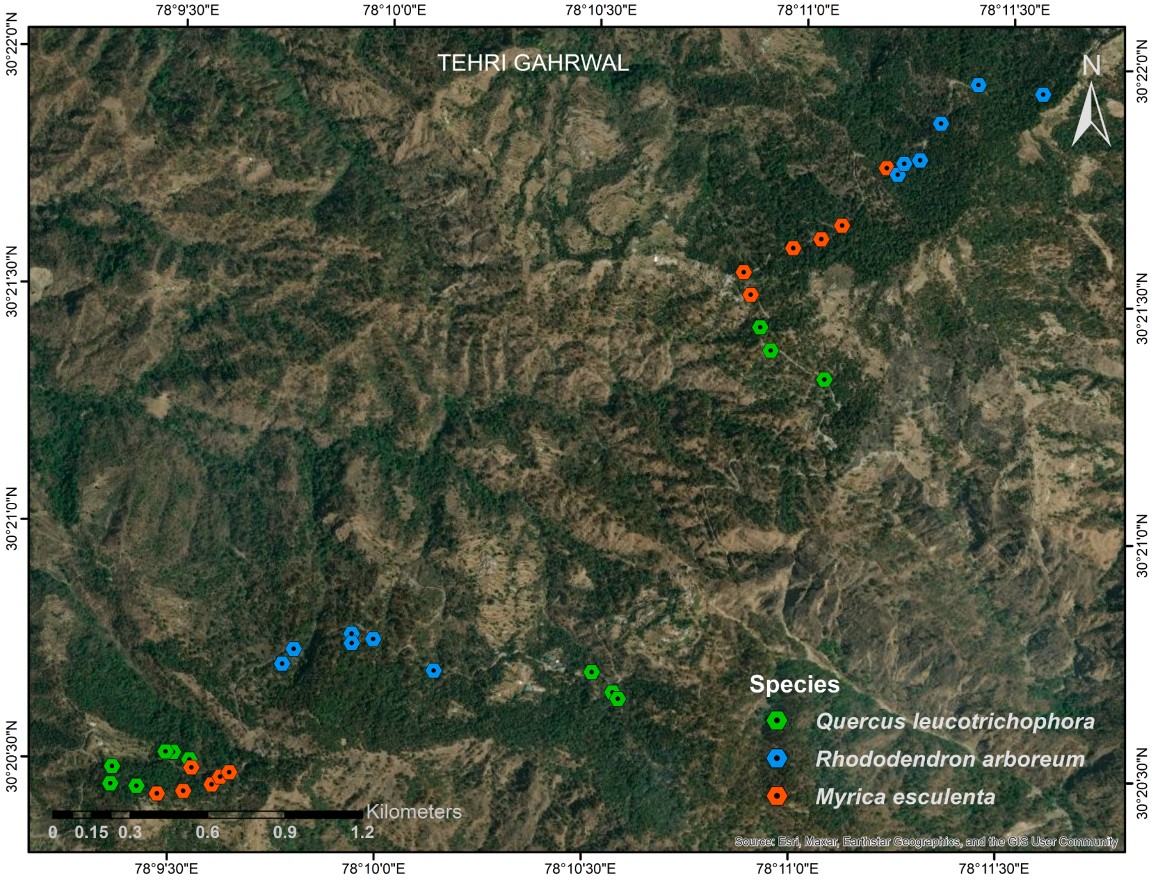
Study was conducted in moist temperate forest of Western Himalaya spread over an area of 210 ha between $30^{0}20'34.06''$ – $30^{0}2'50.53''$ N and $78^{0}09'23.21''$ – $78^{0}12'29.16''$ E at an elevation between 1400 amsl to 1980 amsl (Fig. 1). The average annual rainfall was 1409.21 mm with an average annual minimum and maximum temperate of 12.63 °C and 23.43 °C during 2019–21 (https://power.larc.nasa.gov/). Weather is mainly characterized by three seasons i.e., summer (March to June), monsoon (July to October), and winter (November to February). Soil developed from medium to moderately coarse alluvial texture under the influence of vegetation. The average pH ranges from 5.3 to 5.9, and organic carbon ranges from 1.5 to 6.8 % (Saha et al., 2018). The vegetation survey was conducted through using 0.1 ha plots, and resulted in a total of 67 plant species being present in BOF with 4 trees species, 14 shrubs, and 49 herbs. The tree species were *Quercus leucotrichophora*, *Rhododendron arboreum*, *Lyonia ovalifolia*, and *Myrica esculenta*. The major shrub species were Arundinaria falcata, *Berberis aristata*, *Boehmeria rugulosa, Eupatorium adenophorum,* and *Girardinia diversifolia* in BOF.

3.2. Sampling method

Samples were collected by using stratified random sampling at seasonal basis (winter, summer and monsoon) from two altitudes (1400–1700 amsl and 1701–1980 amsl) for two years (2019–2021). Vegetation composition was criteria for elevation stratification (Fig. 2a).



(a) Map of the study site



(b) Location of sampling point in BOF

Fig. 1. Figure of study site.

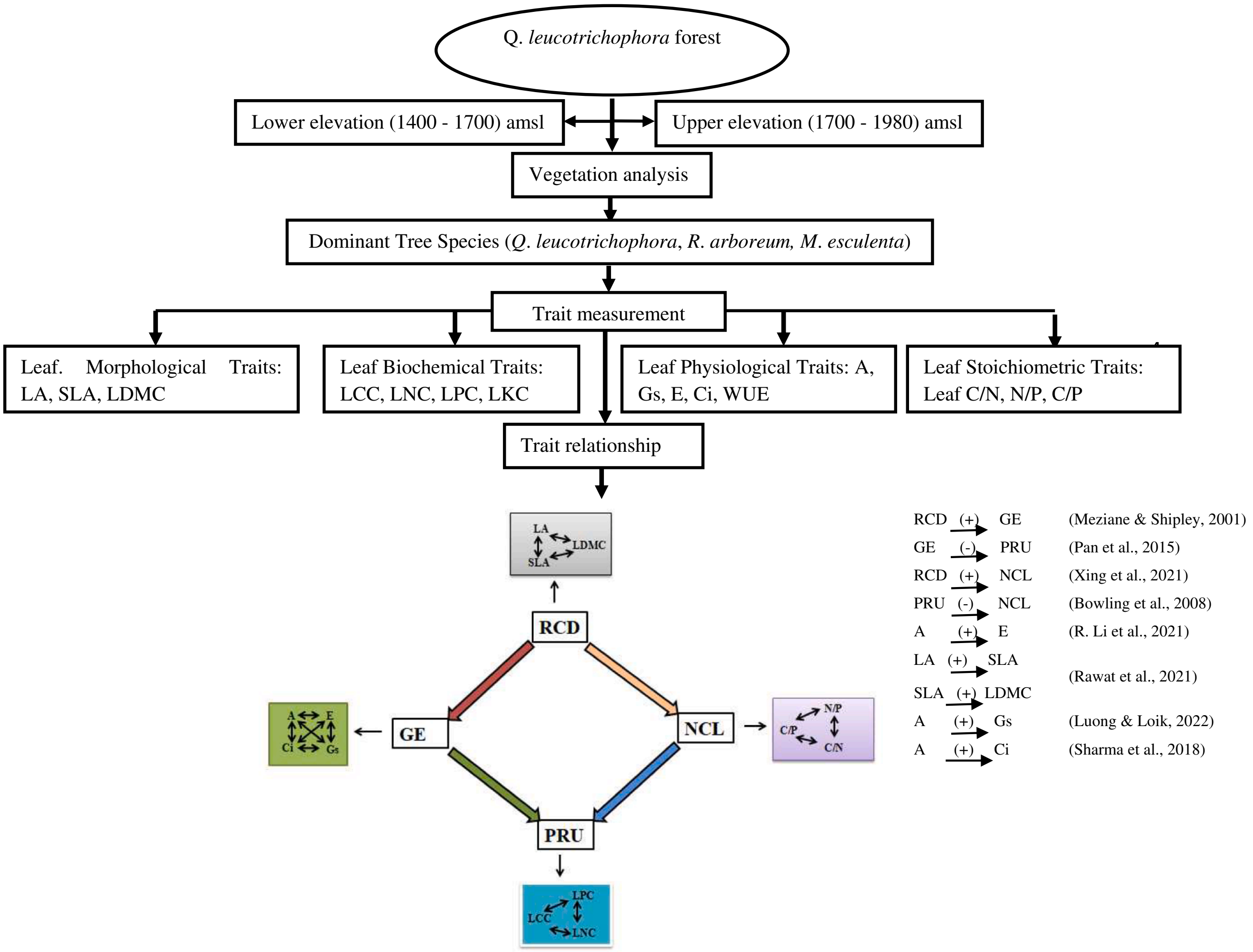


Fig. 2. Study design and Trait relationship (A priori model of relationship between plant functional trait and strategies in BOF Morphological trait; LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; Biochemical trait; LCC = leaf carbon content; LNC = leaf nitrogen content; LPC = leaf phosphorus content; LKC = leaf potassium content,; Physiological trait; A = photosynthetic rate; Gs = stomatal conductance; E = transpiration rate; WUE = water use efficiency; Stoichiometry; leaf C/N, leaf C/P and leaf N/P. Latent variable Resource capture and defense (RCD) (LA + SLA + LDMC), Gas exchange (GE) (A + Gs + Ci + E), Photosynthetic and resource utilization strategy (PRU) (LCC + LNC + LPC + LKC + PNUE) and Nutrient cycling and limitation (NCL) (LCC/LNC + LCC/LPC).

We laid out a total of 28 quadrat size of 31.62 × 31.62 m (0.1 ha) for both altitude (FSI, 2019). Sample size was estimated through the protocol based on primary data on trees (Daniel, 1999). Based on the Importance Value Index (IVI), three dominant species were selected i.e., *Q. leucotrichophora*, *R. arboreum,* and *M. esculenta* for data collection (Table 1). Six individuals of each selected species were marked at each elevation for data collection for two years (3 species × 3 season × 2 elevation × 2 year). Mature and full sun exposure leaves were collected from selected trees.

Table 1

Characteristics of Ban Oak Forests (BOF) in Temperate Himalaya.

Forest type	Slope aspect	Slope position	Slope gradient	Altitude (meter)	Major species	Density/ha	Tree height (meter)	Average DBH (meter)
$12C_1$/ Moist temperate forest	Northwest, North, North south and West	Down to Medium	15 to 28	1400–1700	*M. esculenta*	27.42	16.80 ± 0.95 (11.50–22.45)	0.351 ± 0.018 (0.24–0.42)
					Q. leucotrichophora	199.58	11.48 ± 1.08 (8.05–15.30)	0.237 ± 0.022 (0.14–0.27)
					R. arboreum	41.67	10.64 ± 0.82 (9.20–13.55)	0.268 ± 0.01 (0.21–0.28)
	Northwest, North south and West	Down to Medium	13 to 25	1701–1980	*M. esculenta*	29.59	17.43 ± 0.74 (14.50–22.20)	0.343 ± 0.013 (0.29–0.42)
					Q. leucotrichophora	208.67	14.22 ± 0.50 (11.06–16.00)	0.309 ± 0.009 (0.27–0.35)
					R. arboreum	46.74	9.84 ± 0.72 (7.50–10.55)	0.218 ± 0.012 (0.16–0.26)

Mean ± SE (Minimum and Maximum values).

3.3. Functional trait measurement

Leaf fresh weight measured in the laboratory within 24 h. Other leaf samples were dried. Dried leaf samples were ground in a Wiley mill and filtered through a stainless-steel mesh with a 1 mm pore size (Elosegi and Pozo, 2005) (see Table 2).

3.3.1. Leaf morphological trait

Ten leaves were collected from one individual of each species for measurement of LA (cm^2), SLA ($cm^2\ g^{-1}$), LDMC ($cm^2\ g^{-1}$), and LMA ($g\ cm^{-2}$). LA is one side projected area of the leaf and measured using IMAGE J software. SLA is the ratio of leaf area and oven-dry weight of the leaf. LDMC is the ratio of the oven-dry weight of leaf and the fresh weight of the leaf. LMA is the reciprocal of SLA (Pérez-Harguindeguy et al., 2013).

3.3.2. Leaf physiological trait

Physiological traits i.e., A ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$), E ($mmol\ H_2O\ m^{-2}\ s^{-1}$), Gs ($mol\ H_2O\ m^{-2}\ s^{-1}$), and Ci ($\mu mol\ CO_2\ mol^{-1}$) were evaluated using a portable photosynthetic system (Licor-6800). Water Use Efficiency (WUE) was ratio of A/E (Medrano et al., 2015) and Intrinsic Water Use Efficiency (IWUE) was a ratio of A/Gs (Rekha et al., 2013).

Table 2
Details of leaf traits and their function.

Leaf Traits	Traits/ Abbreviation	Unit	Function (Strategy)	Source
Morphology	Leaf area (LA)	cm^2	Light interception, physical defense (Resource capture and defense (RCD))	Su et al., 2021
	Specific leaf area (SLA)	$cm^2\ g^{-1}$		
	Leaf dry matter content (LDMC)	$cm^2\ g^{-1}$		Qin and Shangguan, 2019
	Leaf mass per area (LMA)	$g\ cm^{-2}$		Smart et al., 2017
Physiology	Photosynthesis rate (A)	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$	Growth regulator (Gas exchange (GE))	Renninger et al., 2015
	Stomatal conductance (Gs)	$mol\ H_2O\ m^{-2}\ s^{-1}$		
	Intercellular CO_2 concentration (Ci)	$\mu mol\ CO_2\ mol^{-1}$		
	Transpiration (E)	$mmol\ H_2O\ m^{-2}\ s^{-1}$		
Biochemical	Leaf carbon concentration (LCC)	%	(Metabolic efficiency) (Photosynthetic and resource utilization strategy (PRU))	Wang et al., 2015
	Leaf nitrogen concentration (LNC)			
	Leaf phosphorus concentration (LPC)			Osnas et al., 2013
	Leaf potassium concentration (LKC)			
Stoichiometry	Leaf stoichiometry	–	Nutrient balancing (Nutrient cycling and limitation (NCL))	Zhang et al., 2017

3.3.3. Leaf biochemical trait

Leaf biochemical traits i.e., LCC (%) and LNC (%) were measured through CHNS analyzer. LPC (%) and LKC (%) was measured through acid digestion method.

3.3.4. Statistical analysis

Pearson correlation was estimated to test the correlation between various leaf traits. Comparison of different species, seasons, and sites was made by three way Analysis of Variance (ANOVA) with interactions and least significant differences by Scheffe test using in SPSS (IBM Statistics, ver. 21). Also, Principle Component Analysis (PCA) was used for identifying the key variables among studied leaf traits. Relationships between leaf morphological, physiological, chemical, and stoichiometric traits were investigated using SEM through JASP software's SEM package.

4. Results

4.1. Variation in leaf morphological traits of major tree species of the BOF

All four morphological traits were significantly different among three species and among three seasons except LA, which was non-significant for season. Non-significant differences were observed between the two elevation ranges for all the four morphological parameters except LA (Table 3). From the two factor interaction between seasons and elevation, no significant differences were observed for the all four morphological traits. LA and LDMC were significantly different for the two factors interaction between species and seasons, however, LDMC was only trait, which was significantly different for species and elevation range interaction; and LA and SLA were significantly different for the interaction among species, seasons and site (Table 3). Maximum and minimum LA was recorded in *R. arboreum* and *M. esculenta* during winter season, respectively. Maximum and minimum SLA was observed for *M. esculenta* and *R. arboreum* during monsoon and winter season,

Table 3
Leaf morphological traits variation during seasons at two elevations.

Species	LA (cm^2)	SLA (cm^2g^{-1})	LDMC (cm^2g^{-1})	LMA (gcm^{-2})
Q. leucotrichophora	32.34 ± 2.91^b	8.74 ± 2.01^a	0.46 ± 0.14^a	0.12 ± 0.03^b
M. esculenta	29.39 ± 2.98^c	9.49 ± 2.41^a	0.41 ± 0.13^c	0.11 ± 0.02^b
R. arboreum	34.22 ± 3.89^a	7.44 ± 2.36^b	0.44 ± 0.14^b	0.15 ± 0.05^a
p-value	<0.0001	<0.0001	<0.0001	<0.0001
Season				
Winter	31.88 ± 4.32	6.81 ± 1.48^c	0.58 ± 0.068^a	0.15 ± 0.04^a
Summer	31.44 ± 3.55	8.53 ± 2.31^b	0.50 ± 0.042^b	0.13 ± 0.04^b
Monsoon	32.63 ± 3.74	10.33 ± 1.95^a	0.26 ± 0.037^c	0.10 ± 0.02^c
p-value	0.194	<0.0001	<0.0001	<0.0001
Elevation				
(1400–1700) amsl	31.42 ± 2.51	8.36 ± 2.07	0.43 ± 0.14	0.13 ± 0.03
(1701–1980) amsl	32.55 ± 3.96	8.77 ± 2.71	0.45 ± 0.15	0.12 ± 0.04
p-value	<0.038	0.221	0.156	0.793
Interaction p-value				
Elevation × Season	0.940	0.228	0.159	0.309
Species × Season	<0.0001	0.175	<0.004	0.084
Species × Elevation	0.236	0.126	<0.021	0.300
Species × Season × Elevation	<0.027	<0.032	0.868	0.309

respectively. Maximum and minimum LDMC was recorded in *Q. leucotrichophora* and *M. esculenta* during winter and monsoon season, respectively. Maximum and minimum LMA was recorded for *R. arboreum* and *M. esculenta* during winter season and monsoon season, respectively (Supplementary Table 1). LA was significant for three-way interaction i.e., species, season and elevation; and maximum and minimum value was observed for *R. arboreum* (37.00) and *M. esculenta* (27.46) during winter season at elevation range 1701–1980 amsl, respectively Supplementary (Table 1). However, for SLA was significant with maximum for *M. esculenta* (11.76) during monsoon season and minimum for *R. arboreum* (5.22) during winter season at elevation range 1701–1980 amsl for both species. LDMC was significant with maximum for *Q. leucotrichophora* (0.64) during winter season at elevation range 1701–1980 amsl, whereas minimum for *M. esculenta* (0.233) during monsoon season at elevation range 1400–1700 amsl.

4.2. Variation in leaf physiological traits of major tree species of the BOF

Significant difference was observed among species, and season for all the six physiological parameters, however, for the elevation range significant differences were observed for A, E and IWTU. No variation was observed for the interaction between elevation range and season for any of the physiological traits i.e., the values for each physiological trait for various elevation ranges under the three seasons did not differ. However, variation in values for each physiological trait was observed for the interaction between the three species under the three seasons. Gs, Ci and IWTU were significantly different for the interaction among species, seasons and elevation range (Table 4). Maximum and minimum A was observed in *R. arboreum* during monsoon and winter season, respectively. Stomata behavior (Gs) in terms of stomatal conductance was recorded maximum for *R. arboreum* which was similar in *Q. leucotrichophora*. Maximum and minimum stomatal conductance was recorded in *R. arboreum* during summer and winter seasons (Supplementary Table 2). Maximum stomatal conductance was recorded in *R. arboreum* during monsoon season and lowest in R. arboreum during winter season at upper elevation (Supplementary Table 2). Ci was recorded maximum in *Q. leucotrichophora* which was similar in *R. arboreum* (Table 4; Supplementary Table 2). Maximum Ci was recorded in *R. arboreum* during monsoon season at upper elevation and minimum in *M. esculenta* during winter season at lower elevation (Supplementary Table 2). Among the different tree species maximum E was observed in *Q. leucotrichophora*, which was similar in *M. esculenta*. Maximum and minimum E was observed in *Q. leucotrichophora* and *M. esculenta* during summer and winter season, respectively. Maximum E was observed during summer season at upper elevation and minimum during winter season at lower elevation (Supplementary Table 2). WUE was recorded maximum in *R. arboreum*, which was similar in *M. esculenta*. Maximum and minimum WUE was observed in *M. esculenta* and *Q. leucotrichophora* during winter summer season, respectively (Supplementary Table 2). IWTU was recorded maximum in *M. esculenta*, which was similar in *Q. leucotrichophora*. Maximum IWTU was recorded in *Q. leucotrichophora* during monsoon season at lower elevation and minimum in *R. arboreum* during monsoon season at upper elevation (Supplementary Table 2). A was significant for three way interaction i.e. species, season and elevation and maximum (11.43) was noted at elevation 1701–1980 amsl during monsoon and minimum (6.48) was noted at elevation 1400–1700 amsl during winter season for *M. esculenta* (Supplementary Table 2). Gs was significant with maximum (0.31) and minimum (0.10) for *R. arboreum* during monsoon and winter season, respectively at elevation 1701–1980 amsl. Ci was significant with maximum (276.80) and minimum (152) for *Q. leucotrichophora* and *M. esculenta,* respectively at elevation of 1400–1700 amsl. Species and season interaction for E was significant with maximum (4.99) for *Q. leucotrichophora* during summer and minimum (1.63) for *M. esculenta* during winter season (Supplementary Table 2). WUE was significant and maximum (5.41) and minimum (2.21) were noted for *M. esculenta* during winter season and monsoon season, respectively. However, interaction of species, season and elevation for IWTU was significant with maximum (77.23) and minimum (31.46) for *Q. leucotrichophora* and *R. arboreum,* respectively, during monsoon season at elevation range 1400–1700 amsl (Supplementary Table 2).

4.3. Variation in leaf biochemical traits of major tree species

Significant difference was observed among species only for LCC and LNC however, significant differences were observed for season for all the biochemical traits except LCC. Among interaction between factors significant differences were observed for LNC, LKC, PNUE, and PPUE for species and season; whereas LCC, LKC, and PPUE and for species, seasons and site (Table 5). LCC was maximum (Table 5; Fig. 3) in *Q. leucotrichophora*, which was similar in *M. esculenta*. Maximum and minimum LCC and LNC were recorded in *Q. leucotrichophora* and *R.*

Table 4

Leaf physiological traits variation during seasons at two elevations.

Species	A (μmol CO_2 m^{-2} s^{-1})	Gs (mol H_2O m^{-2} s^{-1})	Ci (μmol CO_2 mol^{-1})	E (mmol H_2O m^{-2} s^{-1})	WUE (mmol H_2O m^{-2} s^{-1})	IWTU
Q. leucotrichophora	9.25 ± 1.55^{a}	0.186 ± 0.052^{a}	236.61 ± 46.52^{a}	3.70 ± 1.57^{a}	$3.73 \pm 1.22\ ^{a}$	54.45 ± 19.60^{ab}
M. esculenta	8.52 ± 1.47^{b}	0.163 ± 0.036^{b}	189.28 ± 39.89^{b}	3.20 ± 1.51^{ab}	3.62 ± 1.59^{b}	60.67 ± 15.09^{a}
R. arboreum	9.68 ± 1.89^{a}	0.202 ± 0.085^{a}	226.25 ± 51.06^{a}	2.80 ± 1.12^{b}	3.02 ± 1.47^{b}	52.86 ± 7.76^{b}
p-value	<0.0001	<0.0001	<0.0001	<0.004	<0.043	<0.057
Season						
Winter	8.20 ± 1.57^{c}	0.138 ± 0.033^{c}	176.34 ± 34.50^{c}	2.10 ± 0.81^{b}	4.35 ± 1.48^{a}	61.68 ± 14.95^{a}
Summer	9.71 ± 1.07^{b}	0.189 ± 0.036^{b}	218.56 ± 45.44^{b}	3.97 ± 1.52^{a}	3.04 ± 1.37^{b}	56.72 ± 15.01^{a}
Monsoon	10.32 ± 1.44^{a}	0.223 ± 0.077^{a}	257.23 ± 31.58^{a}	$3.63 \pm 0.1.19^{a}$	2.98 ± 1.08^{b}	49.48 ± 20.85^{b}
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.002
Elevation range						
(1400–1700) amsl	9.08 ± 1.49	0.187 ± 0.061	220.08 ± 49.94	3.01 ± 1.40	3.60 ± 1.50	52.42 ± 15.37
(1701–1980) amsl	9.74 ± 1.71	0.180 ± 0.065	214.68 ± 50.22	3.45 ± 1.47	3.31 ± 1.41	59.56 ± 19.32
p-value	0.005	0.379	0.290	0.039	0.220	<0.012
Interaction p-value						
Elevation range × Season	0.911	0.306	0.381	0.303	0.489	0.477
Species × Season	<0.0001	<0.0001	<0.001	<0.041	<0.029	<0.0001
Species × Elevation	<0.026	0.235	<0.0001	0.231	0397	0.172
Species × Season × Elevation	0.109	<0.0001	<0.039	0.490	0.483	<0.004

Table 5
Leaf biochemical and stoichiometric traits variation during seasons at two elevations.

Species	LCC (%)	LNC (%)	LPC (%)	LKC (%)	PNUE	PPUE	C/N	N/P
Q. leucotrichophora	47.46 ± 2.20^{a}	1.59 ± 0.09^{a}	0.289 ± 0.015	0.46 ± 0.24	5.84 ± 0.82	43.84 ± 29.43	29.83 ± 1.39^{ab}	7.60 ± 5.01
M. esculenta	46.65 ± 2.20^{a}	1.55 ± 0.10^{ab}	0.319 ± 0.15	0.47 ± 0.25	6.15 ± 1.08	41.04 ± 30.71	30.19 ± 2.41^{a}	6.97 ± 5.43
R. arboreum	44.50 ± 2.39^{b}	1.54 ± 0.16^{b}	0.299 ± 0.14	0.49 ± 0.22	6.21 ± 1.21	37.94 ± 16.29	29.17 ± 3.14^{b}	6.71 ± 3.90
p-value	<0.0001	<0.005	0.385	0.138	0.138	0.378	<0.048	0.381
Season								
Winter	46.25 ± 2.32	1.57 ± 0.09^{b}	0.14 ± 0.05^{c}	0.25 ± 0.02^{c}	5.18 ± 0.85^{c}	66.12 ± 30.65^{a}	29.38 ± 1.79^{b}	12.57 ± 4.56^{a}
Summer	45.91 ± 2.85	1.62 ± 0.13^{a}	0.41 ± 0.19^{a}	0.80 ± 0.04^{b}	5.99 ± 0.69^{b}	26.13 ± 10.05^{b}	31.09 ± 2.34^{a}	4.37 ± 0.96^{b}
Monsoon	46.44 ± 1.98	1.48 ± 0.11^{c}	0.35 ± 0.09^{b}	0.38 ± 0.06^{a}	7.10 ± 1.14^{a}	30.57 ± 8.98^{b}	28.72 ± 2.54^{b}	4.34 ± 1.53^{b}
p-value	0.524	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Elevation range								
(1400–1700) amsl	45.98 ± 2.25	1.54 ± 0.12	0.301 ± 0.15	0.48 ± 0.25	5.93 ± 1.24	40.78 ± 27.61	29.89 ± 2.54	7.27 ± 5.18
(1701–1980) amsl	46.43 ± 2.53	1.57 ± 0.12	0.304 ± 0.14	0.47 ± 0.23	6.20 ± 1.19	41.10 ± 24.89	29.54 ± 2.34	6.92 ± 4.42
p-value	0.247	0.110	0.860	0.444	0.77	0.924	0.398	0.517
Interaction p-value								
Elevation range × Season	0.320	0.095	0.372	<0.005	0.803	0.899	<0.013	0.532
Species × Season	0.470	<0.002	0.431	<0.001	<0.0001	<0.018	<0.002	0.486
Species × Elevation	0.204	0.138	0.303	0.184	0.108	0.102	0.662	0.110
Species × Season × Elevation	<0.051	0.252	0.191	<0.050	0.220	<0.025	<0.015	0.082

arboreum. Maximum and minimum LCC was observed in *Q. leucotrichophora* and *R. arboreum* during winter and summer season, respectively and maximum LNC was observed in *R. arboreum* during monsoon season. LKC was recorded high during summer season with maximum and minimum was recorded in *Q. leucotrichophora* and *M. esculenta* during summer and winter season, respectively (Supplementary Table 3). Maximum and minimum PNUE was recorded in *R. arboreum* during summer and winter season respectively. Maximum and minimum PPUE was recorded in *Q. leucotrichophora* and *M. esculenta* during winter and monsoon season respectively. Maximum PPUE was recorded in *Q. leucotrichophora* during winter season at upper elevation and lowest in *R. arboreum* during monsoon season at lower elevation (Supplementary Table 3).

4.4. Variation in leaf stoichiometry traits of major tree species

Significant difference was observed among species only for C/N stoichiometry trait; however significant differences were observed for C/N and N/P for season. Among interaction between factors, significant differences were observed for C/N for species and season; and for species, seasons and site (Table 5). Maximum C/N was recorded at upper elevation during summer season, whereas lowest was recorded at upper elevation during winter season (Supplementary Table 3). Highest C/N was recorded in *R. arboreum* during summer season at upper elevation, whereas lowest was recorded in *R. arboreum* during winter season at upper elevation. Species, season and elevation interaction for C/N was significant and maximum (33.23) was observed for *R. arboreum* during summer season at elevation of 1400–1700 amsl, and minimum (26.90) for *R. arboreum* during monsoon season at elevation of 1701–1980 amsl (Supplementary Table 3).

4.5. Relationship among leaf traits of temperate tree species

LA was significantly and positively correlated to SLA, A, Gs ($r = 0.31$), Ci, E and LNC ($r = 0.32$). However, SLA was significantly positively correlated to A, Gs, Ci, E ($r = 0.70$), LCC, LNC and LPC ($r = 0.51$). Moreover, LDMC was significantly negatively correlated with A, Gs ($r = -0.47$), Ci ($r = -0.58$), E, LNC and LPC. Physiological trait i.e., A was significantly positively correlated with Gs, Ci, E ($r = 0.48$), LCC ($r = 0.36$) and LPC. However, Gs was significantly positively correlated with Ci ($r = 0.60$), E, LNC and LPC ($r = 0.41$). Ci was significantly positively correlated with E ($r = 0.31$), LNC and LPC and E was significantly positively correlated with LCC and LPC ($r = 0.43$). Biochemical trait i.e., LCC was significantly positively correlated with LNC ($r = 0.26$) (Fig. 4).

SEM provided information about the various latent relationships between the studied traits and also along the four latent factors i.e., among RCD, GE, PRU, and NCL (Fig. 2b). The test statistics for SEM was $\chi^2 = 1650.001$, d.f. = 98.00, p = < 0.000, AIC = 5208.99, showing goodness of fit of the model (Fig. 5). RCD was directly related to LA ($\beta = 0.32$), SLA ($\beta = 1.37$) and indirectly with LDMC ($\beta = -0.43$). GE was directly related to A ($\beta = 0.50$), Gs ($\beta = 0.12$), Ci ($\beta = 0.27$), E ($\beta = 1.09$) and negatively with WUE ($\beta = -0.79$). PRU was directly related to LCC ($\beta = 0.26$), LNC ($\beta = 0.99$), LPC ($\beta = 0.15$) and negatively with LKC ($\beta = -0.39$) and PNUE ($\beta = -0.46$). PRU was directly related to LCC/LNC ($\beta = 0.90$), and negatively with LCC/LPC ($\beta = -0.09$) and LNC/LPC ($\beta = -0.90$). RCD was positively linked with GE ($\beta = 0.42$), while PRU was negatively linked with NCL ($\beta = -0.90$). LA negatively co-vary with SLA and positively co-vary with LDMC for defining the resource utilization. However, LCC was positively co-vary with leaf C/N (Fig. 5).

Moreover, the PCA analysis results into two factors model with 75.64 percent variability. The first principal component was positively correlated with SLA and E and negatively with LDMC explaining 37.67 percent variability. The second principal component was positively correlated with LA (Table 6).

5. Discussion

5.1. Seasonal differentiation among leaf traits

Our study reported that morphological traits i.e., LA and LMA were significantly higher for *R. arboreum*; SLA significantly higher for *M. esculenta* and *Q. leucotrichophora*, and LDMC was higher for *Q. leucotrichophora* (Table 3). Seasonal variations in these traits were also observed except for LA. No discernible seasonal trend was observed for LA in the study, probably might be due to the evergreen nature of the species (Zhang et al., 2020). Higher LDMC of *Q. leucotrichophora* is evidenced from trade-offs between biomass production and nutrient conservation (Wright et al., 2005) besides adjustments of response of these species to the seasonal change (Tian et al., 2016). Seasonal variation in SLA in coexisting species supports to appropriately use the available resources in response to light intensity against the leaf thickness of the species (Tian et al., 2016), as a result, low SLA was observed in *R. arboreum*, due to high demand for non-structural carbohydrate production in the meristem (Liu et al., 2016). High SLA during monsoon

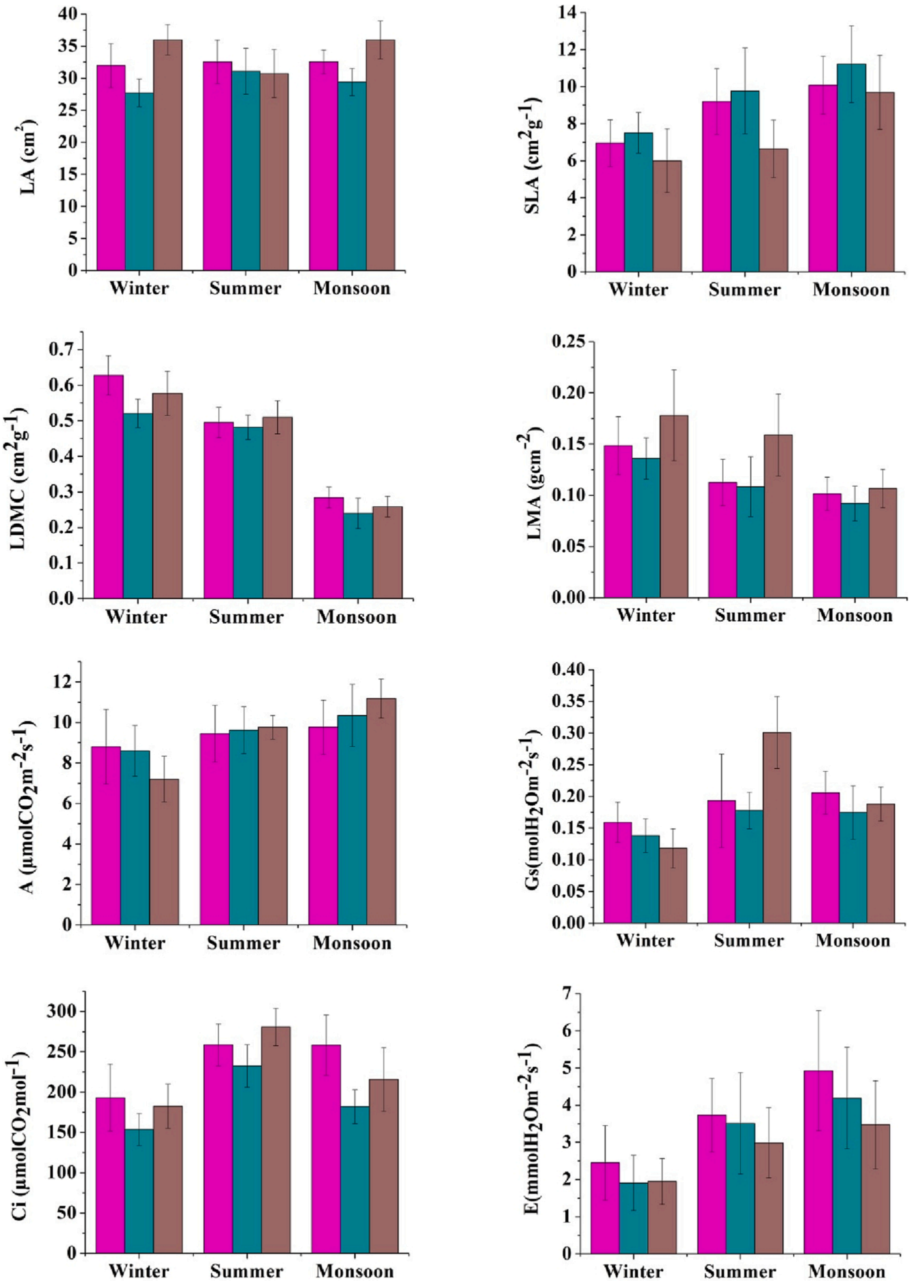


Fig. 3. Leaf traits seasonal variation in major tree species of BOF. Vertical bars indicate (±) standard error.

season is due to the plasticity of leaf traits against the response to light (Liu et al., 2016), while high LDMC during the winter season is due to increased cell wall thickness of mesophyll and structural tissue (Tosens et al., 2012). High mesophyll thickness in *Q. leucotrichophora* leaves, may be characterized by a high LDMC, and affects CO_2 assimilation rate and subsequently enhances WUE through photooxidation as also reported by Bargali et al. (2015). The high LMA in *R. arboreum* determine high leaf thickness during winter season and influences the anatomical tissue and chemical composition as reported by de la Riva et al. (2016). Moreover, higher LMA contributes to long life leaf span, nutrient concentration, and protection from desiccation (de la Riva et al., 2016), in contrast, lower LMA supports an advantage in resource uptake efficiency, by increasing the absorption surface per unit of tissue biomass (Wright et al., 2004). Therefore, *M. esculenta* may has an edge for resource uptake efficiency than the remaining two species of the BOF.

Leaf physiological traits responded significantly towards seasonal changes. *Q. leucotrichophora* had significantly higher value for most of the observed physiological traits than the other studied species, however similar to *R. arboreum* for A and Gs (Table 4). During monsoon season, all physiological traits were significantly higher than summer and winter except WUE and IWTU. Our results determined that the CO_2 assimilation rate was higher for *R. arboreum* and *Q. leucotrichophora* during monsoon. The probable reason for the variation may be attributed to the transition phase of leaves and high photosynthesis rate during the period, which enhance the carbon fixing and capturing in plants as reported by Nasr (2012). Moreover, photosynthesis rate is also influenced by rubisco enzyme, and water availability in temperate broad-leaved deciduous forest (Miyazawa and Kikuzawa, 2005); leaf age, stomatal conductance, nutrient status, and position of leaf axis towards the sun (Liu et al., 2019). Our study also observed significantly higher stomatal conductance in the monsoon season, which might be due to the availability of water in the soil and higher light intensity

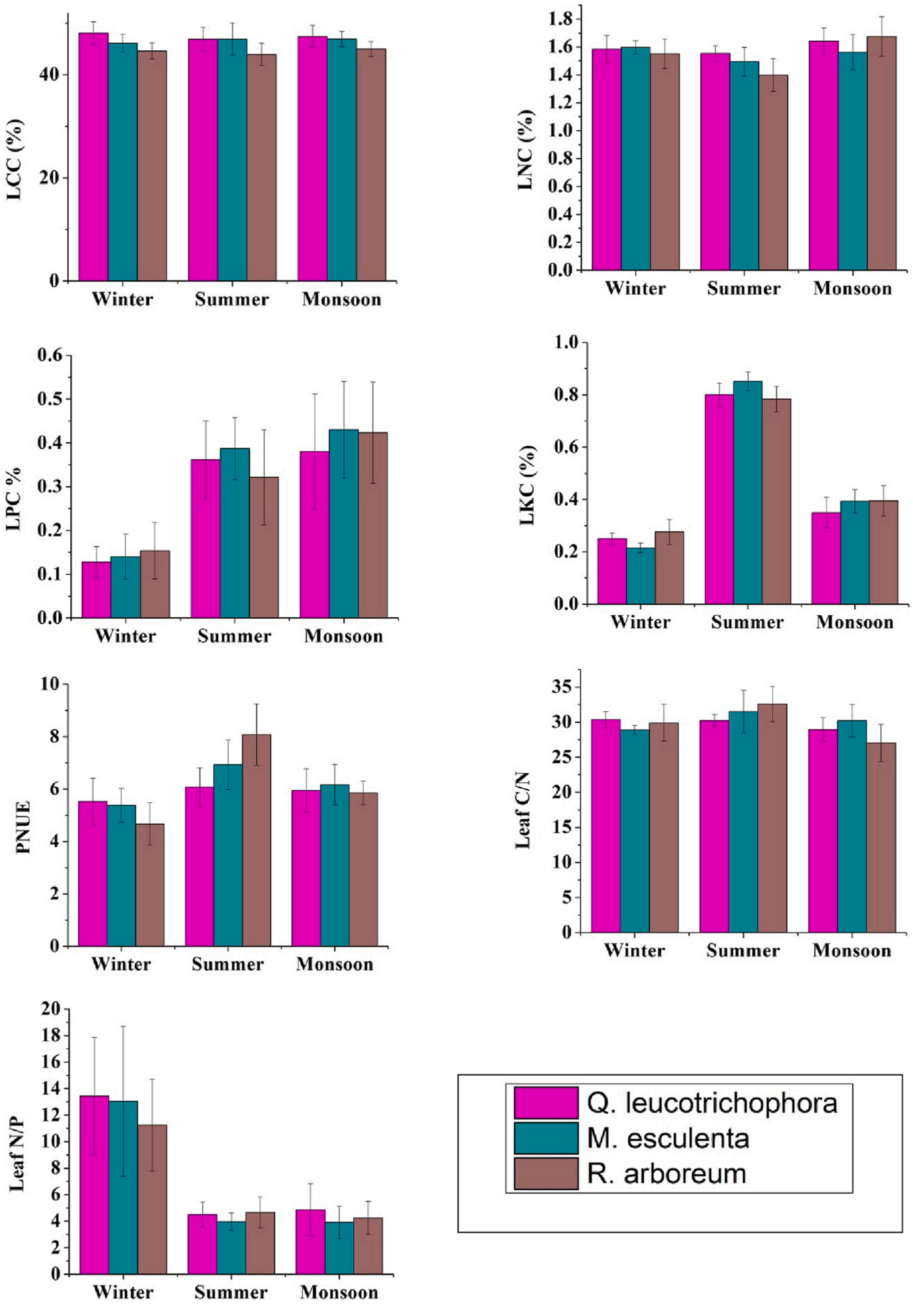


Fig. 3. (*continued*).

leading to enhance the rate of photosynthesis (Carmo-Silva et al., 2010). Water transportation through the xylem is high during monsoon season, putting turgor pressure on the stomatal guard cell and leading to open of stomata, resulting in a higher rate of transpiration and photosynthesis rate in the plant (Kim et al., 2014). Intercellular CO_2 concentration (Ci) was also higher in the monsoon season in present study. Higher Ci in the *R. arboreum* and *Q. leucotrichophora* may enhance photosynthesis rate, as also reported by Boretti and Florentine, (2019). The higher Ci in *R. arboreum* and *Q. leucotrichophora* might be due to more light-independent reaction, which increases the internal CO_2 concentration by increasing the rate of carbon incorporation into carbohydrates (Thompson et al., 2017). Our study results were similar to the findings of Purcell et al. (2018), who reported that the stomatal conductance is increased during summer and monsoon seasons resulting in minimizing the WUE. Furthermore, significantly higher WUE during winter season in *Q. leucotrichophora* is attributed to plants exposed to the dormant period which fix carbon molecules through photosynthesis rate and less investment of fixing water molecule per carbon molecules, as also reported for the subtropical forest (Wu et al., 2018). IWUE was found maximum in the winter and summer seasons and might be due to the efficient relationship between water and carbon coupling (Sharma et al., 2018) or might be due to moisture deficiencies, which alter the balance between vegetative carbon uptake and water loss (Zhang et al., 2019).

Biochemical trait response of species shows that LCC and LNC were significantly higher for *Q. leucotrichophora* and *M. esculenta* (Table 5). Higher value of LCC might be due to higher resource allocation to plant tissues, leading to increase structural carbon concentrations as also reported in *Nepenthes* species (Osunkoya et al., 2008). Variations in LCC indicate differences in the distribution and utilization of photosynthetic products, and different combinations of various compounds with different carbon costs (Han et al., 2011). Structural carbon is primarily concerned with the components of plant cell walls that provide

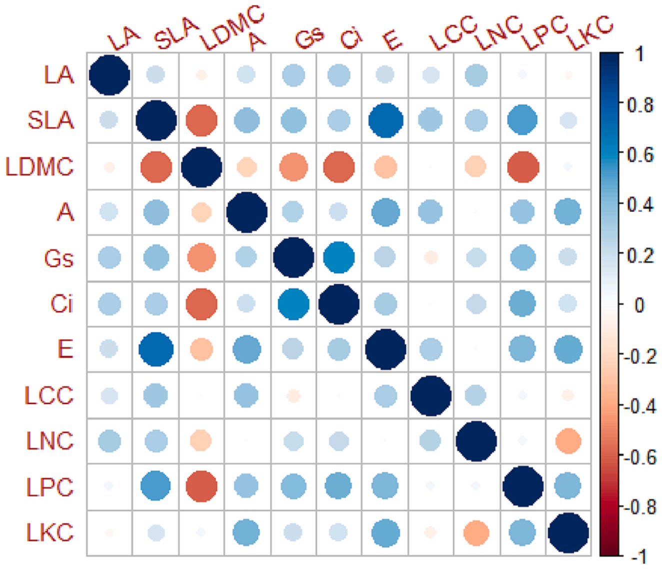


Fig. 4. Correlation matrix between different leaf traits.

biomechanical support and protection to plant tissues (Niinemets and Tamm, 2005). The present study determined that LNC was found maximum during monsoon season, which might be due to increased nutrient re-absorption in plant tissues as reported by Niinemets and Tamm (2005). LNC, LPC and LKC were high during monsoon season due to the high intensity of temperature and precipitation during the period as reported in other plant species of China (Han et al., 2005). Moreover, variation in leaf nutrient concentration at the species level during different seasons is determined by the abundance of species at the community level and the associated trade off and the nutrient uptake capacity of the species from soil in different seasons (Tang et al., 2018). The high PNUE during the monsoon season could be due to high light interception and nitrogen concentration (Alberts et al., 2002). Higher PNUE may indicate that the species invested a higher proportion of N in photosynthetic mechanism as reported by Tang et al. (2018). High PPUE during winter season might be due to low concentration of foliar P and LMA during the period in the present study.

Stoichiometry of leaf macronutrients provides insight into the trade-offs between leaf structural and metabolic investments. In the present study, leaf C/N (Table 5; Fig. 5) was significantly higher during summer season in *M. esculenta* and *Q. leucotrichophora*. High value of leaf C/N is a phenomena of optimum conditions for soil microbial activity in tropical and temperate forests (Zhang et al., 2020) and measures a plant's ability to assimilate carbon and nutrient use, to some extent (Qin and Shangguan, 2019). Leaf N/P was significantly higher during the winter season due to low LPC during the season. N/P<14 showed N limitation in leaf concentration, and mainly due to the acidic soil of the BOF as also reported by Soudzilovskaia et al. (2005). Leaf N/P reflects the

Table 6
Principal components analysis for leaf trait in Banj oak forest.

Variable	PC-1	PC-2
LA	0.32	**0.72**
SLA	**0.86**	−0.25
LDMC	−0.71	**0.37**
A	0.58	0.32
E	**0.74**	0.05
Gs	0.62	0.22
Ci	0.61	0.21
LCC	0.30	0.14
LNC	0.28	0.07
LPC	0.71	−0.19
Percent variation explained	37.67	75.64
Eigen values	4.52	1.16

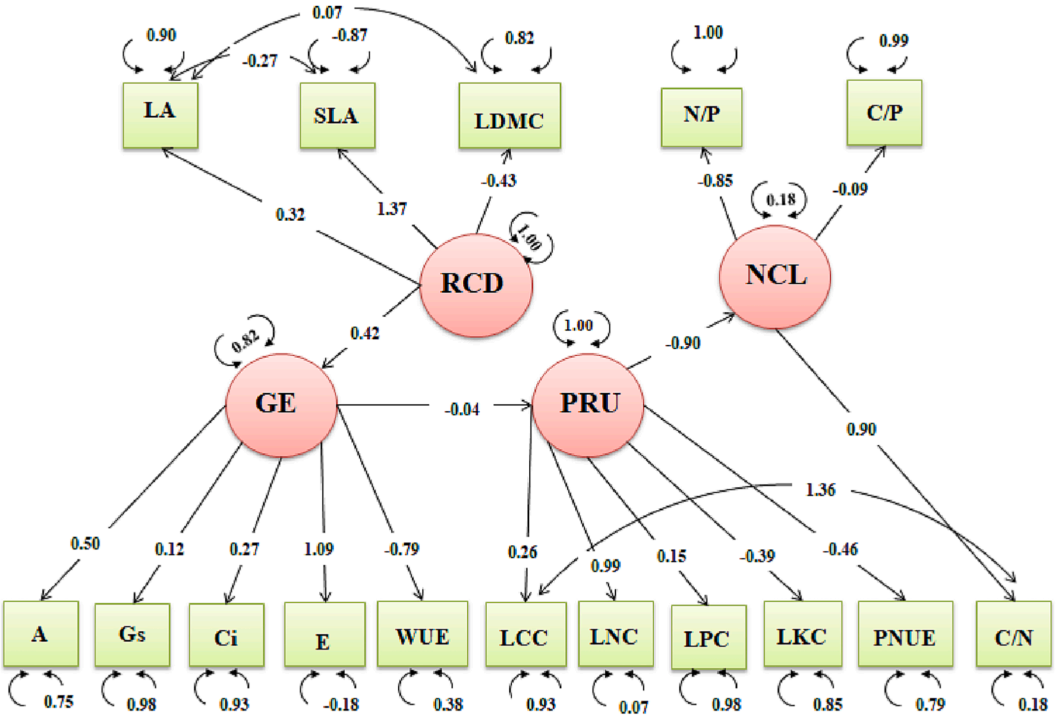


Fig. 5. SEM results of the relationship between latent variables with leaf traits of BOF (Square and circular nodes indicate manifest and latent variables respectively. Directed edges indicate one variable effect on another variable i.e., linear regression parameters, whereas bidirectional edges indicate co-variance between two variables. However, circular curved arrows represent the variable variance. Path coefficients represent standardized partial regression coefficients. Latent variable RCD (LA + SLA + LDMC), GE (A + Gs + Ci + E + WUE), PRU (LCC + LNC + LPC + LKC + PNUE) and NCL (LCC/LNC + LCC/LPC); and regression were GE vs RCD and PRU vs GE and NCL vs PRU and the residual covariance were SLA vs LA and LDMC vs LA and LCC/LNC vs LCC.).

biogeochemical cycle and vegetation composition, functioning and nutrient limitation at the community level and is affected by temperature and latitude (Güsewell, 2004).

Higher SLA indicated that *Q. leucotrichophora* and *R. arboreum* were important tree species as higher SLA control the productivity and biomass accumulation in the forest ecosystem similar result was reported by other studies also (Finegan et al., 2015; Rawat et al., 2019). Higher LDMC in *Q. leucotrichophora* indicates higher efficient use of resources indicating conservation strategies and productivity in comparison to *M. esculenta* and *R. arboreum* reported by other study (Smart et al., 2017). *M. esculenta* has better resource uptake strategies may be due to it capture high light due to its higher LMA reported by other study also (Davi et al., 2008; Poorter et al., 2009) than *Q. leucotrichophora* and *R. arboreum*. WUE and IWTU traits indicated that *Q. leucotrichophora* and *M. esculenta* species performed well in the relationship between carbon coupling and water use as WUE increases with rise in CO_2 concentration in the environment (Mathias and Thomas, 2021; Soh et al., 2019). High stomatal conductance (Gs) and CO_2 assimilation by *Q. leucotrichophora* and *R. arboreum* species was might be due to high photon absorption per unit area to expand vessel cell diameter with respect to seasonal changes other study also reported the similar findings (Kröber and Bruelheide, 2014). The result of LCC, LNC and LPC revealed that *Q. leucotrichophora* was important species in controlling the ecological process i.e. nutrient cycling on BOF forest due to nutrient allocation and re-translocation in different parts of the tree i.e., leaf, stem and root (Khan et al., 2022; Tang et al., 2018).

5.2. Latent relationship for the functionality of temperate species

RCD depicts resource (light and water) uptake strategy of the plant and had a strong positive relationship with SLA and weak positive with LA and weak negative relation with LDMC in the BOF. The relationships of SLA and LA with RCD may assist to high light interception and potential growth rate to the forest community by regulating nutrient cycling and water gradient (Gao et al., 2022), and it also assist in effective resources utilization and accumulation of organic matter for functioning (Evans and Poorter, 2001) by maintaining the CO_2 assimilation rate (Pringle et al., 2011) in forest ecosystem. Strong relationship of SLA with RCD strategy signifies carbon allocation, moderate rate of development, and high tolerance to pathogenic and fungal infection besides facilitating to robustness to mechanical damage (Gianoli and Salgado-Luarte, 2017). The strong relationship between SLA and RCD demonstrate that SLA is major morphological trait to explain resource utilization for the functioning of Ban Oak forests reported by other also (Liu et al., 2016; Rawat et al., 2019).

GE was having a strong and weak positive relationship with E and A respectively, however, had negative relationship with WUE. Positive relation with E shows that the association between transpiration and sap flow has an impact on a plant's vitality and assist a plant under direct sunlight to overheat (Simon et al., 2018) besides better allocation of mineral and water in different structural part of the plant in xeric and mesic condition (Lévesque et al., 2014). Positive relation with A may indicate carbon stability in soil and plant systems (Fig. 5). Moreover, high resource utilization by the plants facilitates high exchange of gases. However, the negative relationship between GE and WUE could be due to stomatal conductance and water loss decreasing in comparison to carbon fixation in plants during drought conditions. (Edwards et al., 2012).

PRU was having positive strong relationship with LNC and weak relationship with LKC and PNUE. High LNC assists to maintain the abundance of rubisco enzyme, increase photosynthetic capacity, and improve leaf longevity and carbon uptake (Onoda et al., 2017). However, weak relationship of LKC with PRU might be due to low availability of K in leaves, which may restrict the metabolism and photosynthesis activity in the plant. In contrast, positive relationship of LKC with PRU supports growth and metabolism activities of the plants (Li et al., 2021; Lu et al., 2019) Negative relation with PNUE might be due to the rapid nitrogen losses by different processes such as denitrification in temperate and tropical forests (Fang et al., 2015).

NCL is having a strong (0.90) positive relationship with leaf C/N and strong negative relation with leaf N/P. The high C/N in evergreen forest community regulates growth, remobilize stored lipid and also facilitate to photosynthetic gene expression (Chen et al., 2015). Biomass dominance may shift from photosynthetic to structural tissue as the C/N ratio in plant tissue rises in broadleaved evergreen forests (Ågren, 2008).

Overall, the obtained results determined that SLA (morphological trait), E (physiological trait), LNC (biochemical trait) and leaf C/N (stoichiometry trait) determine the plant strategies of BOF. Moreover, all the three studied species of the ban oak forest had resource conservative strategies. Moreover, *Q. leucotrichophora* was a major species for the forest functioning in the forest whereas *M. esculenta* had higher resource uptake efficiency. Overall, leaf traits were varied with different species and seasonal changes facilitate an adaptive role in a plant's survival under the existing microclimatic condition.

6. Conclusion

Mechanism of leaf trait variation along with changing climatic conditions is important for understanding the functioning of Himalaya Forest ecosystem. Present study concludes that the major temperate species i.e., *Q. leucotrichophora, M. esculenta and R. arboreum* were associated with different plant strategies i.e., RCD, GE, PRU and NCL. Moreover, species acquire resource assimilation strategy for their growth during winter. However, among all the studied leaf traits SLA, E, LNC, and leaf C/N were the significant traits to control the plant functioning and among the species *Q. leucotrichophora* was a major tree species for regulating the functioning of BOF. Overall, leaf traits were varied with different species and seasonal changes facilitate an adaptive role in a plant's survival under the existing microclimatic condition. The findings of the study provide insight into changes in leaf traits and the plant strategies at the temperate forests of the Himalayas with seasons and provide the foundation for projection future changes in leaf attributes and the environment's adaptation at Himalaya and regional level.

Ethical approval

Not applicable.

Consent to publish

Not applicable.

Author contribution

RS and RP conceptualized and designed the study; RS collected and analyzed the data with the support of RP and written the first draft; RS, MR and RP interpreted the analysis, RS developed first draft with consultation with MR; RP, RS and MR modified the final manuscript. All have contributed extensively for data interpretation and discussions. All authors consented for the publication.

Availability of data and materials

The datasets used during the current study are available from the corresponding author on reasonable request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110212.

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