Treeline species phenology: shoot growth, leaf characteristics and nutrient dynamics

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Abstract: In this study on treeline phenology in Tungnath, Garhwal Himalaya (altitude, 2955–3334 m asl), we (i) collected data on micro-climatic conditions, timing of major phenophases, leaf and shoot growth phenology and leaf nitrogen resorption in four major tree species (*Abies spectabilis, Betula utilis, Quercus semecarpifolia, Rhododendron arboreum*) and a krummholz species (*R. campanulatum*); and (ii) compared the treeline species phenology with mid-altitude forest tree species phenology of this region. Meteorological data reported for this site revealed that the mean monthly atmospheric temperature during growing period (July–September) has increased at the rate of 0.11 °C yr^{-1} in the last two decades. Leaf bud-break occurred in all the species in May, however, the proportion of marked tree population in bud-break phase at the time of first observation in May varied considerably across the species from 10% in *Q. semecarpifolia* to 50% in *R. arboreum*. Leaf initiation and leafing in the treeline species was delayed by about two months, compared to the mid-altitude tree species. Also, the leaf expansion within one month of leafing was conspicuously slower in treeline species than mid-altitude species (43% vs. 83% in *Quercus* spp. and 49% vs. 76% in *R. arboreum*). The treeline species were characterized by short growing period (2–4 months), lower period of steady-state in peak leaf mass and rapid leaf mass loss, low nitrogen concentration in leaves (1.7% vs. 2.5%), slow shoot growth, lower shoot length (5.6 cm vs. 9.5 cm) and shoot growth period, and higher leaf density in shoots (1.2 vs. 0.8 leaves cm^{-1} shoot length) than the mid-altitude forest trees. It is expected that with the increasing rate of warming in Tungnath the phenological behaviour of treeline species would change markedly in future leading to changes in ecosystem properties.

Key words: *Betula utilis*, Garhwal Himalaya, leaf nutrients, phenology, *Rhododendron campanulatum*, treeline ecotone, tree growth forms.

Introduction

Climatically, the Himalayas are predicted to experience a rise in temperature of 5–6 °C, and precipitation increases of 20–30% by the end of the twenty-first century (Kohler & Maselli 2009; Solomon *et al.* 2007), making them among the most threatened non-polar regions of the world. Treeline ecotones are sensitive biomonitors of past and recent climate change (CC) and variability (Kullman 1998), and are well suited for monitoring CC impact (Becker *et al.* 2007; Kullman 1998). The short growing season, snowfall, low air and soil temperature, high exposure to wind, increased exposure to frost and lower availability of nutrients are some of the common features of high altitude regions, which greatly influence plant phenophases and vegetation growth (Germino 2014; Körner 2012). Treelines are considered to be constrained primarily by heat deficiency (Holtmeier 2009; Körner & Paulsen 2004). Both winter and summer temperatures are considered as accurate predictors of occurrence of phenophases (Galan *et al.* 2005; Schwartz 1999; Spano *et al.* 1999; Sparks & Carey

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1995). For the Himalayan region, our knowledge is grossly inadequate on the relationships of the treelines to other ecological conditions and processes, such as meteorological conditions, freezing and frost, drought, soil temperature, wind, snow cover, soil quality, regeneration and other aspects (Schickhoff *et al*. 2015). In recent years, however, some progress has been made on the growth responses of plants to ongoing global warming (Gaire *et al*. 2014; Cui *et al*. 1999; Shrestha *et al*. 2012).

The alpine treeline represents not only a dramatic change in physiognomy, but also an important ecosystem with unique and rich biodiversity (Singh 2017). A few preliminary studies have shown that plant growth and phenophases here are triggered with the occurrence of favourable temperature, snow melt and consequent soil water availability (Nautiyal *et al*. 2001; Negi *et al*. 1992; Ram 1988; Sundriyal *et al*. 1987). Rai *et al*. (2013) have reported that *B. utilis* is highly sensitive to interannual climatic variations and early snowmelt. Liang *et al*. (2014) reported that Himalayan birch at its upper distribution boundary is increasingly at risk of survival. Uniyal & Uniyal (2009) reported that rising temperature during winter leads to increased activities and range expansion of pests in *Picea smithiana* in west Himalaya. In Tibetan plateau, Yu *et al*. (2010) have reported that strong winter warming could slow the fulfillment of chilling requirements, which may delay spring phenology. Phenological shifts (e.g., flowering time, its duration, and synchrony) may affect the interactions of plants with their pollinators and seed dispersers, hence reproductive success and growth of plants. In the mid-elevation forests of this region and other parts of the Himalaya there is growing evidence to show that CC has already induced changes in flowering phenology of trees (viz., *Rhododendron* spp.) (Gaira *et al*. 2014), and alpine herbs (Telwala *et al*. 2013). However, only a few such studies are available on the trees of timberline ecotone of the western Himalaya (Mir *et al*. 2016; Rai *et al*. 2012; Rawal *et al*. 1991).

Trees in seasonal climates often experience major water deficiency, and their physiology and phenology reflect the seasonality of moisture deficits. Soil moisture patterns within treeline ecotones are less frequently documented, but are supposed to be important drivers of treeline formation, and strongly influenced by moisture seasonality (González de Andrés *et al*. 2015). Tree growth may be constrained by lower water availa-

bility due to insufficient snow cover and frozen soils in spring (Balducci *et al*. 2013). Abiotic factors other than temperature, including water availability may serve as other important controls at high elevations, particularly for seedlings (*Picea engelmannii*) (Gill *et al*. 2015). Flower bud expansion and shoot growth involving cell expansion are known to be inhibited by even moderate water deficit. Soil temperature has been found to be the factor with similar importance for tree growth, both at a global and a local scale (Muller *et al*. 2016). It is known to impede photosynthesis (Dong *et al*. 2011), and biological activity in soil (< 5 °C), hence the nutrient supply (Holtmeier 2009; Körner 2012). Examination of soil and foliar nutrients is thus essential as trees are assumed to not being able to use obviously sufficient nutrients for growth as a result of low soil temperature. Several studies have assessed lower N cycling rates and contents in treeline soils, as well as lower foliar N in treeline trees compared to soil at lower altitude (Müller *et al*. 2016). In the nutrient-poor environment, protection against leaching, effective nutrient resorption from senescing plant organs, and high nutrient-use efficiency through long leaf life-span are regarded as important nutrient conservation strategies (Freschet *et al*. 2010). Thus measurements of soil temperature and moisture and related climatic and vegetation variables at high altitudes are required to understand the complexity and adaptations of the alpine ecosystems to CC (Liu & Luo 2011).

Objectives of the study were to: (i) collect first-hand data on various micro-climatic, phenological and leaf nitrogen aspects of treeline ecotone species varying in growth forms; (ii) determine phenological differences of treeline species with those of the mid-altitude (2000–2200 m asl) forest trees; (iii) find out phenological response of treeline species to global warming; and (iv) compare western Himalayan treeline ecotone with the alpine treelines of other parts of the world.

Study area description

Here, we have documented phenology of treeline ecotone species of Garhwal Himalaya in relation to treeline environment and compared its features with mid-elevation tree species phenology. The treeline species were highly diverse in growth forms ranging from *Abies spectabilis* (evergreen conifer with multi-year leaf life-span), *Betula utilis* (winter deciduous broadleaf), *Quercus seme-carpifolia* (semi-evergreen broadleaf), *Rhododendron arboreum* (evergreen broadleaf) and *R. campanu-*

Table 1. Study species in Chopta-Tungnath treeline ecotone. All occurred on North-West aspect, except *B. utilis* which occupied N-E aspect.

Species	Altitudinal range (m asl)	Physiognomy
Q. semecarpifolia	2955–3085	Brown Oak; Evergreen with 1 year leaf life-span
R. arboreum	2965–3233	Tree Rhododendron; Evergreen with leaf life-span between 1 and 2 years
A. spectabilis	2990–3276	Himalayan Fir; Evergreen with multi-year leaves
B. utilis	3250–3280	Himalayan Birch; Winter deciduous
R. campanulatum	3250–3334	Simru; Evergreen shrub (krummholz) with leaf life-span between 1 and 2 years

Fig. 1. Trees marked (1–100 nos.) in each five forest types for phenological observations (Above), and micro-climatic measurements under each forest stands (Below).

latum (evergreen krummholz species) (details given in Table 1), and phenological features considered were vegetative bud-break and shoot extension, leafing and leaf population dynamics, leaf expansion, leaf mass changes, flowering, fruiting and leaf drop. Leaf nitrogen dynamics and nitrogen resorption by leaves were also investigated.

The study was carried out at Chopta-Tungnath (Lat. 30.49', Long. 79.21', Alt. 2955–3334 m asl), located in Uttarakhand Himalaya (Fig. 1; Table 1). Mean monthly temperature at this site during the study year (2017) was 6.2 °C (mean max. = 10.1 °C and mean min. = 3.4 °C), and the annual rainfall in 2017 was 3800 mm, of which ~ 94% was recorded during June-September, the typical monsoon months (Joshi *et al.* 2018). Generally, the mean annual rainfall at this site is 2411 mm (mean value of 2008–2010) (Rai *et al.* 2012). However, 2017 was an unusually wet year. December onwards the site remains under snow for varying periods with mean duration being 85 ± 22.7 days yr^{-1} (Rai *et al.* 2012). At Tungnath, the mean highest sunlight intensity has been reported 79,200 Lux at 12 noon in May, and the least, 2,500 Lux at 12 noon in September (Nautiyal *et al.* 2001). The sunshine is often limiting at this site during monsoon period. In Tungnath, the weathering bedrocks, that provide the bulk of the loose material to soil pool, are crystalline and

Table 2. Mean values of microclimatic parameters during the study period (June to November, 2017).

Forest stand	Mean altitude (masl)	Air temperature (°C)	Soil temperature (°C)	Soil moisture (%)	Atmospheric humidity (%)
Q. semecarpifolia	3020	14.60 ± 1.23	10.30 ± 0.74	20.24 ± 1.40	79.30 ± 3.20
R. arboreum	3099	13.85 ± 2.01	10.10 ± 0.92	17.40 ± 1.97	76.72 ± 3.04
A. sepctabilis	3133	14.30 ± 1.20	10.10 ± 0.73	20.48 ± 1.93	76.58 ± 3.23
B. utilis	3265	12.03 ± 1.21	8.25 ± 0.720	20.23 ± 1.61	77.72 ± 2.72
R. campanulatum	3292	14.40 ± 1.20	10.10 ± 1.00	20.23 ± 1.97	74.60 ± 2.74

metamorphic, with sedimentary deposits of Paleozoic age (Gansser 1964). Soil is sandy loam in texture and acidic with pH between 4.9 and 5.6 (Nautiyal *et al.* 2001).

In the study area forests of *Abies spectabilis* and *Betula utilis* occur on north facing slopes and *Quercus semecarpifolia* and *Rhododendron arboreum* on south facing slopes, with tree associates viz., *Acer caesium, Prunus cornuta, R. barbatum, Sorbus foliolosa* and *Taxus wallichiana* (Adhikari *et al.* 2011). The *R. campanulatum* krummholz formation is common at the site; its seedlings/ saplings grow up to 3,666 m asl (Tungnath peak). None of the other tree species had recruited seedlings/saplings beyond the treeline at 3280 m asl. at this site except for *R. campanulatum* (Rai *et al.* 2012 and our observations).

The alpine meadow beyond the treeline in Tungnath is rich in herbs with 171 species of 5 different growth forms (Nautiyal *et al.* 2001). Tungnath is under varying levels of anthropogenic disturbance with regard to lopping of trees for fuelwood (used in local shops near Tungnath temple during tourist season) and fodder and grazing / browsing, especially by cattle almost during the entire snow-free period that has brought out negative effect on the meadow plants and tree regeneration and growth of under canopy species (Nautiyal *et al.* 2004).

Methods

Mature stands of four tree line ecotone tree species viz., *A. spectabilis* (Himalayan fir; evergreen conifer with multi-year leaf life-span), *B. utilis* (Himalayan birch; winter deciduous), *Q. seme-carpifolia* (brown oak; semi-evergreen), *R. arboreum* (tree rhododendron, evergreen) and *R. campa-nulatum* (evergreen krummholz species) distributed between 2,955 and 3,334 m asl (the upper limit of distribution of these species) were selected for the study (Table 1). Forest stand-specific *in-situ* micro-climatic data (air tempe-rature, atmospheric humidity, soil temperature and soil moisture) were

recorded at a monthly interval amidst the marked stands for each of these five species from May to December 2017. Data on air temperature, humidity and soil temperature (30 cm depth) were recorded three times a day (10 AM–5 PM) with three replications each time. Soil moisture was measured gravimetrically by oven drying the soil samples collected from each of the forest stands at monthly interval from 30 cm depth. To determine soil organic carbon and total nitrogen (N), composite soil samples collected from 30 cm depth were analyzed using CHNS analyzer (Elementar Co.).

Phenological observations on various pheno-phases (viz., vegetative bud-break and shoot emergence, leafing, flowering, fruiting and leaf drop) were made on the above mentioned five species at monthly interval starting from June–December 2017. We wanted to sample more frequently, but the remoteness of the site and logistics was a problem. We compensated for this by keeping sample size large. For phenological records a representative forest stand of 1 ha for each of the five species was selected and 100 mature indivi-duals of each species were marked (for *B. utilis* only 70 trees were available) (Fig. 1). Shoot extension and radial growth were measured at monthly interval on 25 marked current year shoots for each of the tree species. Leaf characters (leaf area and leaf mass) were based on 100 randomly plucked current year leaves from the marked forest stands. Leaf area was recorded using a portable leaf area meter (Biovis LeafAv). These leaves were then oven dried at 60 °C till constant weight and ground in a Wiley Mill and the leaf material was stored in airtight glass vials and subsequently analyzed for total N in CHNS Analyzer (Elementar Co.). Leaf mass loss (an indicator of senescence) was computed as: mature leaf mass − senescent leaf mass, and expressed in terms of percentage to mature leaf mass. Nutrient resorption efficiency (RE, %) was calculated as the ratio of the difference in N mass between mature leaf and senescent leaf stage. In the N resorption study, leaf N leaching

Table 3. Organic carbon, total nitrogen and C:N ratio in soil of Tungnath treeline forests.

Species	Soil organic carbon (%)	Soil Nitrogen (%)	C:N ratio
R. arboreum	6.4 ± 0.7	0.55 ± 0.06	11.7
Q. semecarpifolia	7.4 ± 0.9	0.60 ± 0.08	12.3
A. spectabilis	6.7 ± 0.8	0.53 ± 0.05	12.6
R. campanulatum	5.4 ± 0.5	0.44 ± 0.04	12.3
B. utilis	5.4 ± 0.3	0.37 ± 0.02	14.6
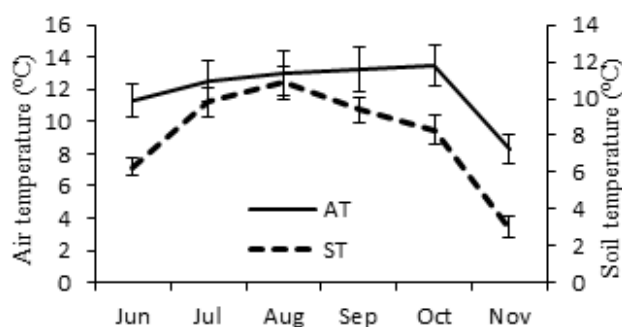
Fig. 2. Air and soil temperature across the study period in *B. utilis* forest stands in 2017.

could not be considered, that makes a negligible part compared to resorption (Freschet *et al*. 2010).

Results

Microclimatic variations among the forests

Mean values of various micro-climatic parameters across the study period varied only marginally among the five study sites (Table 2). The mean air temperature and soil temperature in forests decreased with elevation; being the highest in *Q. semecarpifolia* forest and lowest in *B. utilis* forest, and soil on average was nearly 4 °C cooler than air (Table 2). Among the study sites, *B. utilis* forest site was distinctly cooler (both air and soil temperature) than others. The soil of *R. arboreum* site was relatively drier. During rainy season the difference between soil and air temperatures tended to narrow down as soil warmed up more than the air, where after it widened in autumn because of the rapid cooling-off of soil than air (illustration of this trend for *B. utilis* is given in Fig. 2).

The peak air temperature was recorded in August for two species, and in September for the rest three species, and peak soil temperature was recorded in August for all the five species. Peak soil moisture was recorded in July for all the species except for *R. campanulatum* (August) and it declined in the following months. Peak values of relative humidity were recorded in August for all

the species. The air and soil temperatures were positively correlated (r = 0.789; *P* < 0.01) and the atmospheric temperature and relative humidity were inversely related (non-significant).

Soil nutrients

Mean annual total soil nitrogen in the treeline forests of Tungnath varied from 0.37% to 0.60%, soil organic carbon from 5.4% to 7.4% and C:N ratio from 11.7 to 14.6 (Table 3). In general, soil carbon and soil N tended to decrease with elevation, while C:N ratio tended to increase with elevation, being the highest (14.6) in *B. utilis* forest.

Major phenophases

The occurrence of different phenophases in the five species during the study period is shown in Fig. 3. Leaf bud-break occurred in all the species in May, however, the proportion of total bud break (out of 100 marked trees) that occurred in May varied widely from 10% in *Q. semecarpifolia* to 50% in *R. arboreum*. Leafing was a rapid activity in *R. arboreum* (2 months) and extended activity in *Q. semecarpifolia* (4 months). Leaf drop started earlier in *B. utilis* and *Q. semecarpifolia* in September and October, and by November *B. utilis* trees become leafless. In all the other three species (*A. spectabilis*; an evergreen species with multi-year leaf life-span, and the two *Rhododendron* species with leaf life-span more than one year) previous year (2016) leaves dropped continuously throughout the growing season of 2017, that stopped in August 2017. Again, leaf drop of previous year leaf population started from November onward and continued until next spring (March–April). Flowering occurred in all the species during April-May, except for *B. utilis* (October). It was soon followed by fruiting and fruit maturation in all the species that continued for 3–4 months (Fig. 3).

Phenology of leaf and shoot growth

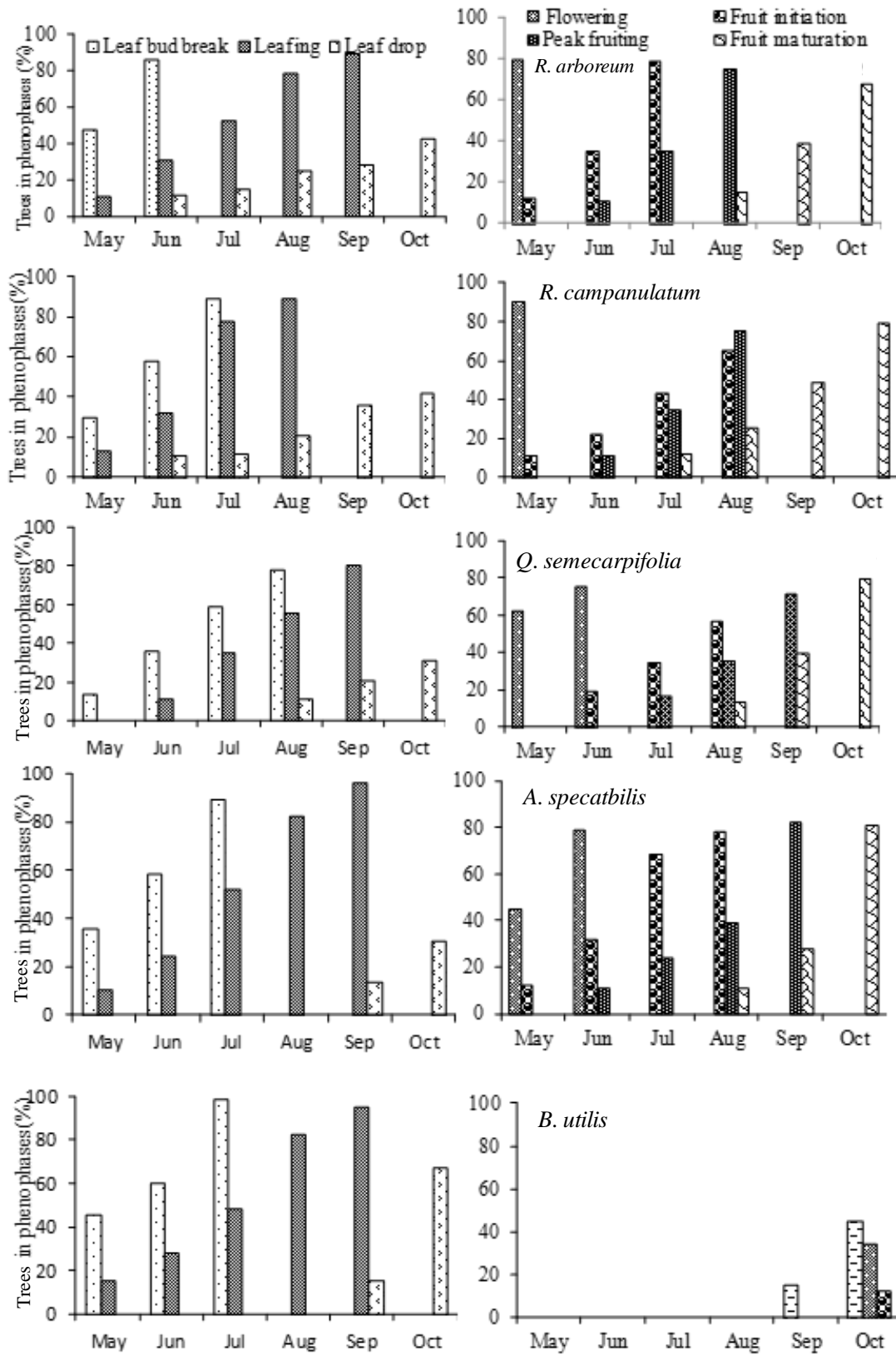In all the species leafing and shoot elongation continued from bud-break until September (Fig. 4),

Fig. 3. Phenological events in different forest trees species expressed as % of 100 marked individuals of each species in 2017.
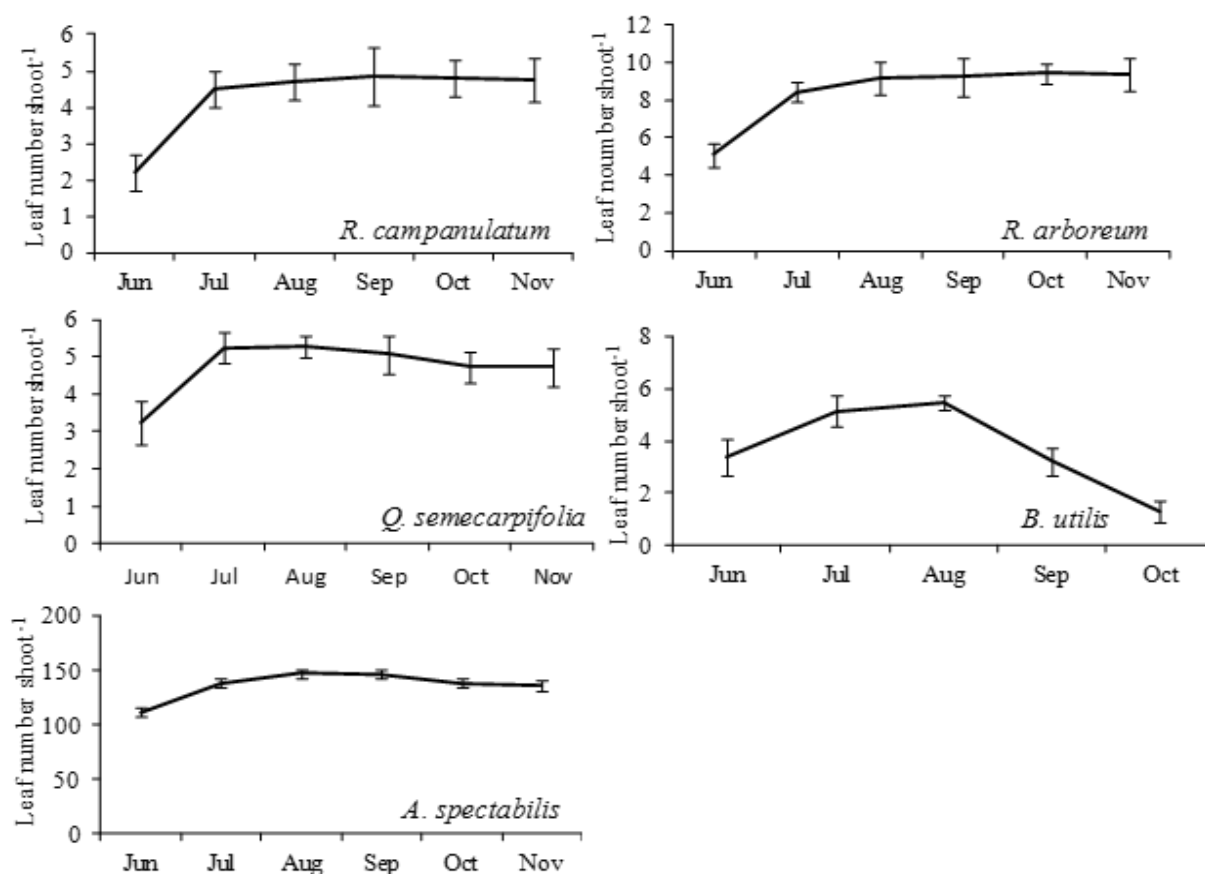
Fig. 4. Number of leaves per shoot in different species in 2017.

however, > 80% shoot extension was attained by July in all the species. Thus much of the canopy was restored by the commencement of monsoon. At the full extension, the shoot length ranged between 4.6 cm in *R. campanulatum* and 13.5 cm in *B. utilis*. The radial growth at full extension of shoot was found ranging from 2.5 mm (*B. utilis*) to 7.5 mm (*R. arboreum*). Leaf number per shoot (current year leaf crop) at mature stage ranged from 4.9 (*R. campanulatum*) to a maximum of 9.4 (*Q. seme-carpifolia*). In *A. spectabilis* it was 147.3 needles/shoot. Leaf density (no. of leaves cm^{-1} shoot length) ranged from 0.37 (*B. utilis*) to 13.3 (*A. spectabilis*).

Leaf expansion took place rapidly in the initial months of leaf formation and attained peak in August in all the species except for *R. campanulatum* in which it continued until September (Fig. 5). Here, it can be stated that as the leaf area measurements were based on 100 leaves (randomly collected at monthly interval from the marked population of current year leaf crop), full expansion of leaves could be considered when the leaves had attained ~90% of

the leaf area on a leaf population basis. Peak leaf area (cm^2 leaf^{-1}) ranged from 0.29 cm^2 (*A. spectabilis*; a conifer) to 64.8 cm^2 (*R. campanulatum*). Time taken to attain peak leaf area was three-four months (except for two months in *B. utilis*). Corresponding to leaf area, gain in leaf mass was rapid in the initial months of leaf formation (Fig. 5). The time when full leaf mass was attained ranged from August in *Q. semecarpifolia* to October in *R. campanulatum*. At the mature leaf stage the leaf dry weight (g leaf^{-1}) was measured lowest for *A. spectabilis* (0.008 g) and highest for *R. campanulatum* (1.37 g). In most of the species leaf mass loss started as early as in August-September except for *R. campanulatum*. Leaf mass loss ranged from 25.3% (*R. arboreum*) to 42.0% (*B. utilis*) (Fig. 5).

Leaf N dynamics

Mean values of leaf N concentration and leaf N mass are depicted in Fig. 6. At the bud-break stage leaf N concentration was maximum in all the species, which declined with the expansion and gain
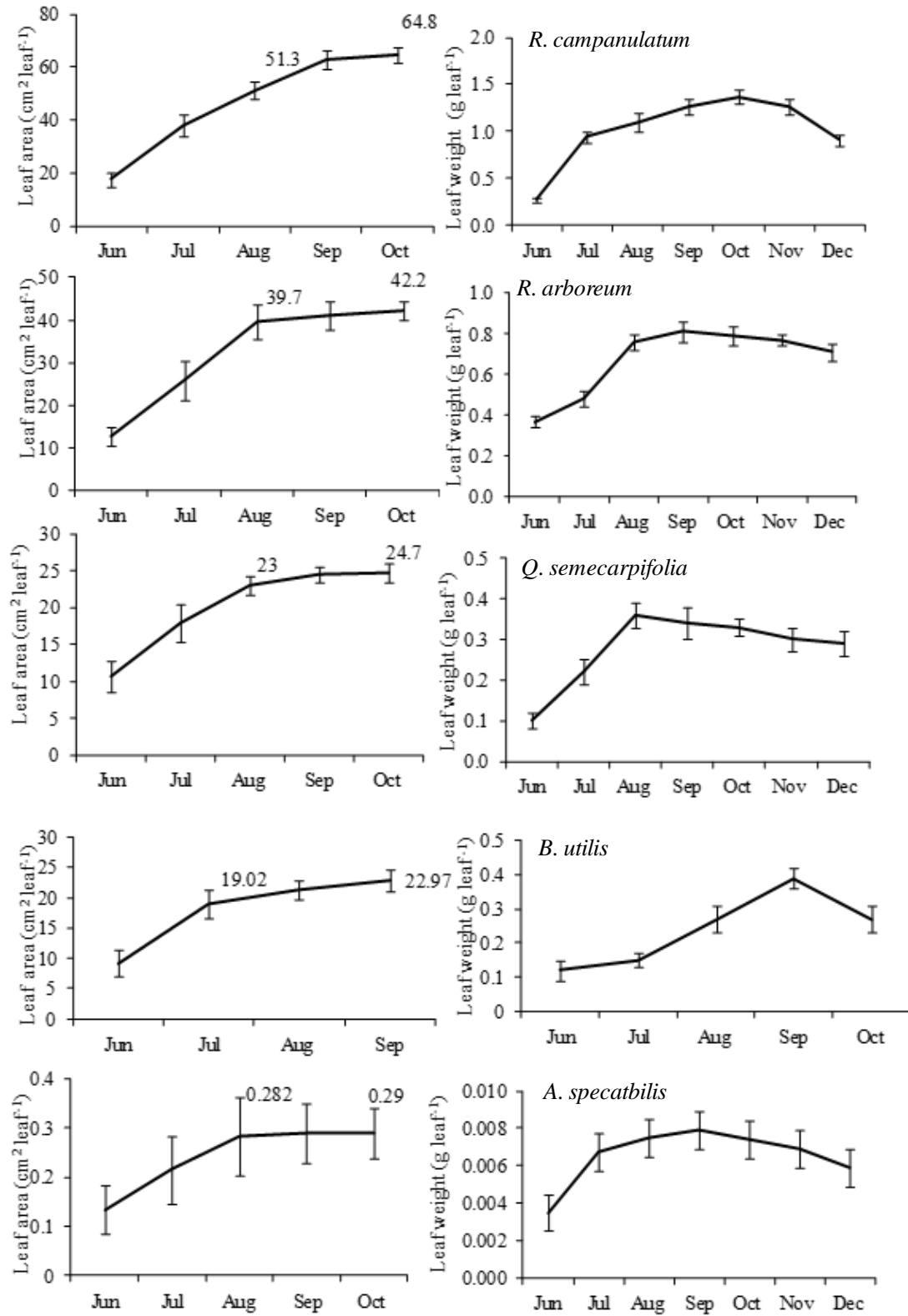
Fig. 5. Leaf area (cm² leaf⁻¹) and leaf weight (g leaf⁻¹) in relation to growing period for different species in 2017. Mean leaf area at fullest expansion (~90%) in August and at the end of the observation in October is given in figures over the line diagram (Left side).
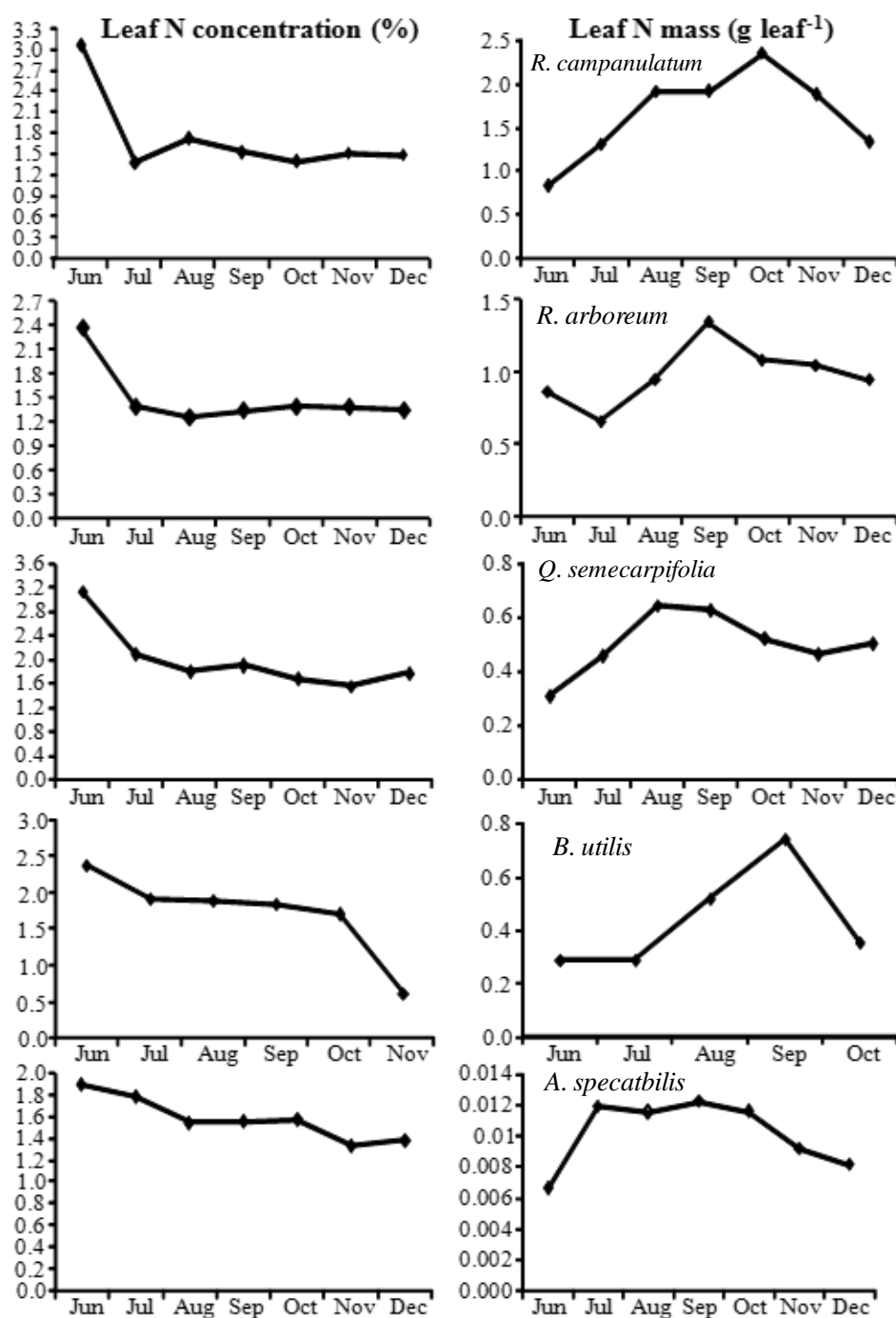
Fig. 6. Leaf nitrogen dynamics of different studied species (Left: leaf N concentration, %; Right: leaf N mass, g leaf^{-1}).

in mass of leaves. At mature leaf stage (steady-state in leaf mass) leaf N concentration varied from 1.53% (*R. campanulatum*) to 1.89% (*Q. semecarpifolia*). The phase of peak leaf N concentration was followed by a gradual decline until the leaf drop. At the senescent leaf stage leaf N concentration varied from 0.63% (*B. utilis*) to 1.3% (*A. spectabilis* and *Q. semecarpifolia*). In terms of leaf N mass all the species attained peak leaf N mass by September, except for August in *Q. semecarpifolia* (Fig. 6). Across the species peak leaf N mass varied from 0.012 g leaf^{-1} in *A. spectabilis* to

Table 4. Atmospheric temperature recorded for Tungnath by various workers. (-) Data not available.

Year of measure-ment	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Growing season mean (Jul –Sept.)	Reference
1985–86	6.3	11.1	15.9	14.4	12.9	7.4	5.6	-	-	11.6	Ram *et al.* (1989)
1985–86	-	-	-	12.3	12.0	9.0	7.2	-	-	11.1	Sundriyal *et al.* (1987)
1990–97	-	10.0	12.0	10.0	9.0	8.0	7.0	-	-	9.0	Nautiyal *et al.* (2001)
2008–10	7.0	8.0	11.0	12.0	11.5	9.0	7.0	4.0	1.0	10.8	Rai *et al.* (2012)
2017	6.7	8.09	10.2	11.7	11.7	10.1	6.4	2.6	-	11.2	Joshi *et al.* (2018)
2017 (Day time)	-	-	12.8	13.9	16.0	15.8	13.2	-	-	15.2	Present study

1.93 g leaf⁻¹ in *R. campanulatum*. N mass resorption efficiency at the stage of leaf senescence was computed ranging from 34% in *A. spectabilis* to 63% in *R. arboreum*. Leaf N mass was steady for only a short period, except in *A. spectabilis*, *R. arboreum* and *R. campanulatum*.

Discussion

This study on phenology, leaf and nitrogen dynamics in forests of varying growth forms in a treeline ecotone of western Himalaya has generated some first-hand data in this least investigated and "data-deficient" system of the Himalayan region. In all the five species studied the onset of growth (vegetative bud-break and leafing) occurred in the first week of May, however, the number of trees (out of 100 marked trees of each species) in the bud-break phase varied from one species to other. In tree stands of *R. arboreum* occupying the lower limit of the ecotone (2965–3233 m asl) about 50% marked tree individuals exhibited bud-break in May compared to 25% in *R. campanulatum* growing at the higher altitudes (3250–3334 m asl) in Tungnath. However, it was quite possible that bud-break in some species might have initiated before May when the site was inaccessible because of snow cover. For this study site, Rai *et al.* (2013) have reported 102 ± 11.5 Julian day (April first week), the average date of bud-break, and appearance of first leaf on 111 ± 14 JD (mid-April) in *B. utilis*. In the dominant trees (both evergreen and deciduous species including *Quercus* spp. and *Rhododendron arboreum*) of mid-altitude (2000–2200 m asl) zone

of this region peak leafing (~90% new leaf crop in trees) is accomplished by the end of April–early May (Negi 2006). The mid-altitude tree species are also characterized by concentrated leafdrop during March–April. Thus, in the treeline ecotone species leafing and accomplishment of full leaf canopy were delayed by about two months as compared to the mid-altitude tree species. A similar delay in treeline ecotone occurred in the time of the highest temperature that occurs in August in Tungnath, and during June in mid-altitude forests. Also, in the evergreen treeline species peak leaf drop occurred during May–June. However, during October-November due to heavy frost and cold winds some leaf drop was recorded in these species. In the Tibetan Plateau, Yu *et al.* (2010) reported that winter and spring warming has resulted in delayed spring phenology. In our study site mean atmospheric temperature for growing period (July–September) has increased by about 1 °C (@ 0.11 °C yr⁻¹) during the last two decades (between 1990–97 and 2017; Table 4). The excessive wet conditions of the year 2017 (annual rainfall= 3800 mm vs. 2410 mm in 2009–10; Adhikari *et al.* 2011) may have prolonged the active growth period.

R. campanulatum krummholzs differ from other treeline species with respect to a slower rate of leafing and simultaneous and prolonged drop of previous year leaves that occurred from June to December. In respect to leafing and leaf drop, it resembled more with *R. arboreum*; a species of tree rhododendron also found in the mid-altitude forests in this region (Negi 1989). Leaf area and leaf mass of *R. campanulatum* were highest among all the species, and its lower specific leaf area indicated

that the leaves were thicker than other species possibly to escape from the stressful conditions of high altitudes (Körner 2012). The krummholz stands were particularly characterized by relatively lower relative humidity and more atmospheric temperature during day time as the stands occurred in open meadows with abundant wind flow.

A comparison of leaf and shoot growth characteristics with the *Quercus* spp. and *R. arboreum* of the mid-altitude forests of this region reveals that the bud-break and leafing takes place about four-six weeks earlier than in conspecifics at Tungnath site (Negi 2006). Also, the leaf expansion within one month of leafing was conspicuously greater in these species of mid-altitudes (83% vs. 43% in *Quercus* spp. and 76% vs. 49% in *R. arboreum*). These observations quantify the limiting effect of heat deficiency in treelines. Leaf area of *R. arboreum* at these sites was almost equal indicating that the difference of temperature in this species results in delay in phenophases, but not in leaf size. Leaf size depends on several other factors, particularly sunlight (James & Bell 2000). A lower shoot extension period (2–5 months vs. 4–6 months) and lower shoot extension growth at the treeline ecotone for *Quercus* spp. and *R. arboreum* than at the mid-altitude site (mean shoot length= 5.6 cm vs. 9.5 cm) was the other striking feature of shoot growth phenology. In terms of leaf number per cm shoot length, leaves were distantly placed in mid-altitude species as compared to densely packed leaves along shoot length in treeline species (0.8 vs.1.2 leaves/cm shoot length). It implies temperature control over the growth of plants in alpine environment (Tranquillini 1979) and warming is expected to increase growth in treeline ecotone.

Phenological events are constrained at high altitudes by the short growing season delimited by cold temperatures and snow cover. The time of snowmelt appears to have an almost universal effect on high-altitude phenology (Inouye & Wielgolaski 2003), and variations in phenology has been usually linked to variations in the accumulation and melting of snow (Holway & Ward 1965; Mark 1970). In the alpine sites of this region it has been reported that because of early availability of snowmelt water, ca majority of the species initiate growth (Negi *et al.* 1992; Ram *et al.* 1989) and do not wait for the onset of the monsoon as required for herbaceous plants of the low altitude of this region (Singh & Singh 1992). At Tungnath, Rai *et al.* (2012) reported that the development of leaves in a shoot and leaf fall at the end of the growth period were highly correlated with soil and air temperature, precipitation and relative humidity. They found that leaf fall was delayed in years with a higher temperature and vice versa, and higher temperatures and delayed monsoon extended the overall growth period of trees.

When considered the growing period between 1990–97 and 2017 (the period using modern meteorological instrumentation) rise in atmospheric temperature has been quite conspicuous (i.e., 2.2 °C in the last two decades @ 0.11 °C yr^{-1}) (Table 4). This rate of warming is in conformity with those reported by several workers for the Himalayan mountains (Schickhoff *et al.* 2015; Shrestha *et al.* 2012; Singh *et al.* 2011; Xu *et al.* 2009). Of particular interest is growing season mean of air and soil temperatures that vary across forests and influence growth of plants. In our study site, considering the wet and warm months (July–September) as active growing season when the foliage is fully developed, the mean air temperature in 2017 (i.e., 11.2 °C) was much higher than seasonal mean ground temperature of 6.7 °C (± 0.8 SD; 2.2 K amplitude of means for different climatic zones of the world), reported by Körner & Paulsen (2004). Thus, it may be pointed out that growing season length at Tungnath is much longer than the climatic treelines, which may have several eco-physiological implications on the treeline vegetation and warrant further studies.

The annual mean of soil temperatures across the five forest sites (range = 8.3 °C to 10.3 °C; mean= 9.8 °C at 30 cm depth) recorded by us was higher than other reports for alpine treelines (Körner 2012) that may have favoured nutrient mineralization. At a global scale, an average growing season soil temperature below 6.4 ± 0.7 °C in 10 cm soil depth is supposed to limit alpine tree growth (Körner 2012), whereas growing season mean soil temperature at a local scale exhibit a large range from 5 °C to 12 °C (Müller *et al.* 2016). In a year (2010) with high air and soil temperatures in Tungnath, Rai *et al.* (2012) found a short growing period that was related with slow rate of leaf expansion, lower leaf area and leaf number in *B. utilis*. Also, low soil temperature led to a slow rate of leaf expansion, shoot growth and fewer leaves in a shoot in Tungnath (Rai *et al.* 2012). Further, higher temperature and delayed monsoon extended the overall growth period, resulting in a delayed and slower leaf fall which is advantageous in terms of longer leaf life-span and photosynthetic gain. A longer leaf life-span is associated with potentially higher carbon gain by the plant and

more efficient nutrient use (Richardson *et al.* 2006).

Plants have developed two main strategies to grow and persist under regimes of nutrient limitations: optimizing nutrient acquisition and reducing nutrient loss. These adaptations are part of a well-known trade-off in and among plants between resource acquisition and conservation (Reich *et al.* 1997; Wright *et al.* 2004). We found that in the *R. arboreum* and *R. campanulatum* krummholz poor in soil nutrients and leaf N, resorption efficiency of leaf N (mean= 60%) was markedly greater than other species growing at similar site conditions. Treeline species at Tungnath were relatively poor in leaf N at mature stage than the mid-altitude forest trees (2.5 vs. 1.7%; Negi 1989). Freschet *et al.* (2010) found inter-specific variation in organ nutrient resorption and leaf leaching in 40 subarctic vascular plants and linked it with "nutrient acquisitive-conservative strategies", and resorption process as a potential importance for the plant nutrient budget. Some studies have found resorption efficiency and leaching resistance decreases with increasing leaf nutrients (e.g., Kobe *et al.* 2005; Pastor *et al.* 1987). Studies elsewhere (e.g., Drollinger *et al.* (2017) have shown that nutrient concentration in soil and trees decreases with increasing elevation in treeline ecotone that might explain why treeline shift and global warming are decoupled (Müller *et al.* 2016). Our data also show that both soil nutrients (total N, $R^2 = 0.30$; and OC, $R^2 = 0.22$) and foliar N decreased with increasing elevation though the relation was weak, indicating nutrient conservation strategy of *R. campanulatum* in poor site conditions. Our values of soil OC were much higher than that reported for mid-altitude forests of this region (range= 0.8–3.3%) but the soil total N was quite comparable (range= 0.25–0.70%; Joshi & Negi 2015). Garkoti & Singh (1994) have reported mean value of soil organic carbon (3.04–3.13%) and N (0.40–0.41%) in *B. utilis* and *R. campanulatum* forests of this region (up to 30 cm depth). Soil organic carbon stock has been reported highest for *B. utilis* across a variety of temperate forests of Kashmir Himalaya (Dar & Somaiah 2015). Decreasing soil C with increasing elevation, however insignificantly (Speed *et al.* 2015), whereas significantly decreasing soil N concentration (Muller *et al.* 2016), thus significantly increasing C/N ratio (Thebault *et al.* 2014) has been reported. Since, leaching of organic acids and organomineral compounds is part of the podzolization process as a whole, N limitation might be a typical factor for treeline ecotones (Müller *et al.* 2016) that requires further research.

To conclude: (i) the treeline species are characterized by a delayed bud-break and leafing, a slow leaf expansion, a short steady-state period in leaf mass, lower shoot growth, higher leaf density per shoot and lower leaf N concentration compared to the mid-altitude forest tree species of the western Himalayan region; (ii) treeline of our study site is characterized by a longer growing season owing to markedly higher mean growing season temperature than the climatic treelines of the world (11.2 °C vs. 6.7 °C). Treeline ecotone vegetation of western Himalayan region may face several eco-physiological implications with the ongoing pace of global warming.

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