

Altitudinal Patterns of Foliar Nutrients in Dominant Tree Species: Are Central Himalayan Forests Nutrient Stressed?

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Abstract

*In forest ecosystems nutrient availability is one of the most important drivers of tree growth and ecosystem function. We studied changes in soil and foliar nutrients (N, P & K) and leaf N and P stoichiometry in eight dominant canopy and sub-canopy forest tree species of Central Himalayan forests occurring between 300 and 2200 m asl. Nutrient (N, P & K) concentration in leaves at bud break, mature and senescent stage varied significantly across the tree species. The nutrient resorption efficiency (NRE) varied significantly across the species and found ranging for N from 48.7 - 76.8%. Both the nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) increased linearly with altitude ($R^2 = 0.647$ for NRE significant at $p < 0.05$; and R^2 for PRE = 0.525; NS) pointing out that trees growing in temperate climate conserve nutrients more efficiently to withstand the slow mineralization due to cold climate. With the increasing altitude leaf life-span increases significantly ($R^2 = 0.0025$; $p < 0.0074$). ANOVA indicates that the foliar N and P and altitude were unrelated. The low N: P ratio, a measure of nutrient status of forest ecosystems at senescent leaf stage, found ranging from 9.97 in *Q. floribunda* to 18.8 in *P. roxburghii* points out that forests of the study region are nutrient stressed, partly due to low P mineralization in temperate climate, leaching of nutrients due to heavy monsoon rain, and poorly developed underlying geology. Thus, the Central Himalayan forests are characterized by high NRE and low growth rate with increasing altitude. Winter season warming might help improve the nutrient availability in the forest floor and nutrient uptake to enhance nutrient cycling and biomass productivity in these forests.*

Keywords: Leaf Growth Characteristics; Leaf Nutrient Dynamics; Dominant Tree Species; Central Himalayan Forests; Nutrient Conservation Strategy.

1. Introduction

Availability of nutrients is one of the most important drivers of tree growth and ecosystem function in temperate forest ecosystems. The leaf nutrient (N and P) concentration reflects plant nutritional status, nutrient uptake, nutrient utilization efficiency and adaptation of plants to the environment during various stages of growth [1, 2]. Nitrogen (N) is one of the most limiting elements for growth of plants in many ecosystems, partly because plants require a large amount of N for photosynthesis [3, 4]. Plants allocate higher N among leaves with higher photo flux density (or sunshine) to maximize photosynthesis [5, 6]. Plants take up Phosphorus (P) in its inorganic form as phosphate [7]. In natural conditions P is often the first limiting nutrient for plant growth as the soil solutions are usually depleted in inorganic P [8]. However, plants can adapt to low P availability by P recycling and remobilization [9]. Potassium (K) is the next most abundant nutrient after N in leaves, and plays an important role in plant metabolic processes and ecosystem functioning [10, 11]. Although, K is more abundant than P, its plant-available form is often low in forest ecosystems [12, 13].

Leaf being an important and most sensitive organ reacts with environmental conditions rapidly and affects the growth and development of plants [14]. Various factors, such as season, and physiological status of trees influence the leaf element concentrations [15]. The N and P are the most limiting nutrients for plant growth, and their resorption is important for plant nutrient conservation [16-18]. Nitrogen is mobilized from senescing leaves to other plant parts, and this N resorption enable plants to reuse and conserve this nutrient for supporting spring bud-break and new leaf crop formation, and vegetative shoot extension thus reducing the dependence on external nutrient supply [19-22]. Nutrient resorption may occur throughout the life of a leaf but most of the resorption occurs shortly before leaf abscission. Nutrient resorption efficiency (NRE) and proficiency, NRP (reduction in the N concentration between green and senescing leaves) may vary with plant species leaf habits and plant organs [4, 18, 23, 24]. Reported that foliar nutrient resorption plays an important role in nutrient conservation, and the NRE varies greatly among nutrients and plant species [25-27]. High NRE and low growth rate are some of the plant characteristics under

nutrient-poor conditions [28].

Plant growth and nutrient uptake is also known to be limited by availability of soil N and P [29]. Nutrient poor habitats are reported to be dominated by nutrient-conserving species, as opposed to fertile habitats those are dominated by species with higher productivity per unit of leaf mass [30]. Still within any given habitat plants with a number of leaf traits may coexist [31]. N and P use efficiency varies within conifers and broadleaved trees as well [32]. Leaf life-span is one trait important in this regard that provides an indirect index of growth rate, nutrient-use efficiency and litter decomposition [33, 34]. Concentrations of leaf N and P in green and senesced leaves are reported to be negatively correlated with leaf life-span, excluding N₂ fixing species [1]. In the Central Himalayan forest trees leaf N (1.8-2.5%), P (0.85-0.180%) and K (0.78-1.05%) concentration in mature tree leaves reported by earlier workers those are comparable to the global values, but slightly lower than the wet tropical forests. In these forests due to low temperature P was found significantly decreasing with increase in altitude [35-37]. Also, the high altitude forests have been found more efficient in nutrient-use than several broad leaf forest communities of low altitudes of this region.

Nitrogen resorption plays an important role in the plant N economy that affects litter quality, litter decomposition and nutrient release [38]. On average, plants reabsorb about 50% of leaf N and P, but this proportion varies widely across species, 5-80% of leaf N, and 0-95% of leaf P [3]. A global meta-analysis of 86 studies on ~ 1000 data points across green and senescent leaves across plants of various climates computed N (62.1%) and P resorption (64.9%), which is significantly ($P < 0.05$) higher than the commonly used global value of 50% [39]. In the dominant tree species of Central Himalayan forests, the RE of N has been found much lower ranging from 21.5% to 54.4% [35, 36]. Another study reported that about 38-68% N, 26-50% and 49-55% K was reabsorbed from senescing foliage of dominant tree species in three Central Himalayan forests.

Although the relationship between plant growth and leaf N or P concentration are yet unclear, still the leaf N: P ratio are used to indicate plant N or P limitations (i.e., N limitation when N: P is < 14 , P limitation when N: P is > 16) [40, 41]. In 54 plant species in China a low N: P ratio (10.8) indicated that the flora was more N limited than P limited. It has been reported that leaf N: P ratio increases with decreasing latitude or increasing mean annual temperature (MAT). P generally decreases with MAT in green leaves, and in consequence the N: P ratio increases with MAT [42, 43]. In general, it is assumed that the tropics are more P-limited while high latitudes are more N-limited [44]. Analyzing a global data set of leaf N and P for 1,280 plant species across 452 sites, reported that leaf N and P declines and the N/P ratio

increases as average temperature and growing season length increases toward the equator [43].

In the mountain forests altitude determines ecosystem structure, functions and process, and often used as a proxy for ascertaining how warming affects plant growth and leaf properties. Reported that the altitudinal pattern of soil and plant nutrients differs among ecosystem components and the relative importance of P vs. N limitation shifts along altitudinal gradients. In the tropical montane forest in Ecuador, foliar nutrient concentration were found decreasing with increasing altitude, with apparent nutrient deficiency at higher altitude, however, the soil nutrients were not affected by altitude and increased significantly with altitude. Reported that both soil and foliar nutrients (N, P, and K & Mg) decrease significantly with elevation across a tree line ecotone in Nepal Himalaya. Therefore, nutrient dynamics studies along altitudinal gradients may improve our knowledge about spatial variation in nutrient cycling and can also enhance our ability to predict how mountain ecosystems will respond to global warming.

This study was undertaken with an objective to determine seasonal changes in foliar nutrient (N, P & K) concentration and leaf nutrient resorption efficiency (NRE) across the gradients of altitude, tree growth form, forest types and soil physico-chemical properties in dominant canopy and sub-canopy tree species of four major forest types in Central Himalaya. The hypothesis tested was: (i) Weather leaf nutrient resorption increases with altitude; (ii) whether leaf stoichiometry (N: P) is controlled by season? And (iii) Whether Central Himalayan forests are nutrient limited? Although, the Central Himalayan forests have been studied for the changes in plant and soil nutrients by few workers, still there is a lack of studies those considered this topic from a stoichiometric and nutrient limitations and conservation perspective along altitudinal gradient [45].

2. Materials & Methods

2.1 Study Area: This study was undertaken in river Gaula catchment, Nainital (Central Himalayan mountains in north India) (29°17' N latitudes and 79° 26' E longitudes) along an altitudinal transect of 300-2200 masl. Between 2014 and 2016. In the study area from lower to higher elevations following forests occur: Sal (*Shorea robusta*) forests < 1000 m; Chair Pine (*Pinus roxburghii*) forests between 1000 and 1600 m; and Oak (*Quercus spp.*) forests between 1700 m and 2200 m (Fig.1). The higher limit of this altitudinal zone is represented by forests of tree species such as Tilonj Oak (*Q. floribunda*), Kharsu Oak (*Q. semecarpifolia*), Blue Pine (*Pinus Wallichiana*) and Deodar (*Cedrus deodara*), etc. These forests represent some of the well-stocked, relatively undisturbed and late successional climax forests of this region except for *P. roxburghii* an early successional forests [46].

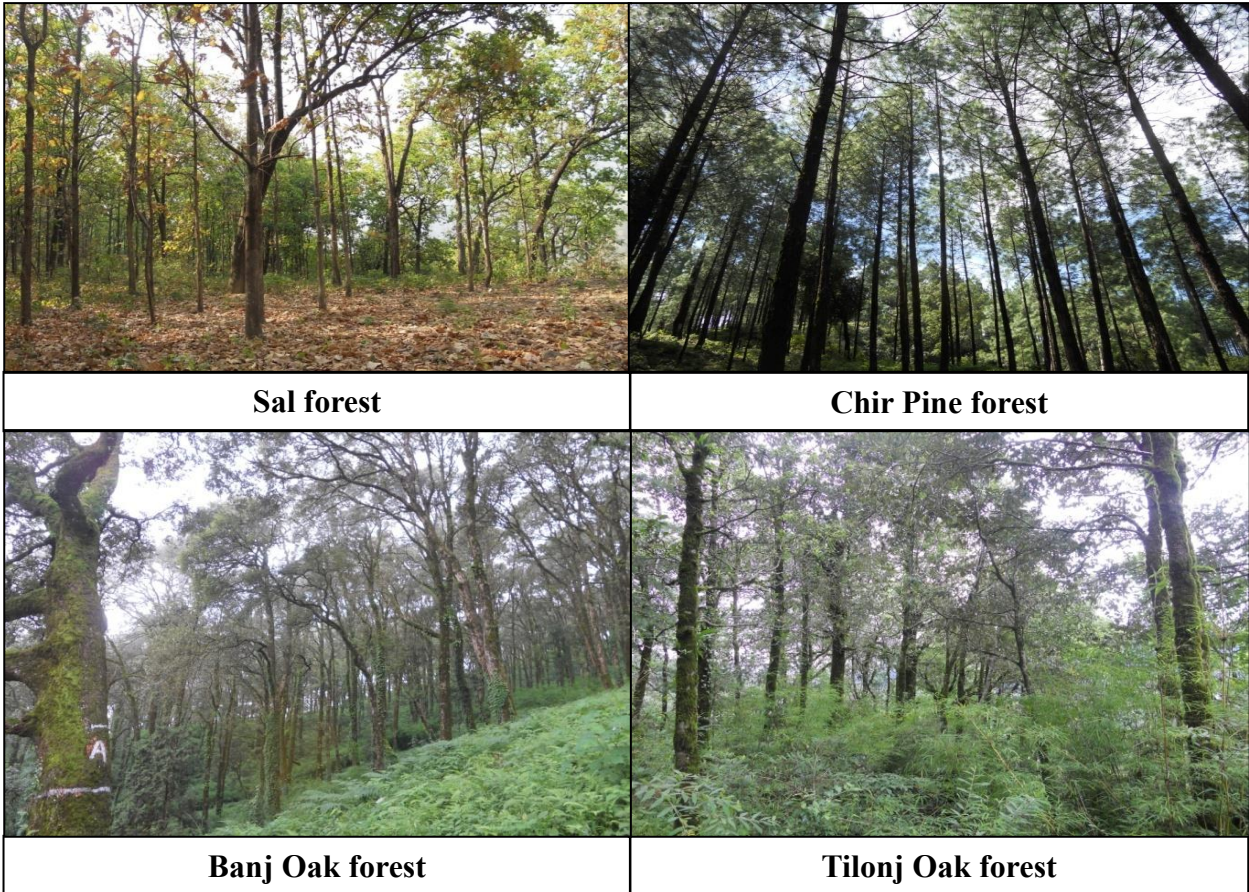
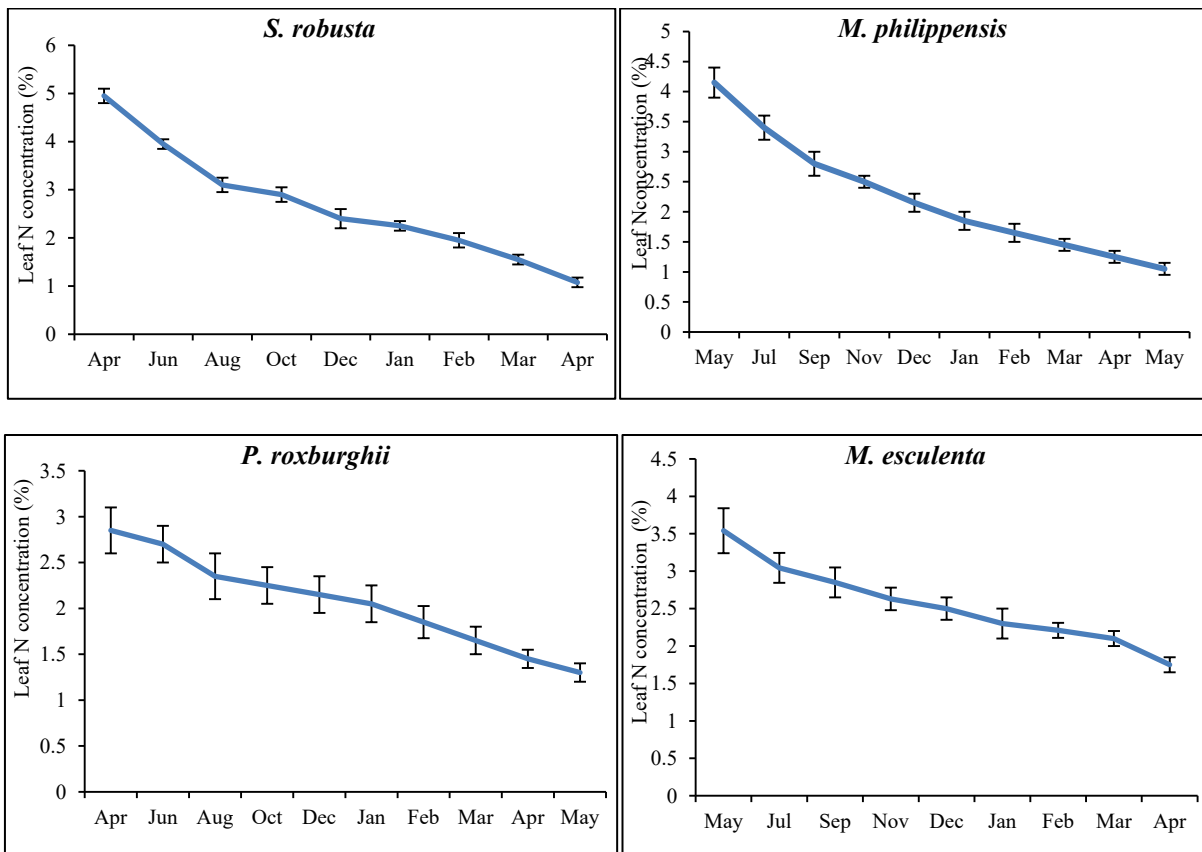


Figure 1: Forests and tree species selected for study in the Central Himalayan region.



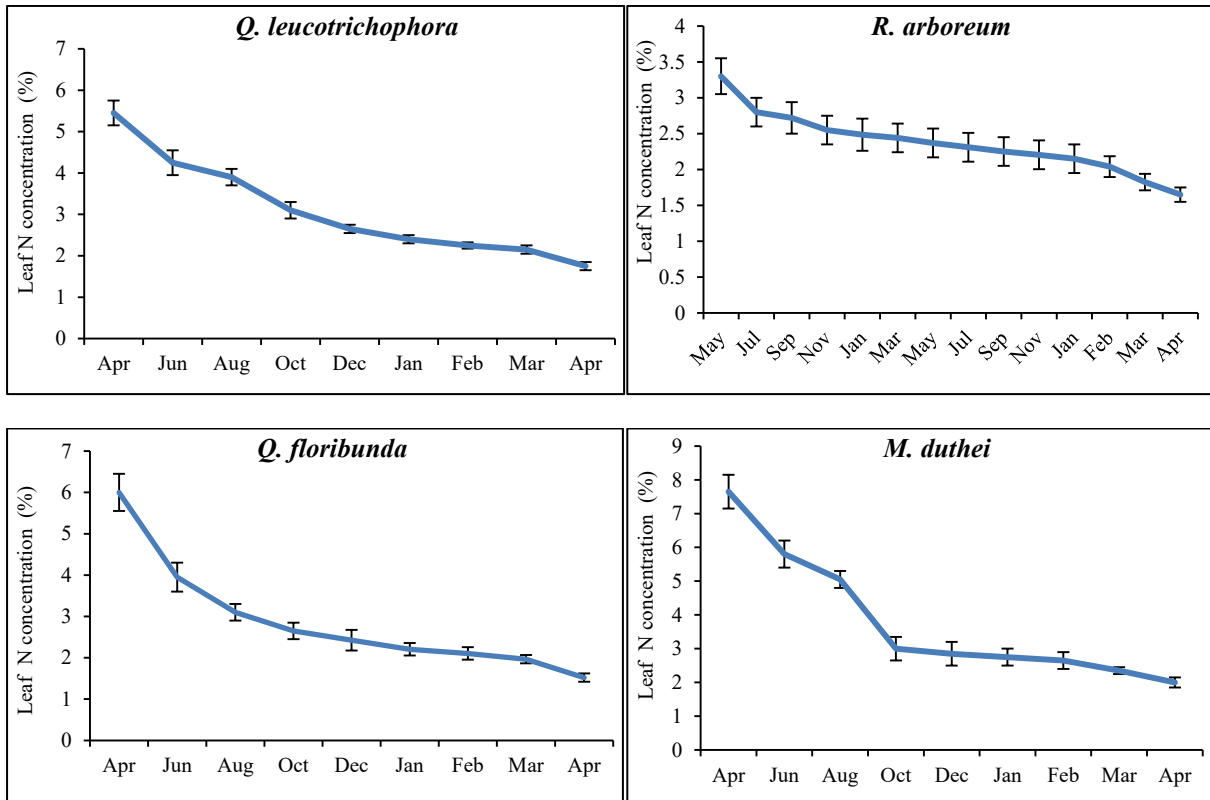
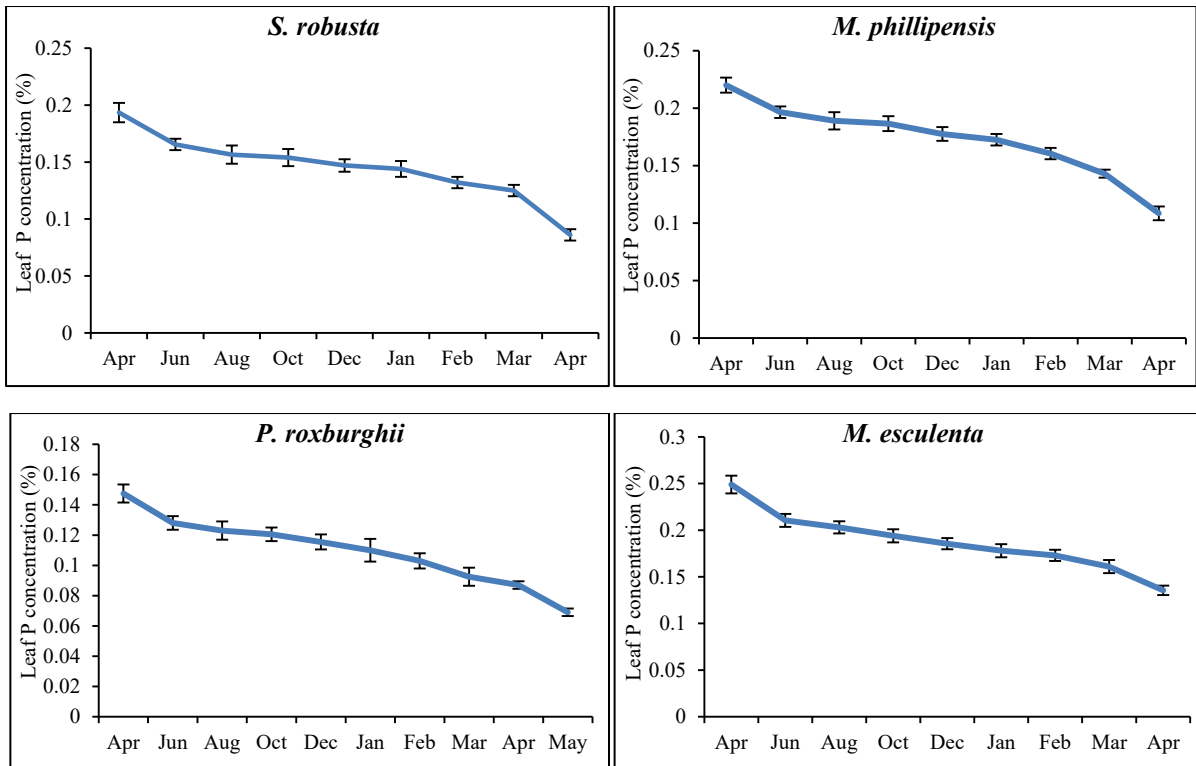


Figure 2: Leaf Nitrogen concentration (%) in tree leaves of different studied species.



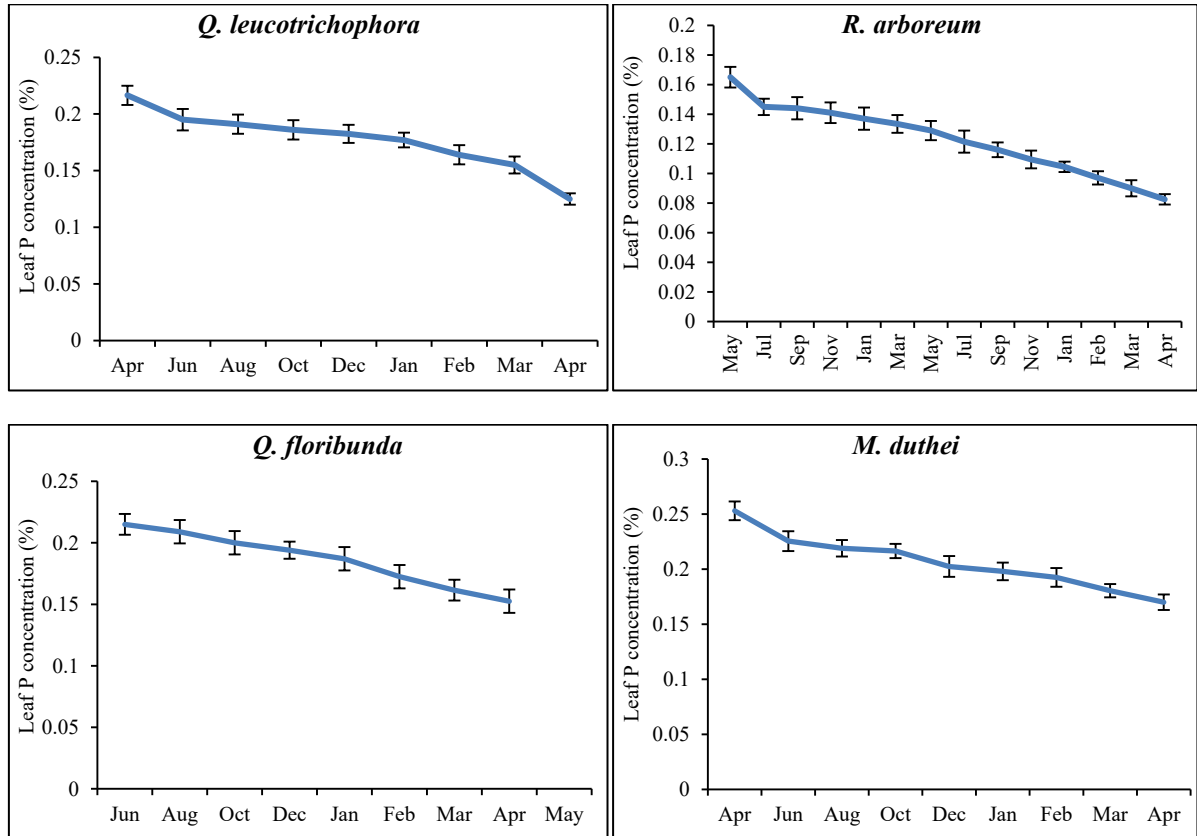
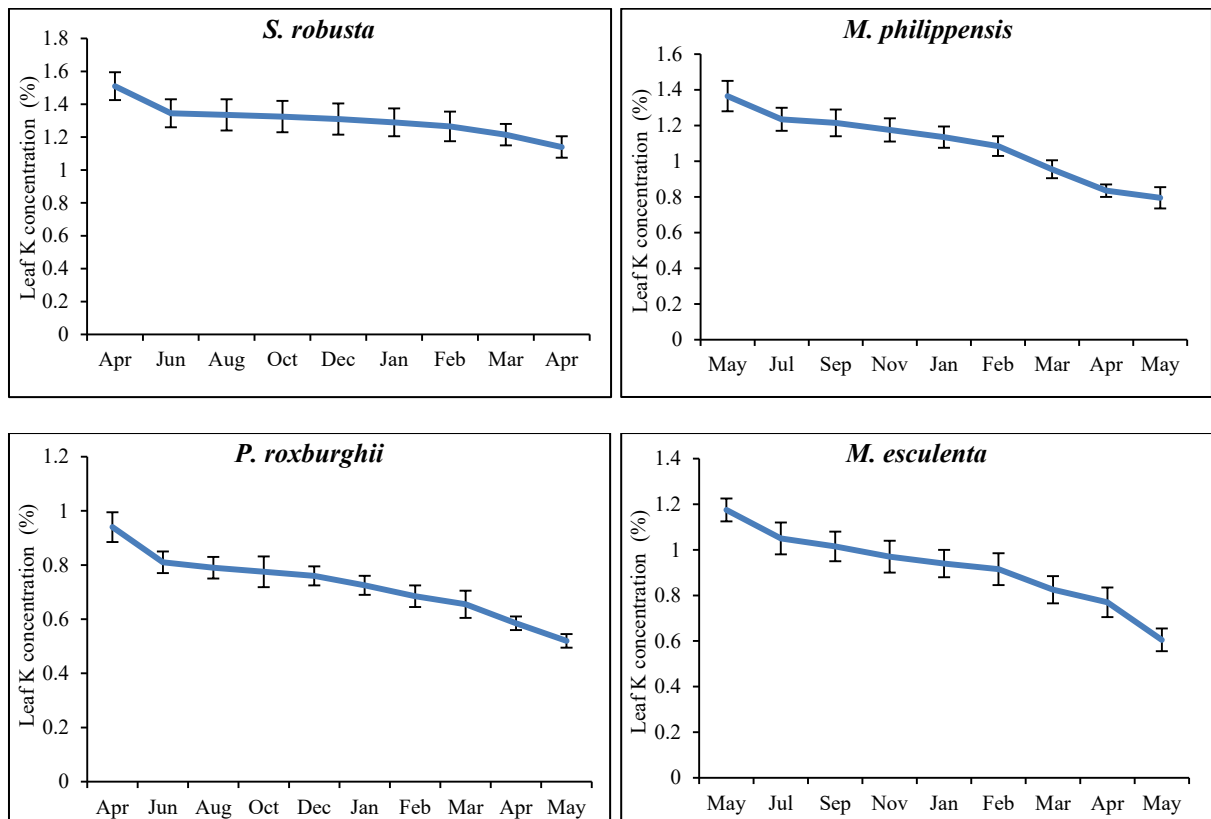


Figure 3: Leaf Phosphorus concentration (%) in tree leaves of different studied species.



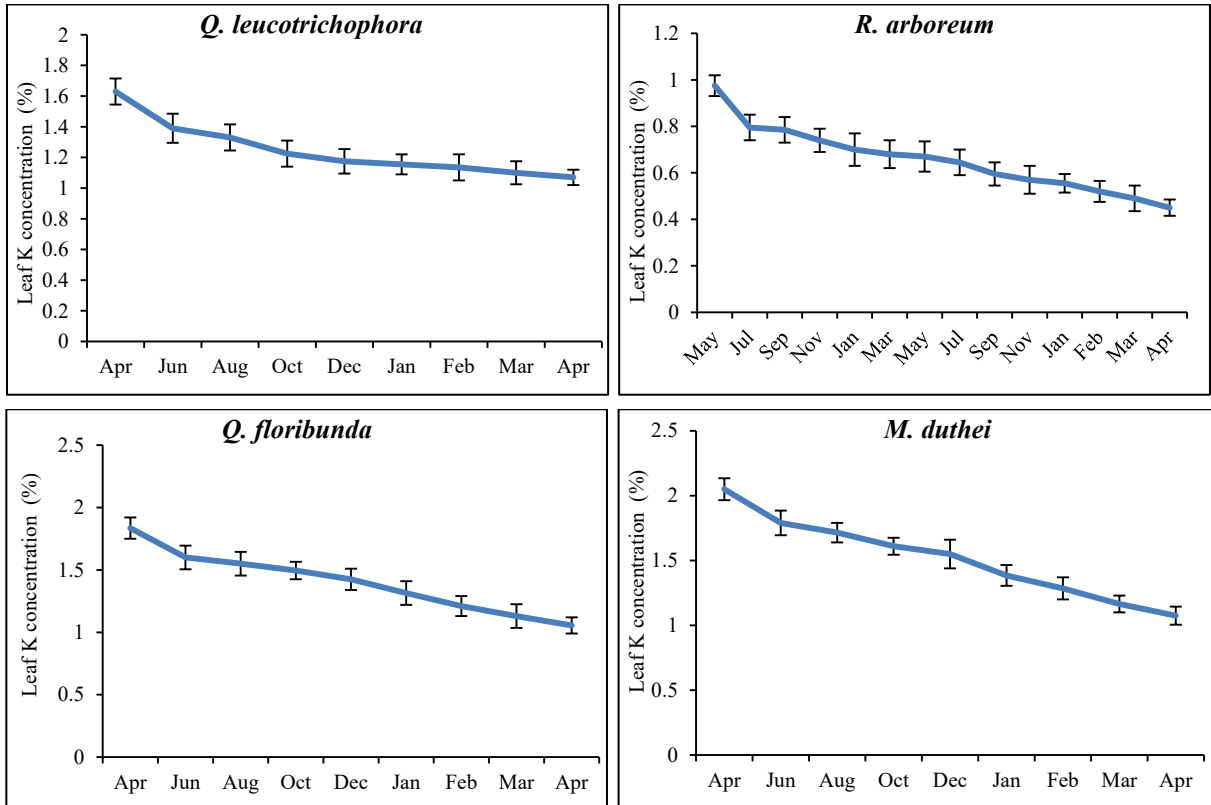
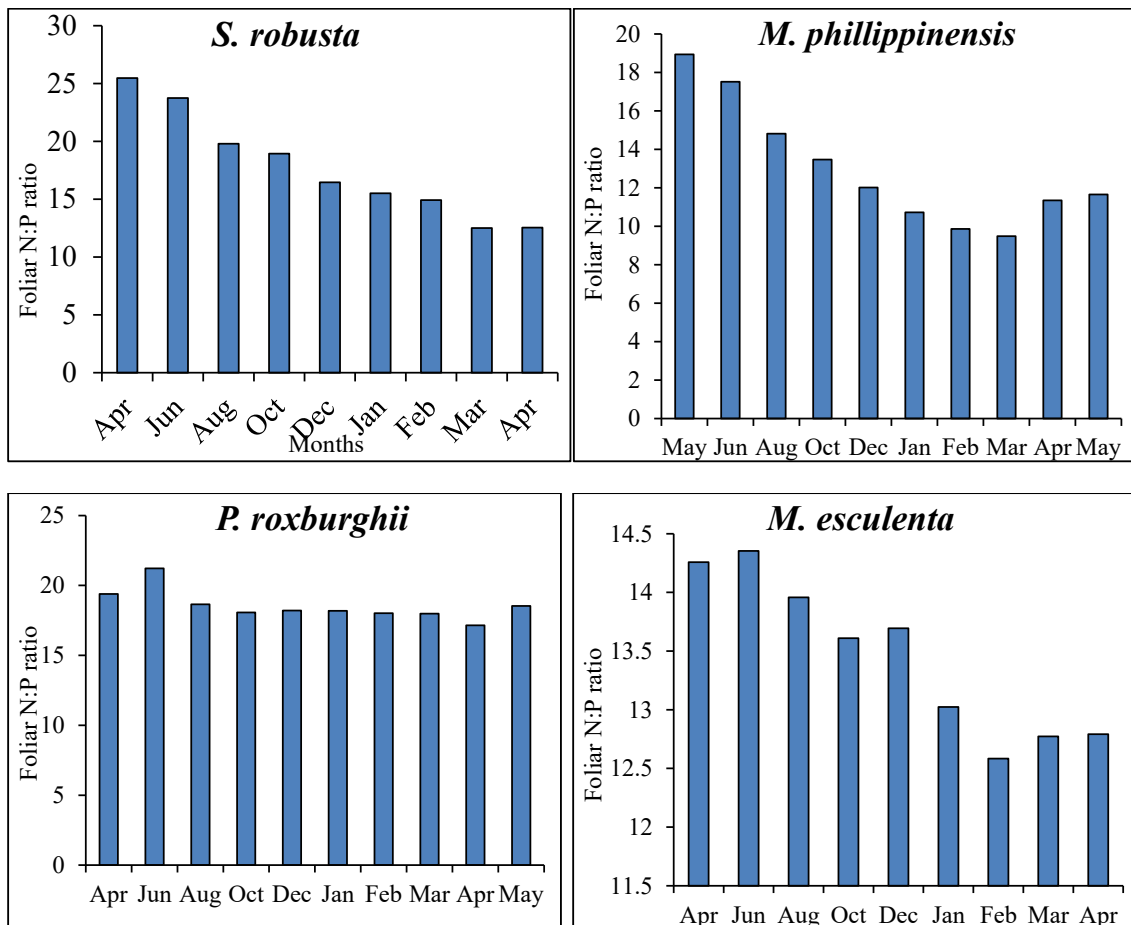


Figure 4: Leaf Potassium concentration (%) in tree leaves of different studied species.



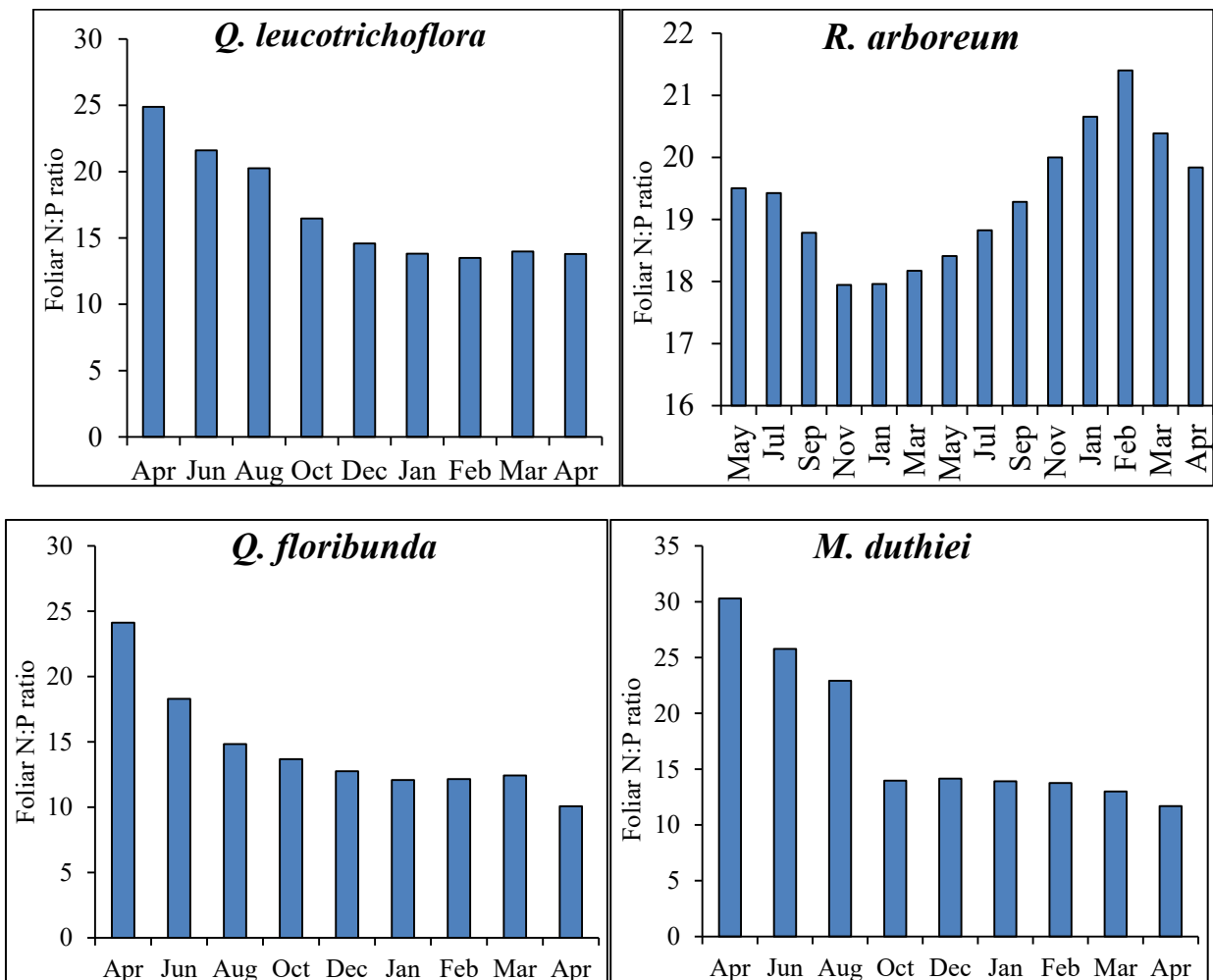


Figure 5: Foliar N: P ration of Central Himalayan forest.

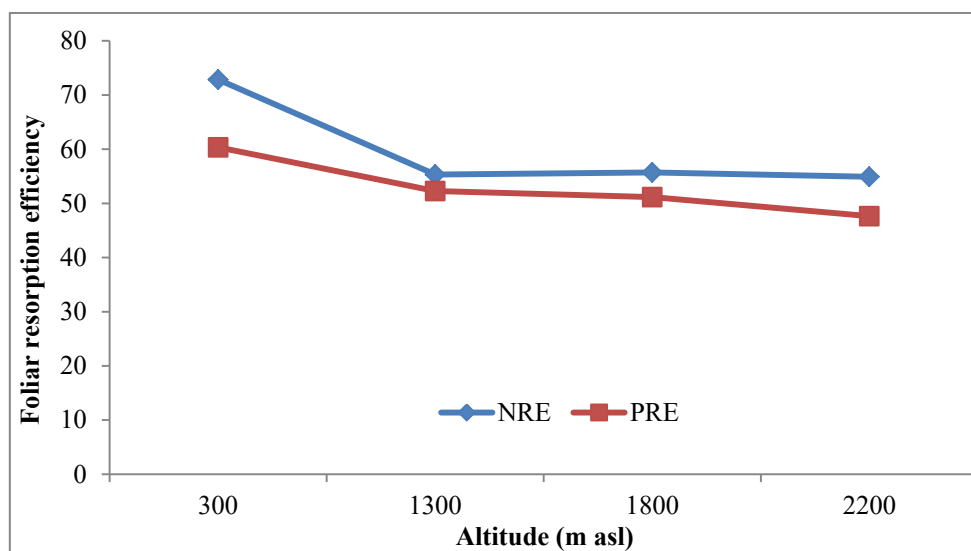


Figure 6: Relationship between altitude and NRE in trees of Central Himalayan forest.

The basic climatic pattern of the study area is controlled by monsoon rhythms. There are three main seasons: a cold and relatively dry winter (mid-December to mid-February); warm and dry summer or pre-monsoon (April to mid-June); and wet summer monsoon (mid-June to mid-September). Monsoon season

accounts for about 80% of the annual rainfall of 150-250 cm, while 15% of the annual rainfall is associated with cyclones in winter season, and 5% with local thunder storms [45]. The dry period sometimes continues for about 6-8 months, with < 10% of the annual rainfall. The winter precipitation associated with

cyclones is received in the form of snowfall in the high mountains. In the study area along the altitudinal transect the mean annual atmospheric temperature (range= 19.1-28.6°C), and mean annual soil temperature (range= 14.4-22.4°C) declines with increasing altitude, but relative humidity (range= 71.9-74.5%) increases with altitude [47]. In general, the mean temperature falls by ~3.5°C with a rise of 1000 m altitude in this region. Climate change impacts are perceptible in the study area, particularly in the last three decades. In the study area the mean air temperature has significantly ($\alpha = 0.05$; $P = 0.000015$; $R^2 = 0.4703$) increased by 0.038oC/yr. and the mean annual rainfall during 1985-87 (2192 mm) and during 2014-16 (1760 mm) has significantly decreased ($R^2 = 0.166$; $p = 0.021$) [47]. Mean daily sunshine hours in the mid-altitude belt varied seasonally and gradually increases from 2-3.3 hrs. In rainy season, 5.6-7.8 hrs. In winter season and 8-9 hrs. In summer season [48]. Majority of forest soils of the region belong to brown forest soil category [49]. In general, soil is sandy loam and poor in soil organic C, total N and P, and the rocks are complex mixture of sedimentary, low grade metamorphosed and igneous in the study area [50].

2.2 Tree Species:

The eight tree species selected for the present study (Table 1) are divisible into: (i) Evergreen; in these species complete leaf fall occurs only after sufficient development of new foliage in spring season (March-April), thus the trees never become leafless, and (ii) Semi-deciduous; as above, but complete leaf fall occurs only when new foliage development is still limited in summer (April-May), rendering some twigs of trees leafless for a few days or weeks. The selected tree species for this study form dominant forests along altitudinal gradient in this region (Singh and Singh 1987). Tree height for canopy species was recorded 15-50 m and for sub canopy species from 7-12 m and the tree girth from 50-290 cm for canopy species and 15-150 cm for sub canopy species, and the tree layer biomass of these forests has been reported ranging from 113-710 t/ha for Sal and Pine forests, respectively [45]. These forests represent some of the most intact stands of the region with high species richness (28 trees, 58 shrubs and 72 herb species). Detailed description of each of these species and forests is given in [51, 52].

Forest sites (m asl)	Canopy / sub-canopy tree species	Tree girth (cm)	Tree height (m)	Trees density /ha	Tree biomass (t/ha)	Total basal area (m ² /ha)	Tree species richness
Sal forest (300)	<i>Shorea robusta</i> (SD)	50-250	30-35	325	526.2	184.0	11
	<i>Mallotus philippensis</i> (SD)	35-110	10-12	205	10.1	16.6	
Chir Pine forest (1500)	<i>Pinus roxburghii</i> (E)	55-290	35-50	230	165.0	134.0	12
	<i>Myrica esculenta</i> (E)	35-120	7-8	95	26.5	27.1	
Banj Oak forest (1800)	<i>Quercus leucotrichophora</i> (E)	60-210	15-20	295	276.5	135.8	17
	<i>Rhododendron arboreum</i> (E)	40-140	8-10	90	41.5	51.7	
Tilonj Oak forest (2200)	<i>Quercus floribunda</i> (E)	65-190	15-20	275	318.5	108.3	13
	<i>Machilus duthiei</i> (E)	45-150	10-15	135	40.3	43.2	

*SD= Semi-deciduous, E= Evergreen

Table 1: Vegetation and soil characteristics of the forests and tree species selected along an altitudinal gradient in outer ranges of Central Himalaya.

2.3 Sampling Methods:

In each of the forest sites as listed under Table 1 (1 ha representative plot at both N and S aspects) 100 mature individuals each for a dominant canopy tree species and a co-dominant sub-canopy tree species across the four forests were (marked) (total marked trees=800) for detailed investigation on leaf nutrients (N, P and K) across annual growth cycle of these tree species, and sampled at monthly interval for a period of two years from April 2014 to March 2016. The selected tree individuals (100 for each of the tree species) were randomly selected within a representative stand of the four forest types across the altitudinal gradient. The tree individuals encompassed all age structure, canopy height and other forest characteristics. To determine the nutrient resorption efficiency (NRE) 100 tree leaves for each of the 8 tree species were sampled at monthly interval that encompassed both at leaf maturation stage (when the leaf had fully expanded

and gained peak leaf mass and nutrient mass) and 100 abscised leaf (determined by coloration, usually yellow) were picked up 5-10 m above in the tree crown from the ground from the trees of each of the species representing the even aged leaves of entire leaf population. The abscised leaves were collected gently shaking the branches/twigs of trees. On each sampling date 100 leaves were collected from the marked tree populations of each of the eight tree species across the four forest sites. Leaves were stored in paper packets, brought to the laboratory and oven dried at 60oC till constant weight in an electronic balance. Leaf mass loss was computed as the difference between leaf mass at leaf maturity and in senescent leaves at leaf drop stage.

The dried leaves were then grinded in a Willy Mill, and the material was stored in air tight glass vials to determine total Nitrogen (N), Phosphorus (P) and Potassium (K) concentrations.

Total N was determined following, total P using UV- VIS Spectrophotometer (UV- 2600) following, and total K using Flame Photometer (Systronics 128) [53, 54]. To compute resorption of N, P and K (nutrient resorption efficiency, NRE), leaf N, P and K mass was computed as the values obtained by multiplying dry

weight of leaves with their N, P and K concentrations at mature and abscised leaf stage. Maximum value of leaf nutrients at leaf maturity (expressed as mg leaf⁻¹) was taken to compute NRE as follows:

$$\text{Nutrient resorption efficiency (NRE)} = \frac{\text{Leaf nutrient mass at steady state of leaf dry weight}}{\text{Leaf nutrient mass at steady state of leaf dry weight} - \text{Nutrient mass in abscised leaf}} \times 100$$

2.4 Forest and Soil Micro-climatic Data:

Micro- climatic data (atmospheric temperature and relative humidity) below the forest canopy of each of the selected forest stands (both at N and S aspects) was recorded at monthly interval using a pocket weather meter (Kestrel 400NV). On each visit to the study sites of about one week period micro-climatic data was recorded within the marked forest stands three times a day from morning till evening (10 am -5 pm). Soil of these forests beneath the marked tree stands was studied for meteorological

data (soil moisture and soil temperature) at monthly interval at 30cm depth across all the four forest sites. Soil temperature was determined using a soil thermometer, and three measurements were taken at each site on every visit. To determine the soil moisture about 10 g of fresh composite soil sample (in triplicate) was collected from 30 cm soil depth, dried in an oven at 80oC for 24 hrs. Or till constant weight and weighed. The moisture content was calculated on oven dry weight basis following:

$$\text{Soil moisture content (\%)} = \frac{\text{Fresh weight of soil} - \text{Dry weight of soil}}{\text{Dry weight of soil}} \times 100$$

To determine soil nutrients status these soil samples were mixed to make a composite sample for each of the summer, rainy and winter seasons. Soil was sieved, air dried and stored in air tight polythene bags and leveled for determination of various soil

physic-chemical properties (pH, N, P, K and OC) following standard methods as used for analysis of leaf nutrients. Soil pH was determined following. The soil organic carbon was determined using following equation:

$$\text{Soil organic carbon (\%)} = \frac{M \times (V_1 - V_2) \times 0.39}{\text{Weight of soil sample}}$$

Where; M= Molarity of FeSO₄ solution; V₁= Volume of FeSO₄ required for blank (ml); and

V₂= Volume of FeSO₄ required for sample (ml).

2.5 Statistical treatment of the data:

Statistical tests (Statistica 8.0) was applied for the meteorological data (daily mean air temperature and mean annual rainfall) for linear trends using regression (R²). Correlation was applied between soil temperature and altitude, between nutrients (N, P) across aspects of the forests (North and South) and NRE and PRE between altitudes. ANOVA was applied for leaf nutrients concentration (N, P) and tree species. All the data for various study parameters given in results section is mean across two growth cycles of trees (April 2014- March 2015 and April 2015- March 2016).

3. Results

Micro-Climature under The Forest Canopy: The effect of altitude on air temperature, soil temperature and soil moisture was evident across different forest sites (Table 2). Mean annual air

temperature declined significantly with increasing altitude from 28.6°C in Sal forest to 19.1°C in Tilonj Oak forest (R²=0.369; P< 0.01). Mean annual soil temperature was recorded maximum in Sal forest (22.4°C) and minimum in Tilonj Oak forest (14.6°C) (Table 2). Soil temperature was found in the order: Sal (22.4°C) > Pine (19.0°C) >Banj Oak (16.3°C) and Tilonj Oak forest (14.4°C). Across these sites, both soil and air temperatures were significantly different (P<0.05), however, the difference in RH was insignificant. Soil temperature declined with increasing altitude significantly (R=0.34; P<0.01), and it was found (mean =18oC) about 5oC lower than the mean air temperature (22.9°C). The Tilonj Oak forests were moist (mean value of soil moisture= 15.9%) and the Pine forest were the driest (10.8%) (Table 2). Across the three seasons and four forest sites soil moisture was recorded maximum during rainy season (mean= 16.8%) and minimum during summer (mean= 11.9%).

Forest sites (m asl)	Soil temperature (°C) (N=288)	Soil moisture (%) (N=96)	Air temperature (°C) (N=288)	Air Humidity (%) (N=288)	Soil nutrients (%)				
					SOC (N=96)	N (N=96)	P (N=96)	K (N=96)	C:N
Sal forest (300)	22.37±1.13	13.7±1.0	28.61±1.41	74.53±1.34	2.30±0.06	0.50±0.06	0.136±0.012	0.205±0.04	4.59±0.8
Chir Pine forest (1500)	19.01±1.12	10.85±0.6	23.12±1.24	72.97±2.34	1.90±0.05	0.305±0.05	0.108±0.07	0.130±0.03	6.23±0.9
Banj Oak forest (1800)	16.27±1.39	14.45±0.7	20.73±1.32	72.37±2.94	2.80±0.07	0.535±0.07	0.135±0.05	0.370±0.06	5.23±0.7
Tilonj Oak forest (2200)	14.55±1.26	15.9±0.8	19.15±1.36	71.86±2.90	3.10±0.09	0.555±0.06	0.121±0.06	0.350±0.05	5.58±0.6

Table 2: Soil microclimatic and physico-chemical characteristic of the studied forests (values are annual means ±).

Soil Physic-Chemical Properties:

Data on physico-chemical properties of soil averaged across summer, rainy and winter seasons of 2014-15 and 2015-16 for all the forests are given in Table 2. The mean N concentration ranged from 0.31% in Pine forest to 0.56% in Tilonj Oak forest. However, the P value was almost the same (mean = 0.12%) across all the forests. The Pine forests were markedly poor in K (0.13%) than the Oak forests (mean = 0.36%) with intermediate value for Sal forest (0.21%). Sal forest had a lower C: N ratio (4.6) than the nutrient poor Pine forest (C: N = 6.2) (Table 2). Across the three seasons soil moisture was recorded maximum during rainy season (mean = 16.8%) and minimum during summer (mean = 11.9%) for all the four forest sites. The Pine forests were poor in both soil moisture and soil nutrients, whereas the Oak forests were rich in both these parameters. Soil of the Sal forests was rich in P and the Oak forests soil in K (Table 2).

Leaf Nitrogen Dynamics

Leaf N concentration varied significantly (ANOVA; $P < 0.05$) across the tree species, season and life cycle of leaves (Fig. 2). In all the species N concentration was the highest in newly born leaves, followed by a pronounced decline during the leaf expansion phase, and then a relatively stable phase of N during winter that declined gradually through leaf senescence in the following summer season (Fig. 2). Across the species mean leaf N concentration immediately after bud-break was found ranging from 2.8% in *P. roxburghii* to 7.6% in *M. duthiei*. At the bud-break stage the mean N concentration in canopy and sub-canopy

species was almost similar (4.79% vs. 4.66%). Notably, at the bud-break stage leaf N concentration was significantly ($P < 0.05$) greater (6.69%) on S aspect, than on the N aspect (4.5%). At mature leaf stage with leaf mass in a steady state mean leaf N concentration varied between 2.3% in *P. roxburghii* and 3.0% in *M. duthiei*. A gradual decline in mean leaf N concentration (N-resorption proficiency) during leaf senescence until leaf drop occurred in all the species (Fig. 2). It was ranged from 30.0% in *M. esculenta* (evergreen) to 57.1% in *S. Robusta* (a semi-deciduous species). The N-resorption proficiency was marginally greater for canopy species than the sub-canopy species (mean = 44.4% vs. 38.4%), and that of S (60.65%) and N aspect (58.73%).

The leaf N mass (mg leaf⁻¹) at mature leaf stage ranged from 4.28 mg leaf⁻¹ (*P. roxburghii*) to 49.83 mg leaf⁻¹ (*S. Robusta*) during post-monsoon season. N-resorption started during November and continued until leaf drop in next April when new leaves of next year growth cycle were born. The period of N-resorption was shortest (2-3 months) in *S. Robusta* and relatively longer in the evergreen Oak species (4-5 months) growing at cooler higher altitudes. Across all the tree species NRE ranged from 48.7 to 76.8% in *M. esculenta* and *M. philippensis*, respectively (Table 3). The mean value of NRE for the canopy species (60.2%) and for the sub-canopy species (59.2%) was similar. N-Resorption efficiency at S aspect was slightly greater than the N aspect (61% vs. 58%). NRE was found inversely related with altitude ($R^2 = 0.89004$, $P < 0.056$).

Species	Mature leaf (%)	Senesced leaf (%)	Leaf N-mass at mature stage (mg leaf ⁻¹)	N-resorption proficiency (%)	N-resorption efficiency (%)
<i>S. robusta</i>	2.40	1.03	49.83	57.08	68.89
<i>M. philippensis</i>	2.50	1.15	11.14	54.00	76.77
<i>P. roxburghii</i>	2.25	1.30	4.28	42.22	61.93
<i>M. esculenta</i>	2.50	1.75	8.89	30.00	48.70
<i>Q. leucotrichophora</i>	2.65	1.75	11.82	33.96	51.64

<i>R. arboreum</i>	2.20	1.40	37.60	36.36	59.80
<i>Q. floribunda</i>	2.65	1.52	9.29	42.64	58.15
<i>M. duthiei</i>	3.00	2.00	14.14	33.33	51.68
Average	2.52	1.49	18.37	40.84	59.70

Leaf Phosphorus Dynamics

The leaf P concentration also varied significantly (ANOVA; $P < 0.05$) across the tree species, season and life cycle of leaves (Table 3; Fig. 3). Across the tree species mean P concentration in leaves immediately after bud-break ranged from 0.147% in *P. roxburghii* to 0.253% in *M. duthiei*. At the bud-break stage mean P concentration for sub-canopy species (0.22%) and canopy species (0.20%) was almost equal. At mature leaf stage mean leaf P concentration varied between 0.119% in *P. roxburghii* and 0.214% in *M. duthiei*, and the mean P concentration was almost similar for canopy and the sub-canopy species. At the senescent stage of leaf, P concentration varied between 0.069% in *P. roxburghii* and 0.170% in *M. duthiei* (Table 3). At steady-state phase of leaf nutrient concentration in the leaf mass, P- resorption efficiency (PRE) varied from 45.38% to 66.05% across the species. At the S aspect it was slightly greater than the N aspect (mean= 61% vs. 58%). PRE was found inversely related with altitude ($R^2 = 0.89004$, $P < 0.056$).

Leaf Potassium Dynamics

Dynamics of leaf K concentration throughout the growth cycle of leaves in the tree species is given in Fig. 4. Potassium concentration in leaves immediately after bud-break was found ranging from 0.94% in *P. roxburghii* to 2.05% in *M. duthiei*. At the bud-break stage mean K concentration for canopy species was slightly greater than the sub-canopy species (1.48% vs. 1.39%). At mature leaf stage mean leaf K concentration varied between 0.78% in *P. roxburghii* and 1.6% in *M. duthiei*. At the senescent leaf stage K concentration varied between 0.52% in *R. arboreum* and 1.14% in *M. duthiei*. At the steady- state phase the leaf K mass varied widely from 1.5 mg leaf⁻¹ in *P. roxburghii* to 24.5

mg leaf⁻¹ in *S. Robusta*. Across all the species the leaf K mass resorption efficiency (KRE) was computed ranging from 42.4% to 65.2% in *Q. floribunda* and *S. Robusta*, respectively. The average KRE was subsequently higher for the sub-canopy species (55.6%) than for the canopy species (54.9%). K- Resorption efficiency at S aspect was slightly greater than the N aspect (61% vs. 58%). PRE was found inversely related with altitude ($R^2 = 0.89004$, $P < 0.056$).

Leaf N: P Ratio

Leaf N: P ratio is a measure of nutrient deficiency in plants. In the present study the leaf N and P ratio varied markedly from mature to senesced leaf stage (Table 5). At mature leaf stage N: P ratio was found 12.9 in *M. esculenta* to 18.9 in *P. roxburghii*, and at senesced stage it varied from 9.97 in *Q. floribunda* to 16.7 in *R. arboreum*. The mean N: P ratio across all the species at mature leaf stage (14.7) and senescent stage (13.4) was similar. In the canopy species at mature leaf stage (15.4) it was slightly higher as compared to sub-canopy species (13.9). In senesced leaf stage N: P ratio was almost the same for both the canopy and sub-canopy species (12.7 vs. 13.1) (Table 5). Leaf N: P ratio during the bud-break and leaf development phase was higher for all the species with gradual decline throughout the leaf life cycle (Fig. 5). Exceptionally in *R. arboreum* after a rapid decline in N: P ratio in the first year of leaf life-span it increased again during the second year of leaf growth cycle. Also, in *P. roxburghii* the N: P ratio remains almost stable throughout the leaf life-span. Characteristically in all species (except *R. arboreum*) the N: P ratio is lowest during winter months with a slight increase in summer.

Species	Bud- break leaf	Mature leaf	Senesced leaf
<i>S. robusta</i>	25.58	15.58	11.92
<i>M. philippensis</i>	18.85	13.55	10.59
<i>P. roxburghii</i>	19.31	18.91	18.84
<i>M. esculenta</i>	14.18	12.88	12.91
<i>Q. leucotrichophora</i>	25.13	14.24	14.01
<i>R. arboreum</i>	19.98	15.25	16.95
<i>Q. floribunda</i>	24.23	13.24	9.96
<i>M. duthiei</i>	30.23	14.01	11.76
Mean	22.19	14.71	13.37

Table 5: Leaf N: P ratio of different forest tree species.

4. Discussion

The dominant canopy and co-dominant sub-canopy forest forming tree species of the four major forest types occurring along an altitudinal gradient studied by us exhibit a variety of leaf nutrient patterns and its dynamics across the leaf life cycle. The vari-

ations in foliar nutrient concentration were mainly contributed by the season, developmental stages of leaves (leaf formation to leaf drop) and altitude, and rather marginally by the aspect and canopy position as reported elsewhere [27]. Also, across the S and N aspects some variations were notable. The S aspect was

characterized by high N, P and K concentration (notably for N by 0.10 - 0.40% greater at N aspect), than the N aspect. In all these species the concentration of N, P and K in leaves was the maximum at bud-break, which declined gradually with ageing leaves (owing to dilution effect caused by expansion of leaf area and leaf weight, in conformity with earlier studies in this region [55, 35, and 36]. The mean leaf N concentration at mature leaf stage (range =2.25 - 3.0%), P (0.119 - 0.214%) and K (0.77 - 1.61%) and at the senescent leaf stage (N= 0.52 - 1.30%; P= 0.03 - 0.28%) varied significantly ($P < 0.05$) across the studied tree species. The nutrient concentration at senescent leaf stage is an important character of trees that determines the NRE and nutrient conservation strategy in the trees. Trees with more nutrient concentration in their senescent and leaf drop stage contribute to the soil fertility build up and ensuing ecosystem process that is reflected in greater nutrient concentration in the top soil of the Oak forests of this region. The nutrient concentrations at the time of leaf drop stage measured by us (mean N= 0.52 - 1.30%; P= 0.03 - 0.28%) fall within the range reported by earlier workers for the dominant forest trees of Himalayan region, in 31 tree species in warm temperate forests of China (N=1.8% and P=1.32%), in Oak (N= 0.03 - 1.85% and P= 0.001 - 0.015%) and Pine (N= 0.029 - 1.34% and P= 0.015 - 0.242%) trees reported globally, but slightly lower than the wet tropical forests of South Assam, Eastern Himalaya (range= 1.14-2.51%) [35, 56, 57, 36, 58, 59, 37, 60]. However, poor nutrients in Oak (N= 0.03%; P= 0.001%) and Pine (N= 0.79%; P= 0.05%) forests have also been reported [37]. The marginally higher leaf N concentration in sub-canopy (2.55%) than the canopy species (2.49%), at mature leaf stage reported in the present study implies that tree species

are adapted under sub-canopy conditions of lower solar radiation [61].

Altitude vs. nutrient relations

In the mountains altitude determines the ecosystem properties and processes. In sub-tropical China reported that with increasing altitude in the leaf litter N: P ratio had non-linear relationship with altitude. We also did not find a relationship in foliar N: P ratio with altitude as reported by. In general, both N and K leaf concentration increased with altitude, whereas P remains almost the same (Table 6; Fig. 6). Both NRE and PRE were significantly negatively related with altitude (Table 4), however, the relationship between foliar N and P with altitude was weak ($P < 0.00215$; $F = 4.686$). In montane cloud forests in the Andes, did not found a trend of foliar N: P ratios with altitude that did not indicate N limitation expect at 3000 m altitude. However, it has been pointed out that bedrock geology interaction across altitude and plant growth is poorly understood, which is reported on par with climate as a regulator of vegetation in Sierra Nevada mountain ecosystem. Our results on relationship between foliar N and P with altitude are contrary to the results of foliar N always decrease with altitude reported by. These workers suggested that a shift from P limitation to N limitation in plant growth with increasing altitude (sub-tropical to montane forests). Other studies, however, did not reported a significant change or even an increase in foliar N concentration along altitudinal gradients. Our study area falls within sub-tropical latitude, however due to rapid rise in altitude (300-2200 m ASL) the mean annual atmospheric temperature drops with rise in altitude leading to nutrient limited temperate conditions.

Species	Mature leaf (%)	Senesced leaf (%)	Leaf P-mass at mature stage (mg leaf ⁻¹)	P- resorption proficiency (%)	P- resorption efficiency (%)
<i>S. robusta</i>	0.154	0.086	3.20	44.16	54.62
<i>M. philippensis</i>	0.1845	0.1085	0.89	41.19	66.05
<i>P. roxburghii</i>	0.119	0.069	0.23	42.02	55.53
<i>M. esculenta</i>	0.194	0.1355	0.69	30.15	49.03
<i>Q. leucotrichophora</i>	0.186	0.125	0.83	32.80	45.38
<i>R. arboreum</i>	0.144	0.0825	2.46	42.71	56.96
<i>Q. floribunda</i>	0.20	0.1525	0.70	23.75	48.31
<i>M. duthiei</i>	0.214	0.170	1.01	20.56	46.95
Average	0.174	0.116	1.25	33.43	52.85

Table 4: Mean phosphorus concentration and P-resorption in the studied tree species (N= 624).

Parameter	Test	r ²	Significance (S)/Non-significance (NS) at (P<0.05/0.01)
Canopy/Sub-canopy (NRE)	correlation	0.890	S
Canopy/Sub-canopy (PRE)	correlation	0.033873	NS
Canopy/Sub-canopy (KRE)	correlation	0.998208	S
NRE/Leaf life-span	correlation	0.040443	NS
PRE/Leaf life-span	correlation	0.199689	NS

Altitude/NRE	correlation	0.647282	S
Altitude/PRE	correlation	0.524903	S

Table 6: Statistical relationship between altitudinal and nutrient responses of the trees in Central Himalayan forests.

In general, decline in leaf N concentration during leaf abscission was rapid in canopy species than in the sub-canopy species (2-3 months, December-February). The duration of N resorption (reckoned as decline in leaf N concentration) was shortest in *S. Robusta* (2-3 months) than the other species (4-5 months). *S. Robusta* grows at lower altitude, in the sub-tropical climate where mean annual temperature (MAT) was higher than the high altitude forest sites 21.9 vs. 16.4°C and this species exhibited highest NRE across all the species (Table 3) [62]. Studies have shown that variations in nutrients in green and/or senesced leaves are related with climate, plant functional type and soil condition [63, 64, and 38]. Reported that the leaf nutrient resorption traits (NRE and NRP) were significantly related with MAT and mean annual precipitation, and soil nutrient content (soil N/P concentration and N: P ratio) [65]. We found a significant positive correlation between altitude and NRE ($R^2= 0.647$) and PRE ($R^2= 0.524$) (Fig. 6; Table 6). However, a weak positive correlation was found between leaf life-span NRE ($R^2= 0.040$) and PRE ($R^2= 0.199$), which implies that leaf life-span is a genetically controlled phenomenon of trees.

Leaf N mass retranslocation (NRE) reported in the present study (range= 48.7 - 78.5%) is much higher than 22 - 55% reported for trees and shrubs of this region, but comparable to that reported (43.8 - 62.1%) for sub-tropical species of south Assam, and temperate forests of China (N= 35.6% and P= 43.7%; indicating resorption is one of the most important mechanisms of N conservation in the forests of Central Himalaya [35, 60, 66]. In our studied tree species there existed a weak correlation between leaf N concentration at mature stage and decline in leaf N concentration (NRE) at senescent stage ($R= 0.46$; $P< 0.05$). Also, this relationship was weakly positively correlated for P ($R^2= 0.36$; NS). It has been reported that plants with high nutrient status withdraw more nutrients from senescing leaves to conserve higher amount of soluble N molecules [67]. In conformity to this we found a positive correlation ($R^2= 0.7697$; $p= 0.004$, $P<0.05$) between leaf N concentration (mean=2.52%) and P (mean= 0.174%) at mature leaf stage and NRE (59.70%) and PRE (52.85%). Also, the canopy and sub canopy species differ significantly ($R^2= 0.890$; $P<0.05$) with respect to NRE.

Soil nutrient status has also been found related with NRE by a few workers [68, 69]. In our study, the Pine forest was characterized by poor soil nutrients (N= 0.31%, P= 0.11% and K= 0.13%) with NRE= 61.93%. Earlier workers have reported 12.6 -39.1% N resorption in Radiata Pine; 75.5 - 80.4% in chestnut Oak forest; and 62.3% in Oaks, and 76.7% in nutrient poor sites [70, 71, and 72]. The mean value of N resorption (60%) in this study is also comparable to the global average (62.1%), and that reported by for certain boreal forest species (mean= 52%) [39, 73]. A higher NRE and N- resorption proficiency among the tree species of forests and between the forests in infertile habitats was weakly supported in our study, as has been reported elsewhere [74].

Leaf N and P stoichiometry

As mentioned earlier the foliar nutrients vary along forests, altitude and season. The N: P ratio was wider during summer that declined gradually during winter, except for *R. arboreum*, an evergreen species with over 2 years leaf life-span. The slow release of organic P in the higher altitude is a well-established phenomenon [56]. In our study sites the mean annual soil and forest under-canopy air temperature declines significantly ($R^2= 0.9773$; $P< 0.05$) with altitude (Table 6). Apart from low temperature, the high soil C: N ratio and low concentration of nutrients in leaf litter at senescent stage just prior to leaf drop on forest floor, also hinders the decomposition of litter and organic matter, and therefore help explain why soil organic carbon and other nutrients increased with altitude, as has been reported elsewhere [45, 56]. Low temperature at high altitude probably limits the release of organic N in soil and/or the uptake of N by fine roots. The non-linear changes in P with altitude may have resulted from non-linear changes in P resorption capacity, and from interactions among topography, micro-climate and vegetation. The non-linear relationships observed in the present study suggest that the common assumption about plant and soil properties change linearly with altitude may not always hold.

Plant and Soil Nutrients Stoichiometry

Plant and soil nutrient ratios indicate the nutrient balance between each other and can have important implications for nutrient cycling and plant growth. In this study, C: N ratios of leaves and soil were lower than the global mean, indicating high N status in the studied forests. The high N status may be attributed to these old growth intact forests those do not face any anthropogenic disturbance, except for *P. roxburghii*, which is prone to recurrent forest fire between 3-5 years natural cycle. This is also a reason that the early succession and fire adapted *P. roxburghii* forests are perpetuating in the study area at the expense of adjoining late successional Oak and Sal forests [45]. Significant linear increases in C: N ratio of soil with altitude indicate the increase in N limitation with altitude and season; the C: N ratio become wider during non-rainy season.

In our study, NRE was calculated on a mass basis, i.e., the loss of N mass per unit leaf mass, however, some workers have calculated NRE on a leaf area basis, i.e., the loss of N mass per unit leaf area [74]. Reported that decrease in leaf mass during senescence could underestimate mass-based RE by 20% because the translocation of carbon is not taken into account [19, 75]. Specially for leaves having high N content, they have less structural material per dry weight as N also accounts for the mass of leaves that shows great change in leaf mass during senescence, and the resorption by these species can be underestimated if changes in leaf weight are ignored [76]. However, area-based measures are not perfect in that leaf area shrinkage may also occur during leaf senescence and can underestimate NRE by 10% [76, 77]. The NRE (N= 59.7%; P= 52.9% and K= 55.3%) and RP (N= 40.8%;

P= 33.4% and K= 30.4%) we reported in this study were thus different, and NRP tended to underestimate the N resorption. Nitrogen resorption can also be biased in other ways, like leaching, which has been reported $\approx 25\%$ of the N disappearance from leaves during autumn rains [30]. Generally, leaching of soluble nutrients in green leaves takes place rapidly and in higher concentration [78]. Our study area owing to immature geology is a sub-surface flow system where the rain water percolation and seepage is high owing to monsoon pattern of rainfall, contributing to high leaching loss of nutrients (0.11 - 2.80 kg/ha for N; 0.03 - 0.47 kg/ha for P and 0.10 - 2.86 kg/ha for K that was not measured in this study [79]. Soil P is also known to decrease with altitude due to leaching effect from up slope to downslope [80].

Are These Forests Nutrient Stressed?

Plants have developed two main strategies to grow and survive under regimes of nutrient limitations: optimizing nutrient acquisition and reducing nutrient loss. These adaptations are part of a well-known trade-off between resource acquisition and conservation among plants [81]. In 386 woody species of China, reported that leaf N and P were both negatively related to MAT and annual precipitation, while positively related to soil N and P concentrations [63]. However, in this study we did not find a definite trend between soils N, P and K status to that of leaf N, P and K at mature leaf stage, and also between soils N, P and K status with the RE of these nutrients. The trees we studied recorded a high amount of nutrient RE (mean= 60.0% for N and 55.3% for P), which is higher side of the usually accepted world value (50% for N). Leaf N and P ratio recorded in this study at mature leaf stage across the tree species ranging from 9.97 - 18.8 indicate that forests of the study area are both N and P limited [41]. Thus, considering the N:P ratio at mature leaf stage the tree species studied by us were both N limited (*M. philippensis*, *M. esculenta*, *Q. floribunda*) and the *P. roxburghii* was P limited, and rest of the species were both N and P limited. It implies that trees of the forests of this region optimize nutrient acquisition through reducing nutrient loss in litter fall and leaching and adapt themselves in the nutrient poor conditions by maximizing leaf life-span and NRE. Pine (*P. roxburghii*), an early successional tree that has been expanding in the late successional Oak forests is particularly adapted to the nutrient poor habitats of the region and efficiently retranslate nutrients (NRE= 51.6% for N; 50.92% P and 45.4% K) mass per shoot basis far greater than other tree species.

To conclude, the Central Himalayan forests are N and P deficient in general, owing to an interplay of low temperature, poorly developed and low weathered underlying geology and sub-surface and overland flows in hilly terrain leading to high leaching of nutrients due under the influence of monsoon rainfall pattern. These forests are characterized by high NRE and low growth rate with increasing altitude. Thus, winter season warming might help improve the nutrient mineralization and availability in the forest floor and nutrient uptake by the forests to enhance biomass productivity and ensuing ecosystem functioning and services.

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