Modulation of plant functional traits under essential plant nutrients during seasonal regime in natural forests of Garhwal Himalayas

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Abstract
Aim We estimated how seasonality in conjunction with key climatic variables affects morphological and physiological plant functional traits (PFTs) and soil essential (micro and macro) nutrients in oak, pine, and mixed forests.

Method The different PFTs were tested using several laboratory methods and using the portable photosynthesis system Li-COR 6400 XT, Lincoln NE, USA. Likewise, some chemical traits and soil nutrients were analyzed by using CHNS analyzer.

Results In this study, physiological traits such as CO₂ assimilation rate, stomatal conductance and transpiration rate were significantly higher in the rainy season followed by summer and winter seasons. Among the different forest land uses, physiological traits and resource use efficiency have been significantly higher in oak forest (OF) compared to the mixed forest (MF) and pine forest (PF). Likewise, the concentration of macro–micro nutrients was also recorded higher during the rainy season. The concentration of macro–micro nutrients was higher in OF than in MF and PF in different forest land uses.

Conclusion Changes in PFTs ultimately affect the ecosystem services imparted by the different forests. Such changes lead to the local adaptation of these forests through the interaction between PFTs and soil nutrients.

Keywords Macro–micro nutrients · Physiological traits · Resource use efficiency · Seasonal climate

Introduction
Nutrients are indispensable for plants and alteration of nutrient composition adversely affects the physiological and metabolic functioning of plant systems. The deficiency of essential nutrients causes stressful plant conditions, leading to several changes in the morphological and physiological behavior of plants. These changes lead to alternating metabolic pathways and show some disorders in plants, such as accumulation of anthocyanin, chloroplast disintegration, and chlorophyll loss (Jun-Hao et al. 2016; Farhat et al. 2016). Besides, some micronutrients such as manganese (Mn), zinc (Zn), copper (Cu) and iron (Fe) also play a key role in plant physiological functioning and under deficient conditions, they limit the synthesis of many enzymes in the plant system that further adversely affect plant metabolism and physiological functioning (Terauchi et al. 2010).

The difference in seasonality like drought (summer), wetness (rainy), and transition phase between autumn and spring have a significant effect on morphological and physiological traits such as
photosynthesis and stomatal activity and transpiration. These modified changes in seasonality and plant physiological traits also affect the carbon allocation (above and below ground), plant nutrient absorption and other related features of soil and plant (Kassem et al. 2008; Perez-Harguindeguy et al. 2013). For instance, litterfall is caused in a particular season which decomposes in optimum climatic conditions and contributes various nutrients to the soil in the form of organic compounds.

There is little information on the status of macro and micro-nutrients and their critical levels in forest soils. The physiological traits are responsible for regulating the metabolic activities of the plant system, which ultimately affects plant growth and development. These metabolic processes are regulated by the nutrient uptake capacity of the plant, which is associated with the amount and distribution of nutrients in the soil (Paudel and Vetaas 2014; Farhat et al. 2016). There is an urgent need to establish a physiologically based critical approach for diagnosing nutrients in different parts of the plant, their connection with productivity, and ensuring optimum plant functioning. The diagnosis of plant mineral deficiencies by visual symptoms and biochemical techniques are well established (Pandey et al. 2017), physiological techniques can be a new nutritional diagnostic method if in-situ physiological trait measurement is performed, so that data may be used to estimate and improve productivity. Globally, most mineral nutritionists only work on agricultural crops, not on forestry crops (Singh et al. 2018). Most of the research is also under refined conditions and does not include the relationship between functional traits of plants and macro–micro nutrients of the soil.

These macro–micro nutrients have been shown to be a sensitive indicator of forest types, topography, and changing climatic conditions across the seasons. Seasonal conditions have a direct effect on soil nutrients and their availability to the plants through interactions with other factor such as forest types, topography and landscape. The oak and pine are two dominated forest species in Garhwal Himalaya of India which is characterized by marked seasonality of rainfall and temperature that influence the nutrient cycling and net primary productivity. Nutrient availability in forest ecosystems is determined by the release of nutrients from the litter produced by the trees after decomposition. The decomposition process is influenced by the type and quality of substrate, composition, activity of microorganisms, and, more strongly on the climatic factor (i.e. rainfall, temperature and humidity). The availability and quantity of nutrients in forest ecosystems are thus primarily determined by the decomposition process, which is characterized by extreme seasonal variation in climatic variables (Ajwa and Tabatabai 1994). The existing knowledge on oak and pine forests, as well as mixed forests of these two species and their functioning in Garhwal Himalayas, shows that these forests are facing the problem of climate change (IPCC 2007; Kumar and Chopra, 2017; Kumar et al. 2021a). Because of changes in environmental variables in the Garhwal Himalaya, the functioning of these forests in terms of nutrient cycle and physiological process has been altered (Grierson and Adorns 2000; Kumar et al. 2012; Rawat et al. 2019).

Different leaf habits in trees, such as broadleaved (Quercus leucotrichophora) versus coniferous (Pinus roxburghii), are usually associated with different functional traits. In comparison to coniferous species, which tend to exhibit more-conservative traits, broadleaved species are characterized by acquisitive traits such as lower SLA, higher rates of photosynthesis and respiration, and higher nutrient concentrations (Rawat et al. 2020). The acquisition of resources is coupled and linked among plant organs. Resource acquisition is coupled and linked among plant organs. Thus, rapid acquisition and processing of water and nutrients via roots would necessitate fast acquisition and processing of carbon through leaves (Reich, 2014). A strong coordination between root morphology and leaf traits was also reported by several workers (Singh and Thadani 2015; Maranon et al. 2020).

The nutritional status and physiological functioning of these forests are still unknown, particularly about micronutrients. Difficulty in measuring these traits is a significant gap in information on the physiological functioning of forest crops. The relationship between nutrient usage effectiveness and physiological characteristics needs to be explored to enhance nutrient use efficiency. A limited study has been reported on the inter-relationship between physiological traits and essential nutrients (Micro and Macro-nutrients). With this background, we conducted this study with the following objectives (1) to assess the plant functional traits of different forests during seasonal regimes and (2) to elucidate the influence
of macro–micro nutrients on PFTs during seasonal regimes. We proposed two hypotheses in these two objectives: 1) The seasonal climate will have a significant impact on the PFTs of various forest land uses; 2) Macro–micro nutrients will strongly modulate the PFTs of different forest land uses during the seasonal regimes.

Materials and Methods

Study Site

The study was carried out in the Kempty watershed of Garhwal Himalaya, India from 2018–2019. The Kempty watershed is situated between 30°28.01′–30°28.54′ N, 78°1.50′–78°2.30′ E, with an average elevation of 1662 m and an average slope of 5.5%. The watershed is located in the middle part of the Indian Himalayas. The total area of the watershed was 870 hectares, of which 227, 188 and 211 hectares were covered by OF, PF and MF, respectively and the remaining area (244 hectares) was under rivers and open land. The area covered by respective forests, rivers and open land was calculated using the ArcGIS software. The selected forests come under the Himalayan temperate forest. The watershed is comprised of two types of forests i.e., Quercus leucotrichophora and Pinus roxburghii forest. Despite this, the forest consists of some other scattered tree species i.e., Quercus leucotrichophora A. Camus ex Bahadur, Quercus floribunda Lindl. ex A. Camus, Pinus roxburghii Sarg., Pinus wallichiana J. Jackson, Daphniphyllum himalayense Benth., Toona serrata M. Roem., Acer oblongum Wall. ex DC, Pyrus pashia Buch. & Ham., Cornus macrophylla Wall. and Myrica esculenta Buch.-Ham. Thus, in the present study, we focused on Quercus leucotrichophora forest (OF) and Pinus roxburghii forest (PF) and mixed forest (MF).

Climate and soil

The watershed climate varies from subtropical to temperate, annual precipitation ranges from 850 to 2200 mm with mean annual precipitation of 1250 mm. The snowfall in winters is a common characteristic of the area. The mean annual maximum air temperature in this watershed varied between 25.12 to 26.82 °C, and the mean annual minimum temperature fluctuated between 7.15 to 10.25 °C. However, the mean annual air temperature varied between 16.26 to 18.02 °C. Annual precipitations in the watershed ranged from 664.50 mm to 1370.80 mm and mean annual relative humidity varied from 55.60 to 95.15%. The texture of the soil is loamy clay, with moderate prone to erosion. The soil of the watershed was slightly acidic with average pH 6.4, bulk density 1.28 g cm⁻³, and organic carbon 2.58%. Mean annual soil moisture varied from 15.15% to 37.46%.

Vegetation analysis and field sampling

The forest of the watershed was surveyed before the data collection. The survey revealed that the watershed contains three types of forests i.e., Q. leucotrichophora forests (OF), P. roxburghii forests (PF) and mixed forest (MF). In a pure stand of Q. leucotrichophora and P. roxburghii forest, more than 80% of the trees in the main canopy were from a single species, whereas less than 80% of the trees in the main canopy were from a single species in a mixed forest (Bargali et al. 2018). The proportion of each species in mixed forest was approximately 45% (P. roxburghii) and 50% (Q. leucotrichophora) and 5% (some other scattered tree species) (Kumar et al. 2021b). The present study focused on these three types of forests and the samples were collected by using stratified random sampling. According to the structure of the watershed, we stratified the entire watershed into three strata i.e. Q. leucotrichophora forests (OF), P. roxburghii forests (PF) and mixed forest (MF). The oak species initiates leaf (bud) formation in the late winter season; it matures in the rainy season and sheds leaves in the early summer. Oak species begin flowering in early summer, fruiting in late summer, and fruit ripening in the winter (Kumar and Chopra 2017). In pine species, leaf initiation, male cone appearance and female cone ripen during the early winter season, while male and female cones dry up and wither during the summer. Leaf fall begins in the late summer, and male and female flowering begins in the late rainy season (Kumar and Sati 2016).

Sampling of plants and soil was performed in three different seasons: rainy (mid June–September), winter (October-February) and summer (April-mid June).
Randomly 10 (10×10 m) quadrates were staked out in each forest stratum, using a gridded randomization method in which the quadrates were selected on a non-replacement basis (Rawat et al. 2020). Three individual trees of each *Q. leucotricophora* and *P. roxburghii* forests were selected at random within each quadrate for the assessment of each trait. As a result, a total of 30 individual trees from each of the *Q. leucotricophora* and *P. roxburghii* forests were studied across the 10 quadrates. However, in mixed forest, four individual trees (2 trees of each species i.e. *Q. leucotricophora* and *P. roxburghii*) were selected at random within each quadrate to assess each trait. The leaf samples were collected from the bottom, middle and upper canopy of the tree. Then, the collected samples were composited, and ten samples were taken to analyze leaf traits. Ten leaf samples were collected from a tree, but a total of 300 (10 leaves × 3 trees × 10 quadrates = 300) leaf samples were taken from 10 (10×10 m) quadrates in each stratum of *Q. leucotricophora* and *P. roxburghii* forests and 400 (10 leaves × 4 trees × 10 quadrates = 400) leaf samples were taken from 10 (10×10 m) quadrates in for mixed forest. The measurement of plant traits and collection of soil samples was performed simultaneously (same sampling time was followed for the plant and soil samples) from all forest land uses. The plant and soil sample collection sites were also the same; soil samples were collected from the same quadrat from which plant samples were collected in all land uses.

**Leaf trait measurement**

In each of the 10 quadrates healthy and adult trees DBH > 10 cm at 1.3 m above the ground of *Q. leucotricophora* forest (OF), *P. roxburghii* forest (PF) and mixed forest (MF) were selected for the trait measurement. Healthy trees were categorized based on their physical appearance, i.e. a canopy with minimum dead branches and disease-free twigs, leaves, and bark was considered a healthy tree (Kumar et al. 2021a). The leaf area was measured by using Imagej software. For the analysis of leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC) and leaf carbon concentration (LCC), the fresh leaf was collected from each sampling points of each stratum. The collected samples were air-dried and then oven-dried to make powder for digestion. For the determination of total P in the leaf, the samples were digested using tri acid (HNO₃, HClO₄, and H₂SO₄ in 10:4:1 ratio) then the stock solution was prepared from the digested samples and phosphorus was determined by vanado molybdo- phosphoric yellow colour method by using spectrophotometer (Lu 2000). The total nitrogen and carbon concentration in leaf samples were analyzed using the CHNS (Euro, EA-3000) analyzer (Pansu et al. 2001). The all collected samples were analyzed separately for each stratum.

**Physiological traits measurement**

The physiological traits were measured in a natural condition (intact leaf to the canopy) with the help of a ladder at the seasonal interval (rainy, winter and summer), the healthy trees were selected and their canopy was stratified into three-layer i.e., bottom, middle and upper canopy then eight observations were taken from each layer of the canopy of all selected trees in each stratum. The physiological traits were measured in fully expanded leaves using an infrared gas analyzer (IRGA) (portable photosynthesis system Li-COR 6400 XT, Lincoln NE, USA instrument).

The following physiological traits were directly measured delta CO₂ and delta H₂O, leaf temperature, light intensity in the chamber and gas flux; while the following were indirectly measured, based on the algorithms, by the software of system; internal CO₂ concentration (Ci- μmol CO₂ m⁻² s⁻¹), transpiration (E- mmol H₂O m⁻² s⁻¹), stomatal conductance (Gs- mol H₂O m⁻² s⁻¹) and CO₂ assimilation rate (A-μmol CO₂ m⁻² s⁻¹), water use efficiency (WUE; A/E-μmol CO₂ mol⁻¹ H₂O), instantaneous carboxylation efficiency (CE; A/Ci), instantaneous mesophyll efficiency (ME; A/Gs-), physiological nitrogen use efficiency (NUE; A/N concentration in leaf sample) and physiological phosphorus use efficiency (PUE; A/P concentration in leaf sample) (Singh et al. 2018; Sharma et al. 2018).

The range of average monitored photosynthetically active radiation (PAR) was 1308, 1356 and 956 μ mol m⁻² s⁻¹ during rainy, summer and winter seasons. The average temperature of the site was 29 °C, 35 °C and 11 °C during rainy, summer and winter seasons, respectively. Likewise, the relative humidity of the
site was 93%, 82% and 88% during rainy, summer and winter seasons, respectively. The average precipitation for rainy, summer and winter seasons was 960, 85 and 300 mm, respectively.

Macro and micronutrient analysis

Soil samples (0–30 cm soil depth) were collected from each of the 10 (10×10 m) quadrates in each stratum, and the collected samples were composited to make four replications in each stratum (total 4 replications×3 forests = 12 samples were taken). The collected samples were air-dried and sieved, and then different macro–micro nutrients were analyzed. The total N (nitrate and ammonium form) was estimated from fresh and processed soil samples using the CHNS (Euro, EA-3000) apparatus (Pansu et al. 2001). The standard technique for preparing samples into small tin capsules, in the form of tiny pellets was followed. About 15 mg of soil, which was finely ground and passed through a 0.2 mm sieve, was taken and placed into the tin capsules. The open end of the capsule was sealed carefully with the help of a pair of forceps and then the sealed capsules were placed in the sample distributor of the CHNS (Euro, EA-3000) apparatus. Those samples ran with the help of a software program of the CHNS analyzer. Soil total P was measured by the molybdenum blue colorimetric method using HClO₄-H₂SO₄ solution for digestion.

For micronutrient 1.0 g of the soil sample, weighed into a 120 ml Teflon PFA microwave digestion vessel and 10 ml of concentrated HNO₃ was added (EPA Method 3051, USEPA, 1986). Then samples were capped and weighted to determine possible acid loss during digestion. The samples were then digested in a CEM 2000 Microwave digester at 100 lb per square inch (PSI) for 5.5 min (CEM Corporation, Matthews, NC). Samples were then filtered through Whatman 42 Filters and transferred to 100 ml volumetric flasks. Samples with weight loss of greater than 10% were re-digested. The final samples were kept in the refrigerator at 4 °C until the analysis of different micronutrients. After that, the concentration of different micronutrients like (Mg), manganese (Mn), zinc (Zn), copper (Cu), and iron (Fe) were analyzed using flame atomic absorption spectroscopy (FAAS) (PerkinElmer, LI-5310).

Statistical Analysis

The significance of all PFTs and macro–micro nutrients were assessed by two-way analysis of variance (ANOVA). Comparison among the PFTs and macro–micro nutrients in all seasons under all forest land uses were made with Duncan’s multiple range test at the significant difference (p<0.05). Principal component analysis (PCA) was analyzed between PFTs and macro–micro nutrients for land uses. The R Studio statistical (4.0.2 version) software was used to analyze the data.

Results

Change in physiological plant functional traits

The present study showed that plant functional traits in different forest types were highly influenced by seasonal variation. Among them, the rate of CO₂ assimilation (A–μmol CO₂ m⁻² s⁻¹) was one of the traits which directly or indirectly affected by the seasonal

|          | A       | Gs      | E       | Ci      | LA      | SLA     | LNC     | LPC     | LCC     |
|----------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| Rainy    | 11.93±0.65 | 0.38±0.01 | 9.56±0.55 | 295.70±5.45 | 13.12±1.02 | 3.69±0.90 | 1.29±0.01 | 0.11±0.01 | 50.39±0.24 |
| Winter   | 4.45±0.45  | 0.18±0.01 | 1.22±0.25 | 322.92±3.64 | 14.80±0.98 | 4.97±1.14 | 1.21±0.03 | 0.13±0.01 | 47.77±0.35 |
| Summer   | 9.41±0.37  | 0.29±0.01 | 7.08±0.87 | 319.53±3.21 | 14.05±1.05 | 4.80±1.14 | 1.45±0.02 | 0.12±0.01 | 50.26±0.26 |
| F        | =87.05,   | =45.57,  | =142.35, | =326.40, | =557.09, | =133.42, | =83.74,  | =319.53, | =10.57,  |
| p        | <0.0001   | <0.0001  | <0.0001  | <0.0001  | <0.0001  | <0.0001  | <0.0001  | <0.0001  | <0.0004  |

Means followed by a common letters in the column are not significantly different
These different letters denotes significant differences among treatment. Data with same letters in the superscript does not differ significantly
variations and recorded significantly (p < 0.05) higher in the rainy season (11.93) followed by summer (9.41) and winter (4.45) (Table 1). Besides that, the rate of CO₂ assimilation in forest land-use types was recorded higher (Fig. 1a) in OF (9.38) followed by MF (8.50) and at par with PF (7.92). Similar trends were also recorded in the case of stomatal conductance (Gs-mol H₂O m⁻² s⁻¹), which was recorded significantly (p < 0.05) higher (Table 1) in rainy (0.38) followed by summer (0.29) and winter (0.18) seasons. However, among the different forest land uses, the highest Gs (Fig. 1b) were recorded in OF (0.31), followed by MF (0.28) and PF (0.26). The interaction between season and forest land-use types on stomatal conductance was significant (p < 0.0001). Likewise, transpiration rate (E-mmol H₂O m⁻² s⁻¹) was significantly (p < 0.05) higher (Table 1) in rainy (9.56) while lower in summer (7.08) and winter season (1.22). Irrespective of forest land uses (Fig. 1c), OF had the highest (6.82) transpiration rate than MF (5.94) and PF (5.10). The interaction between season and forest land-use types on E was significant (p < 0.001). However, intercellular CO₂ (Ci-µmol m⁻²) was observed significantly (p>0.05) higher (Table 1) in winter (322.92) and lower in autumn (295.70), whereas during summer, it was at par (319.53). Notwithstanding this, in forest land uses types the Ci (Fig. 1d) was increased in MF (320.17) and decreased in MF (312.91) and OF (305.07).

Change in morpho-biochemical plant traits

Leaf area was recorded higher (Table 1) during winter (14.80 cm²) whereas lower during rainy season, which was at par in summer (14.05 cm²) season. Among the different forest land use types, the highest (Fig. 2a) leaf area was observed in OF (26.73 cm²), followed by MF (13.52 cm²) and PF (1.72 cm²). Specific leaf area (SLA) was also found significantly higher in winter followed by rainy and winter season (Table 1). However, in the case of forest land uses types, the trend was OF > MF > PF (Fig. 2d & e).

Change resource use efficiency

Water use efficiency is inversely proportional to CO₂ assimilation rate and transpiration rate. Our results showed that WUE was significantly (p<0.05) highest (Table 2) during winter (4.0) while lowest during summer (1.40). However, under different forest land-use types,
it was significantly higher in PF than MF and OF (Fig. 3a). Similarly, Carboxylation efficiency (CE) is directly proportional to CO$_2$ assimilation rate and stomatal conductance, recorded significantly ($p < 0.05$) higher in rainy (0.04) followed by summer (0.03) and winter (0.01) season (Table 2). However, among the different forest land uses, it was higher (Fig. 3b) in OF (0.03) and lower in PF (0.02), which was at par with MF (0.03). The interaction between season and forest land-use types on CE was significant ($p < 0.001$). Likewise, mesophyll efficiency was recorded significantly ($p < 0.05$) higher Table 2) in winter (1826.9) and lower in summer (1107.2) and autumn (773.6) seasons. Under different forest land uses, it was recorded higher (Fig. 3c) in PF (1373.3) followed by MF (1218.8) and OF (1115.6). The interaction between season and forest land-use types on ME was significant ($p < 0.0001$). Nitrogen use efficiency (NUE) followed the similar trends i.e. rainy (9.23) > summer (6.50) > winter (3.67) season (Table 2). Among the forest land-use types, NUE was recorded higher (Fig. 3d) in OF (6.87) and lower in PF (6.06). In the present study, phosphorus use efficiency (PUE) also followed a similar trend as NUE, i.e., rainy > summer > winter season (Table 2). However, in the forest land-use types, PUE was recorded maximum (Fig. 3e) under MF than PF and OF.

Change in macro and micronutrient

Macronutrients like total N under different season was observed highest (Table 3) during summer season and decreased during winter and rainy season. Among the different forest land uses the highest N (Fig. 4a) was recorded in OF and decreased in MF and PF. The interaction between season and forest land-use types on total N was found to be non-significant. Likewise among the seasons, the highest concentration of total
Fig. 3 Resource use efficiency under different forest land uses. Vertical bars indicate (±) standard error. Bars superscripted by a different letter in same forest types are significantly different at P < 0.05. OF = Oak forest, PF = Pine forest, MF = Mixed forest

Table 2 Resource use efficiencies (Means ± standard error) during different seasonal regimes

|         | WUE  | CE    | ME    | NUE  | PUE  |
|---------|------|-------|-------|------|------|
| Rainy   | 1.25b±0.04 | 0.04a±0.001 | 773.60a±40.30 | 9.23a±0.50 | 114.32a±6.39 |
| Winter  | 4.00a±0.66 | 0.01b±0.001 | 1826.90a±89.56 | 3.67a±0.35 | 35.54a±4.57  |
| Summer  | 1.40a±0.17 | 0.03b±0.001 | 1107.20b±47.26 | 6.50a±0.23  | 76.16b±4.37  |

Means followed by a common letters in the column are not significantly different
These different letters denotes significant differences among treatment. Data with same letters in the superscript does not differ significantly

Table 3 Macro–micro nutrients (Means ± standard error) concentration (N=36) during different seasonal regimes

|        | N     | P     | Mg    | Fe    | Cu    | Zn    | Mn    |
|--------|-------|-------|-------|-------|-------|-------|-------|
| Rainy  | 783.01±44.34 | 122.55±6.69 | 69.36±2.59 | 41.46±2.41 | 14.83±1.70 | 68.57±2.72 | 55.24±1.84 |
| Winter | 1004.08±50.98 | 155.11±5.05 | 59.46±2.16 | 33.00±1.93 | 12.49±1.50 | 59.62±1.67 | 43.42±1.72  |
| Summer | 1104.11±48.22 | 144.21±6.31 | 48.85±2.72 | 29.25±1.11 | 10.70±1.03 | 47.41±2.07 | 35.09±2.02  |

Means followed by a common letters in the column are not significantly different
These different letters denotes significant differences among treatment. Data with same letters in the superscript does not differ significantly

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P was recorded (Table 3) during winter season and decreased in summer and rainy. However, among the forest land uses it was recorded highest (Fig. 4b) in OF followed by MF and PF. The interaction between season and forest land-use types on total P was found to be non-significant.

Micronutrient concentration in soil was also varied significantly under the forest land uses during the different seasons. The significantly \( p < 0.05 \) higher (Table 3) concentration of magnesium (Mg) was recorded during rainy season followed by winter and summer season. Among the forest land uses the
highest (Fig. 5a) concentration of Mg was observed in OF and decreased in MF and PF. The interaction between season and forest land-use types on Mg concentration was found to be non-significant. The concentration of Fe was also significantly higher (Table 3) in rainy season and decreased in winter and summer season. Among the different forest land-use types, it was highest (Fig. 5c) in OF followed by MF and PF. The interaction between season and forest land-use types on Fe was found to be non-significant. Similarly, the concentration of Cu was also significantly high (Table 3) in rainy season followed by winter and summer season. However, under different forest land uses the concentration of Cu was high (Fig. 5d) in OF and decreased in MF which was at par in PF. The interaction between season and forest land-use types on Cu was found to be non-significant. The concentration of Zn was also recorded significantly high (Table 3) in rainy season followed by winter and summer season. Among the different forest land use types the significantly higher (Fig. 5b) concentration of Zn was observed in OF followed by MF and PF. The interaction between season and forest land-use types on Zn was found to be non-significant. Significantly high (Table 3) concentration of Mn was also recorded during rainy season and it was decreased in winter and summer season. Similarly under different forest land uses it was significantly high (Fig. 5e) in OF followed by MF which was at par with PF. The interaction between season and forest land-use types on Mn was found to be non-significant.

Relationship between plant functional traits and macro–micro nutrients

The PCA analysis between PFTs and macro–micro nutrients (Fig. 6) showed that forest land-use types are separated in a 2-dimensional ordination diagram by species-level PFTs, and displayed the correlation between PFTs and macro–micro nutrients in each season. Plant functional traits and macro–micro nutrients differed among the seasons, as revealed by PCA. The first PCA axis in Fig. 6 illustrating 65.6 percent of differences in PFTs and macro–micro nutrients in different seasons. The axis showed that A is passively correlated with another trait, i.e., Gs, E, CE, NUE, PAU and LCC, while negatively correlated with Ci, WUE, SLA, and LPC. Likewise, A is positively correlated with macro–micro nutrients like Mg, Fe, Zn and N while negatively correlated to P concentration. Gs is also positively correlated to Mg, Fe, Cu, Mn, Zn, and N and negatively correlated to P concentration. The same trend was followed in the case of transpiration. However, Ci is negatively correlated to the Mg, Cu, Mn, and N while positively correlated to P concentration. The same trend was observed in the case of WUE and ME. CE, NUE and PUE are also positively related to Mg, Fe, Cu, Mn, Zn and N and negatively correlated to P concentration. WUE and ME are positively correlated to SLA and LPC; however, negatively correlated to LA, LNC and LCC. CE and NUE are positively correlated to LA, LNC and LCC while negatively correlated to the SLA and LPC. PUE is positively correlated to LNC and LCC and negatively correlated to the LA, SLA and LPC.

Discussion

Change in plant functional traits

In general, traits decide plant performance in the forest ecosystem, and these traits are significantly influenced by seasonal variation at the species level. These variations alter the metabolic activity of the plant system, which suppresses the growth and productivity of
plants and ultimately affects ecosystem services governed by the plant community. In the present study, rainy season had the higher CO$_2$ assimilation (photosynthesis) due to the transition period from summer to rainy season. Hence, growth and productivity also increase, leading to carbon stabilization in plants and soil systems (Wang et al. 2008; Kohler et al. 2010). Similarly, stomatal conductance was also recorded significantly higher in the rainy season due to abundant water in the soil and high light intensity leading to increased photosynthesis rate. Moreover, water transportation was also high and exerts turgor pressure on the stomatal guard cell resulting in the opening of stomata, thereby leading to a higher rate of transpiration and carbon assimilation in the plants (Wang et al. 2008). However, these traits were declined in the summer and winter seasons in all forest land uses due to the limited water availability. Generally, water and temperature play a key role in determining the plant’s growth and productivity by inhibiting the important enzyme, i.e., Rubisco, limiting the rate of carbon assimilation in plants (Sharma et al. 2018; Kumar et al. 2021a). Similarly, the rate of mesophyll efficiency in the cell is higher due to higher photosynthesis rates and relative quantity yield of PSII at steady-state photosynthesis (Kumar et al. 2021b).

Change in resource use efficiency

In the present investigation, water use efficiency (WUE) and mesophyll efficiency (ME) increased significantly during winter season compared to the summer and rainy seasons in all forest land uses. Nonetheless, due to increased transpiration and decreased intercellular CO$_2$ (CI), the rainy and summer seasons showed increased stomatal conductance which forces to minimize WUE and ME. The reason for increased WUE and ME might be attributed to plants exposed to winter season fixes more carbon molecule through assimilation and investment of water molecule per fixed carbon molecule is less, ultimately improving WUE and ME (Sharma et al. 2018). Owing to increased CO$_2$ accumulation in the sub-stomatal cavity, the winter season causes a stomatal closer induction and decreases partial CO$_2$ pressure in the leaf. This CO$_2$-dependent amplification of stomatal response may enhance WUE and ME at the leaf as well as canopy level. The findings for WUE, ME, and CE in the present study follow the observations of other researchers (Singh et al. 2017; Purcell et al. 2018, Singh et al. 2018).

The concentration of nitrogen and phosphorus and their distribution in tree species determines biomass productivity. In the present study, we found that NUE (defined as mol CO$_2$ assimilated g$^{-1}$ leaf N) and PUE (defined as mol CO$_2$ assimilated g$^{-1}$ leaf P) also decreased from rainy season to winter (rainy $>$ summer $>$ winter). It is consistent with other NUE and PUE reports in drought-affected deciduous tree species (Reich et al. 1995; Kumar et al. 2021b). High NUE and PUE during the early rainy season came at the cost of maintaining high water-use efficiency (WUE; CO$_2$ assimilated per mol of H$_2$O transpired). The enhanced ability of water and nutrient absorption through the roots of plants is encouraging increased yield as well as nitrogen and phosphorus use efficiencies (Palta et al. 2007). The relative nutrient abundance in the litterfall was in order C $>$ N $>$ P, which coincides with studies from various forest ecosystems (Kaushal et al. 2012). The nutrient inputs were within the range as reported in many temperate broadleaved forests in the central Himalayas (Singh et al. 2009). Higher concentrations of nutrients in summers may be attributed to increased nutrient re-absorption in summer from senescent tissues. However, the wood litter in the forests has lower N, P, and C concentrations than the leaf litter and shows no significant seasonal variations than the leaf litter (Rawat et al. 2019).

Change in macronutrients

Results of the present study showed that the concentration of total N was significantly higher in OF during the summer season which might be due to more litter accumulation, low soil compaction, least exposers of particulate organic matter to microbial attack and quick oxidation in forest land uses (Twongyirwe et al. 2013; Zhang et al. 2013). Notwithstanding this, various factors such as compactness, low litter and residue input, increased exposure of organic particulate matter to microbial attack, and rapid oxidation is the factors that reduce N in PF soils compared to OF soil (Kumar et al. 2020).

The summer season had the higher N over the rainy and winter season in various forest land uses. The rate of mineralization and nitrification may increase
during the summer season due to higher temperatures in Himalayan temperate forests. Because of less rainfall during the summer, increased mineralization and nitrification resulted in a higher total nitrogen concentration in the soil (Kumar et al. 2020). Mineralization and nitrification may also increase during the rainy season, but nitrogen loss may be greater due to higher rainfall. The increased concentration of N during the summer season could be attributed to the increased activity of nitrogen-fixing microbes. Plant nutrient intake is significantly reduced during the winter season because N-mineralization and nitrification are either immobilized in microbial biomass or stored in the soil as inorganic nitrogen, resulting in a reduction in nitrogen concentration (Singh and Singh, 2006).

Similarly, total P concentration was also significantly ($p < 0.05$) higher in the winter and minimum in summer. It might be due to the more minerals accumulation and less rainfall during the winter season than summer, leading to less leaching of nutrients from the soil. Nevertheless, a lower concentration of total P during the rainy season could be due to heavy rainfall and soil erosion, which results in the majority of P being leached down (Ashraf et al. 2014). When the level of P and organic carbon in the soil is high, the amount of potential seasonal variation in phosphorus values tends to increase (Semwal et al., 2009; Salim et al. 2015). Another reason for the higher concentration of P in OF is the highest organic matter content which is present in the OF and has a great potential to supply a sufficient amount of organic phosphate from the soil to the plants (Miller and Donahuer 2001; Gupta and Sharma, 2008).

The litter of Chir-pine decomposed slowly, resulting in a slow release of nutrients, increased soil compaction, and decreased available pore space in soil, resulting in a high soil bulk density. Since mixed oak-pine forest produces both types of litter, its bulk density values varied between those of oak and pine forests in terms of soil physical/chemical properties (Bargali et al. 2018). The chemical properties for all forest types across all seasons revealed that mixed oak-pine forests were rich in all chemical properties when compared to the other two forest types (Bargali et al. 2018). Changes in nutrient cycling processes caused by changes in a flora may reflect changes in the soil microbial community due to difference in the quantities and quality of inputs to the soil by different plant species (Kaushal et al. 2012).

Change in micronutrients

The nutrient uptake is greatly influenced by seasonality due to the availability of different temperatures and moisture. Plants absorb micronutrients in a complex way from their roots, but to optimize the uptake of micronutrients, certain conditions are required. The results revealed that the highest concentration of micronutrients was recorded in OF during rainy season and lower in PF during summer season due to the availability of optimum temperature and moisture content during rainy season than summer. Earlier studies reported that low temperature and moisture levels reduce root growth rate, microbial, metabolic activity, organic matter decomposition, and micronutrient bioavailability (Fahad et al 2017; Pandey et al. 2017).

Some micronutrients exit at low concentrations in the soil, so they are transported by diffusion from soil water to the surface of the roots and are limited in the soil and plants due to the enhanced tortuosity of the diffusion path (Barber 1995). A few studies have also reported that micronutrient deficiency is most likely occurring during the summer season due to reduced mass flow and diffusion to roots which ultimately affects the translocation of micronutrients from root to shoot (Baghour et al. 2002; Singh et al. 2017). Notwithstanding this, during rainy season, the water-saturated condition of soil has shown that micronutrients are transferred from exchangeable and soluble forms to oxide forms (Zheng and Zhang 2011).

Relationship between plant functional traits and macro–micro nutrients

The macro–micro nutrients are essential elements that are required for the physiological functioning of the plants. Nitrogen (N) deprivation causes deviations in a vast range of physiological and morphological functioning of the plants (Zhao et al. 2005). N is an essential component as it forms a major component of chlorophyll and plays an essential role in the photosynthesis process (Tang et al 2019). Its effect on CO$_2$ diffusion conductance (both stomatal and mesophyll conductance) in photosynthesis has received a lot of attention in future climate change. Some changes in photosynthetic electron transport rate or actual photochemical efficiency of photosystem II (PS II) can occur due to high nitrogen application.
Phosphorus (P) in the form of phosphate is also one of the least available macronutrients to plants. Phosphate is essential for the maintenance of photosynthesis, plant development, and physiology in many plant processes. It serves as a structural component of the plant and regulates carbon metabolism, energy transfer, sugar and starch transformation, and nutrient movement. As a result, plants have evolved several adaptation strategies to cope with low P conditions, including physiological and metabolic changes (Vance 2008). Plants have devised various physiological strategies for obtaining P, with an emphasis on increased soil exploration and uptake. This is primarily accomplished by increasing root growth, which results in a higher root:shoot ratio. Magnesium also has a significantly strong association with physiological characteristics. It is an essential mineral nutrient that plays a key role in photosynthesis and subsequent long-distance transport of photo-assimilates (Thuynsma et al. 2016). Most metabolically active Mg is bound or incorporated into cellular compartments with the highest concentrations in chloroplasts (Karley and White 2009). The possible effects of Mg on the diffusion of CO₂ through the leaf mesophyll (Tang et al. 2012; Yang et al. 2012; Farhat et al. 2016). In the present study, Iron also has a significant correlation with physiological traits. It is required as a cofactor for a protein involved in several metabolic processes like photosynthesis and respiration (Terauchi et al. 2010). Similarly, manganese also plays a key role in the physiological functioning of the plant (Alloway 2008). It has relatively low phloem mobility in plants, resulting in deficiency symptoms appearing in the younger leaves. It is also observed that copper was also showing a positive connection with the physiological traits and activates several plant enzymes involved in lignin synthesis (Yruela 2005). It is also actively involved in photosynthesis and respiration processes and regulates the protein and carbohydrate metabolism. Zinc is a necessary component of certain enzyme structures, such as carbonic anhydrase. Carbonic anhydrase is an enzyme that catalyzes the reversible hydration of carbon dioxide to bicarbonate and hydrogen ions, which is essential for photosynthesis. The enzyme is closely related to zinc. Consequently, zinc deficiency in plants inhibits plant growth and development, resulting in increased reactive oxygen species (ROS) as a result of photodioxidative damage, decreased net photosynthesis, and photosynthetic electron transport (Kosesakal et al. 2009; Zhao and Wu, 2017). It also participates in the synthesis of chlorophyll, which increases the net rate of photosynthesis, stomatal conductance, and transpiration rate in higher plants, resulting in an increase in photo-assimilates in plant leaves (Sun and Yang 2002; Wei et al. 2005).

Conclusion

This study indicated that most leaf traits (i.e., photosynthesis rate, transpiration rate, leaf carbon and nutrient-use efficiencies) of all selected forests decreased during winter season and increased in rainy season. It can be largely explained by different ecosystem and environmental characteristics, indicating that the ecological strategies of forests varied from resource acquisition to resource conservation during the seasonal regimes. The relationships between leaf traits and the concentration of micro and macro nutrients in forests also varied during seasonal regimes, indicating that the selected forests used different trade-off strategies depending on the season. The high resource (macro–micro nutrient) assimilation efficiency of forest species during the rainy season could support their rapid growth and, as a result, relative low nutrients in that season. Therefore, the present findings revealed that selected forests can regulate the nutrient cycle against the different seasonal variations and could be used to select other forests that have the potential to regulate the nutrient cycle in the Indian Himalayan region. However, additional studies are needed to clarify influence of seasonal climate on plant functional traits and its relationship with soil macro–micro nutrients in the Indian Himalayan region.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.
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