Structure and Functioning of Timberline Vegetation in the Western Himalaya: A Case Study

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An ecological assessment of timberline vegetation was carried out during 2008–2011 at selected locations in the Indian Himalayan states of Uttarakhand and Himachal Pradesh. The objectives were (i) to establish baseline data on the vegetation structure and composition along the timberline ecotone, (ii) to assess the functioning of major communities (net primary productivity, litter decomposition, and nutrient dynamics), and (iii) to study the effects of interannual climatic variation on the phenological responses of the tree species forming the alpine timberline in the study area. Geospatial analysis of the timberline ecotone (3,000–4,000 masl) showed that fir (Abies spectabilis) occupied the greatest area within the timberline (1,886 km²) followed by oak (Quercus semecarpifolia, 1,142 km²), birch (Betula utilis, 433 km²), and krummholz (412 km²). An area of approximately 81 km² had undergone major change during the last three decades, with a proportionally greater change in the last ten years (44 km²) than in the previous decades. Fir forest had increased by 33 km² since 1980. The phenological study showed that the broadleaf deciduous species Betula utilis was more sensitive to interannual climatic variation and early snow melt. This Paper discusses the broad findings of the study, especially the extent and changes in the forests along the timberline ecotone, the pattern of tree species regeneration, the population structure, and phenological responses under different conditions.

Keywords: change detection; phenology; remote sensing; timberline; Western Himalaya

Introduction

The timberline ecotone, marked by the culmination of the forested zone, is the most prominent ecological boundary in the high mountains governed by climatic factors (Holtmeier 2003). The microclimate, topography, altitude, and herbivory play a significant role in determining the structure and function of plant communities along the timberline. In addition, several anthropogenic, topographic, and climatic factors influence the overall physiognomy and
community structure of the timberline. Often the interfaces resulting from these factors lead to a complex spatial heterogeneity in forest structure and mosaics of forest succession (Timilsina et al. 2007; Shugart et al. 2010). All ecotones are known to be sensitive to biotic and climatic stressors because species are adapted to their own microclimatic conditions. It is predicted that with increasing global temperature, the altitudinal timberlines will advance to higher altitudes, while latitudinal timberlines will move towards higher latitudes in the northern hemisphere (Parmesan 2006; Weiser and Tuasz 2007). However, several authors have suggested that this pattern may not hold true for all regions due to the dependence upon local and regional conditions such as terrain type, orographic influences, herbivory, diseases, and anthropogenic influences (Cairns and Moen 2004; Weiser and Tuasz 2007).

Although several authors have documented the floristic structure of high-altitude vegetation in the greater Himalayas (e.g., Naithani 1984; Rawat 1984; Semwal 1984; Singh and Rawat 2000), detailed ecological studies of the community structure, phenological response of major species to inter- and intra-annual climatic variation, and dynamics of vegetation at a landscape level are lacking. Baseline studies covering these aspects along the gradients of precipitation (east-west axis) at selected sites would go a long way towards developing appropriate models for predicting the response of timberline communities to climatic and non-climatic drivers. This paper discusses the results of a geospatial analysis of the timberline ecotone (3,000–4,000 masl) in the Western Himalaya in two Indian states, and looks at recent changes in the vegetation cover at a landscape level, patterns of tree species regeneration, population structure, and phenological response under different conditions.

**Study area**

An extensive survey was carried out along the sub-alpine-alpine ecotone of the Western Himalayan mountains in the Indian states of Uttarakhand and Himachal Pradesh (Figure 9). The phenology of the dominant timberline forming tree species was monitored within Kedarnath Wildlife Sanctuary (KWS) in the upper catchment of the river Alaknanda, a major tributary of the Ganges. The sub-alpine forests in this area are characterized by a preponderance of shade loving species on north facing slopes (*Betula utilis* and *Abies spectabilis*) and light demanding species on south facing slopes (*Quercus semecarpifolia* and *Rhododendron arboreum*), with low tree species richness. The krummholz formation in the study area is dominated by *Rhododendron campanulatum*. Towards higher altitudes, the krummholz formation gives way to extensive alpine grasslands and meadows characterized by the presence of *Danthonia cachemyriana*, several species of *Carex*, *Kobresia*, and a variety of dwarf herbs. The study area has three main seasons: a long winter (October to April), short summer (May to June), and rainy season (July to September). The mean annual temperature along the timberline ecotone (3,300 masl) ranged from -8.9°C in January to +25.6°C in July, with an annual average of 6.6 ± 0.7°C. The mean temperature of the warmest month was 12.6 ± 1.2°C, in July. Annual precipitation was 2,411 ± 432 mm, of which 89.5% was recorded during June-September; snow cover lasted for 85 ± 22.7 days/year.
Methodology

Timberline structure and composition

Vegetation sampling was carried out along the entire timberline in the study area. Forest types were selected based on physiognomy and variation in topographic features. Ten 10×10 m quadrats were laid within each hectare plot (n=26) for trees and saplings. A smaller 5×5 m quadrat was laid within each 10×10 m quadrat for shrubs and tree saplings. Twenty-five quadrats of 1×1 m were laid randomly within the hectare plot for herbaceous vegetation. The tree canopy cover, tree height, canopy depth, and canopy width of trees were measured with the help of a densitometer, clinometer, and measuring tape. The tree, shrub, and herb layers were analysed separately for species richness, density, diversity, and regeneration of tree species following Curtis and McIntosh (1950) and importance value index (IVI) calculated following Phillips (1959).

Vegetation mapping and change detection

Figure 10 shows the methodological framework of the classification adopted for timberline mapping. The field data used for image classification and accuracy assessment of thematic maps were collected during the summer in 2009–2011. Data were collected in the form of
geographical locations of different vegetation classes and non-vegetated surfaces using the Garmin-72 global positioning system (GPS). Landsat images downloaded from the EROS data centre online archive (http://glovis.usgs.gov) were used for the study. Deciduous species only attain full maturity after April. Hence images from earlier period of the year could not be used. Images from the peak growing season (July–August) show poor discrimination of alpine meadow from deciduous forest, and it is very difficult to obtain cloud-free images in the pre-monsoon months. Thus, images from September and early October from the years 1998 and 2009 were selected for the study.

In the first pre-processing step, multispectral scanner (MSS) images were registered with thematic mapper (TM) images and resampled at 30 m to match the resolution. Radiometric correction was performed by converting the raw digital value of the image to at-sensor spectral radiance ($L_{\lambda}$) using standardized rescaling factors (Chander et al. 2009) and finally to top-of-atmospheric reflectance (Markham and Barker 1986). Relative radiometric normalization (RRN) was used to adjust the reflectance of the target (TM) image according to the base (MSS) image (Hall et al. 1991).

As no training samples or ground truth data were available for supervised classification, an unsupervised classification approach through isodata clustering was used. Each individual subset image was classified into 120 clusters. Data collected during the fieldwork were used
to sort the clusters into 12 land cover classes. To avoid the impact of diffuse sunlight on steep slopes, the normalized difference vegetation index (NDVI) calculated from the reflectance band, tasselled cap derived brightness, and the wetness index were used as additional layers with four multispectral bands.

The change detection method used in the study was based on a vegetation index (VI) differencing technique. Residual difference images were created by subtracting the VI of the MSS image from the TM image. The resultant difference image contains negative, zero, and positive values, which can be interpreted as a decrease, no-change, and increase, respectively, in the vegetation parameters. The threshold for derivation of a change/no-change image was based on the standard deviation of the difference image. A higher standard deviation threshold (2) was selected to avoid changes due to the different radiometric response of the images.

The accuracy of the thematic map was assessed using field inventory data; the accuracy of the change/no-change binary map was assessed from randomly generated points that were interpreted visually by overlaying the images from different periods. The accuracy assessment procedure was performed in Arcview 3.2 kappa extension; all the above mentioned steps were performed using ERDAS Imagine 9.3 software. The classification accuracy of the thematic maps was assessed using error metrics. The overall accuracy was 83% for Himachal Pradesh and 82% for Uttarakhand.

**Plant phenological study**

The phenophases of selected species representing the timberline ecotone were studied using the BBCH scale (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie; Meier 2003). Five timberline species were selected for phenological monitoring in the KWS: *Betula utilis* (Himalayan birch, winter deciduous), *Abies spectabilis* (Himalayan fir, evergreen coniferous), *Quercus semecarpifolia* (brown oak, semi-evergreen), *Rhododendron arboreum* (tree rhododendron, evergreen), and *Rhododendron campanulatum* (evergreen shrub-krummholz). Five individuals were selected and marked along the elevational gradient from 3,300 to 3,450 masl, the upper limit of distribution in the intensive study area. Buds were marked after the onset of winter dormancy. After marking, the buds were monitored for the entire study period, every second day during the active growth period, at 10-day intervals in the later stages of growth, and monthly during the peak of winter. The important phenophases include bud swelling, breaking, leaf separation, senescence, leaf fall, and stem development. After dormancy, bud size was monitored during winter to observe changes in the size and initiation of growth in the late winter months. Shoot length and diameter of the marked buds after bud breaking, leaf dimensions (number, length, and width), and girth of marked trees were also measured to assess growth. The phenological parameters such as the occurrence of different stages and the developmental stages and growth were correlated with the environmental parameters. The phenological attributes of one of the broadleaved deciduous and pioneer tree species are presented in detail in the results section.
Results

Extent of the timberline ecotone and changes

The total area within the elevation zone between 3,000 and 4,000 masl in the study area is 10,965 km², with the greater part in Himachal Pradesh (6,818 km², Figure 11). Although Himachal Pradesh has a larger proportion of the timberline zone, it has less forested land than Uttarakhand (2,101 km² compared to 9,908 km²). Fir occupied the greatest area of any species within the timberline (1,886 km²), followed by oak (1,142 km²), birch (433 km²), and krummholz (412 km²). The area of alpine scrub was smaller in Uttarakhand (223 km²) than in...
Himachal Pradesh (354 km²). However, Himachal Pradesh had less representation of mixed broad-leaved forest (68 km²) than Uttarakhand (97 km²). The extent of area classified as alpine meadow depends on the snow deposition pattern and is quite variable; Himachal Pradesh had a much greater area of alpine meadow (2,697 km²) than Uttarakhand (955 km²).

The overall area statistics for the timberline ecotone showed that 81.5 km² had undergone major change in the last three decades. The magnitude of change in the last ten years (44.1 km²) was higher than in the preceding decades. Fir dominated forest had the most area of any species and also had the most change in area, followed by birch (with a 12 km² increase in area during 1980-2010, of which 1.8 km² occurred in 1998–2010). There was also an increase in sub-alpine forest and alpine scrub.

The total change in land cover within protected areas was 20.3 km² and outside 61.2 km², mostly as a result of increase (17.8 km² within protected areas and 52.9 km² outside). The increase has been continuous in recent decades in both protected and unprotected areas. Both increase and decrease were greater outside protected areas. Most of the decrease outside the protected area occurred during 1998 to 2010, while that within the protected area was less but continuous, indicating that it may be natural rather than due to disturbance.

Vegetation structure and composition

Figures 12-15 show the population structure of the various forest types along the timberline ecotone. The *Abies spectabilis* community had the highest tree density (650±147 individuals ha⁻¹), with *A. spectabilis* contributing more than 70% of the total number (Figure 12). *Betula utilis* was the co-dominant species in the community followed by *Sorbus foliolosa*. The *A. spectabilis* community showed very poor regeneration with a low conversion ratio of seedlings to saplings, the timberline is generally lowered in the absence of natural regeneration. The *Betula utilis* community had the second highest tree density (526±94 individuals ha⁻¹), with *Betula utilis* contributing 67% of the total (Figure 13). *Sorbus foliolosa* was the co-dominant species; other species had a very low representation. The density of *S. foliolosa* varied most across the microhabitats. *Abies spectabilis* was also present in small patches in some pocket areas. The average total basal area of the community was 14.9±8.6 m² ha⁻¹ with close to two-thirds contributed by *Betula utilis*. The population structure with all girth classes well represented indicates intense regeneration of *B. utilis*, and the high seedling and sapling density indicates favourable conditions for regeneration in recent years. The high girth class trees were only found in the areas of abrupt termination of the forest at the timberline ecotone. Establishment of seedlings beyond the canopy at the timberline ecotone indicated upward movement of the tree species with invasion of alpine meadows.

Although Uttarakhand has five species of oak (*Quercus* spp.), only *Q. semecarpifolia* is found in the timberline ecotone. *Q. semecarpifolia* dominates the sub-alpine forest (65%) on drier aspect (NW, W to S, SE) and forms a sharp timberline with only a narrow ecotone bordered by
Figure 12: Population structure of *Abies spectabilis* community along the timberline ecotone

![Population structure of *Abies spectabilis* community along the timberline ecotone](image1)

Figure 13: Population structure of *Betula utilis* community along the timberline ecotone

![Population structure of *Betula utilis* community along the timberline ecotone](image2)
Figure 14: Population structure of *Quercus semecarpifolia* community along the timberline ecotone

![Population structure of *Quercus semecarpifolia* community along the timberline ecotone](image)

Figure 15: Population structure of *Rhododendron arboreum* community along the timberline ecotone

![Population structure of *Rhododendron arboreum* community along the timberline ecotone](image)
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Krummholtz vegetation. The *Q. semecarpifolia* community had a tree density of 548±162 individuals ha⁻¹ (Figure 14). *Rhododendron arboreum* and *Sorbus foliolosa* (6% each) were the major associate followed by *A. spectabilis* (4%) and *Betula utilis* (3%). There was good regeneration all along the timberline ecotone in undisturbed and naturally protected areas and all girth classes were present. Establishment of seedlings and saplings beyond the canopy and towards the alpine meadows was observed in many places (e.g., Tungnath and Rudranath).

*Rhododendron arboreum* has a wide range of distribution from warm temperate to timberline ecotone (1,400–3,600 masl) and is well adapted to mild and harsh conditions (Figure 15). This species forms timberlines on rocky slopes above the sub-alpine forests of *Q. semecarpifolia* and was found at many localities with steep and rocky slopes with a south to southwestern aspect facing strong solar radiation. Such areas are unfavourable for large tree species such as *Q. semecarpifolia* due to the ruggedness of the slope, very thin soil layer, and lack of suitable places for seeds to stabilize and germinate, and tree species richness was lowest in this community. *R. arboreum* has a high adaptability and advantages over other species as a result of its small seeds and ability to adapt from a tall tree in the sub-alpine region to a stunted tree in the timberline ecotone. Timberline formed by *R. arboreum* generally had very low stature trees with sparsely distributed individuals and very low canopy cover (27%). The total basal area was 4.6 m² ha⁻¹ and the total tree density of the community was 530 individuals ha⁻¹. All the individuals were of low girth (<70 cm), but good sapling density was observed (610 individuals ha⁻¹) indicating good regeneration of *R. arboreum* along the ecotone with some upward movement.

**Phenological attributes**

The average occurrence of different phenophases in *Betula utilis* at 3,300 masl in three consecutive years, calculated in Julian days (from January 1, JD), is shown in Figure 16. Bud swelling started in *Betula utilis* 18±6 days on average after the snow melted. The average date of bud break was 102±11.5 JD at 3,300 masl (timberline on NW facing slopes) and 104±10.5 JD at 3,450 masl (timberline on SE facing slopes). As a pioneer species, *Betula utilis* has the shortest leaf life span and growth period among all the timberline tree species. The average growth period from bud break to initiation of senescence was 100±27.7 days. Initiation of leaf fall began 110±17.1 days after bud break. The first leaf separated on 111±14 JD. Leaf separation was earlier in 2010, a year with high air and soil temperatures. Senescence is initiated by a sudden fall in temperature and started in July/August, on average on 202±16.6 JD. The date of leaf fall also depends on temperature and was later in years with a higher temperature and vice versa. On average, elongation of the stem by 10%, 20%, and 50% was observed on JDs 114, 133, and 150, respectively. Low soil and air temperature had a negative effect on shoot growth, whereas a delayed monsoon and higher air temperature accelerated shoot growth.

The average surface area of individual mature leaves was measured. The average leaf surface area was 2,221 mm² in 2010, a year with an extended growth period as a result of an
extended monsoon and high rainfall, and 1,612 mm² in 2008, a year with low soil and air temperatures and a short growing period. The leaf area had a high positive correlation with soil temperature at 20 cm depth (Pearson’s correlation = 0.547, p (2 tailed) < 0.05). Low soil temperature led to a slow rate of leaf expansion and fewer leaves in a shoot. The average leaf area per shoot was 12,435 mm² in 2010 and 6,292 mm² in 2008. The development of leaves in a shoot and leaf fall at the end of the growth period were highly correlated with all environmental factors (soil and air temperature, precipitation, relative humidity). Air temperature had the highest positive correlation (r = 0.804, p < 0.001). Higher temperatures and delayed monsoon extended the overall growth period and leaf fall started later and at a slower rate. There was a high positive correlation between the phenophases and air temperature prior to the occurrence of a particular phenophase. Correlation with the average temperature 30 days prior to the phenophase was more significant than correlation with the temperature 15 days prior to a phenophase (Pearson’s correlation 0.749, p (2 tailed) = 0.000, cf. 0.693).
Discussion

The fir, *Abies*, clearly occupied the greatest area among the five major species forming the timberline ecotone in the survey area. However, two different species of *Abies* were actually identified within the timberline ecotone, *A. spectabilis* and *A. pindrow*. These species may have a different response to the climatic conditions, but spectral separation is extremely difficult at present. Thus there is a need to set up long-term monitoring sites in places where both species occur. The distribution pattern of the oak, *Quercus semecarpifolia*, the species with the second largest area in the ecotone, is markedly affected by human disturbance, and the reasons for the absence of this species from some areas, including Kugti WS, is yet to be ascertained. Fir forest formed the largest plant community in the timberline areas in Himachal, and oak forest in Uttarakhand. The timberline ecotone vegetation has undergone changes in all the protected areas, but there was no clear pattern for a particular species or geographic situation (elevation, aspect) so that it is difficult to interpret these changes as a response to recent changes in climatic pattern. Although the method used to detect the changes in cover classes along the timberline ecotone is fairly reliable, explanation of the causes of such changes would require in-depth and long-term studies along the high-altitude forest-grassland interfaces. The results of the present study support the finding of field researchers that timberline ecotones have shifted slightly towards higher altitudes during recent decades in response to current warming (Payette and Filion 1985) at both regional and local scales (Masek 2001).

The study indicates that normalized difference vegetation index (NDVI) is able to detect changes in highly rugged topography, but for better results, imagery must be selected on the basis of phenological similarities rather than simply annual dates. The study found an overall increase in the vegetation of the timberline ecotone over the period 1980–2009. Locally, there was some decrease in some areas which may be attributed to both anthropogenic pressure and natural mortality; e.g., die back of *Rhododendron campanulatum* due to disease was noticeable in Great Himalayan National Park (GHNP). Little or no change was found for *Quercus*, whereas in Kugti and *Pinus* showed increased density near the upper limit of the timberline. These observations support the view that an abrupt timberline will respond less quickly than a diffuse timberline. The changes in Kugti WS were more prominent at lower elevations and in GHNP they were more significant at the upper limit of the timberline, thus these sites should be considered for further detailed study. Green biomass has increased in the upper part of the ecotone. Most of the changes on the northern slopes are associated with *Abies* spp., *Betula utilis*, and *Rhododendron campanulatum*. The major species associated with change on the southern slope were *Quercus* and *Juniperus*.

The timberlines in the Western Himalaya are lower than would be expected naturally because of excessive anthropogenic pressure. Dead remains and stumps of many trees were found well above the present timberline. Further evidence for the lowering of the timberline is that the average temperature in the warmest month for the timberline ecotone in the intensive study area was 12.6°C, whereas worldwide 10°C is considered to be the isotherm for the limit of
tree growth and location of the upper timberline (Tranquillini 1979; Körner 2004). Timberlines are known to be controlled thermally, but recent studies related to the effects of disturbance, such as herbivory (Cairns and Moin 2004), indicate that biotic factors are important and can determine the position of timberlines. The increased regeneration observed in many localities in the study area may be due to the more favourable climatic conditions for growth during past decades, and/or to land use changes in the high-altitude regions. Long-term studies are required in these areas through establishment of permanent plots with weather stations. The upper limit of survival of the timberline species is still unknown for these areas as the region has been under high anthropogenic pressure since time immemorial.

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 and Wielgolaski 2003), and variations in phenology can usually be linked to variations in the accumulation and melting of snow (Holway and Ward 1965; Mark 1970). Billings and Bliss (1959) and Knight et al. (1977) reported that full development of plants was accomplished more rapidly at high altitudes where snow persists longer.

The climate during the study period fluctuated markedly; the longest duration of snow cover and highest snowfall was recorded in 2007/08. In contrast, early snowmelt was observed in 2009. The highest rainfall was recorded in 2010 accompanied by an extended monsoon; this followed an early dry period during spring and summer. Evergreen and deciduous species have different strategies to overcome climatic constraints and respond differently to interannual climatic variation. More adapted species are less affected by extreme climatic events. Species may differ in the dates of phenological phases and the order in which these events occur, and some phases may be more apparent in some species than in others.

The life cycle of most deciduous plants goes through recognizable phases such as bud break, leafing, flowering, fruiting, leaf colouration, leaf fall, and bare tree. The phenology of Betula utilis was strongly influenced by the interannual climatic variation because it is deciduous. The spring phenophases are particularly sensitive to the temperature during late winter and early spring, which are also considered as accurate predictors of phenophase timing (Sparks and Carey 1995; Diekmann 1996; Heikinheimo and Lappalainen 1997; Schwartz 1999; Spano et al. 1999; van Vliet et al. 2002; Galan et al. 2005). A large amount of snow, late melting, and lower winter temperature seemed to have a positive correlation with the growth of Betula utilis in the following growing season. The dry period (snow-free soil) during February/March initiates bud swelling in this species, but bud break only takes place after the average temperature rises above 5°C. If this is delayed, there is a longer period from initiation of swelling to breaking.

The average temperature one month before bud break is positively correlated with this event. For Betula utilis, the average temperature was 4.9°C one month prior to bud break and 5.9°C
15 days prior to bud break. The time from initiation of bud swelling to bud break was longer when the average temperature prior to bud break was below 3°C, and shorter when the average temperature exceeded 5°C. Early melting of snow had a negative effect on the growth of the species for the entire season (2009), whereas late melting resulted in a form of accelerated growth (2008 and 2010). Although longer duration of snow is associated with lower temperatures for a longer time, it leads to more growth and accelerated development of shoots and leaves in *Betula utilis*. Menzel and Fabian (1999) found that 70% of the interannual variation in bud break in a group of European species was explained by daily temperature patterns, and that average February and March temperatures explained 75% of the variation in flowering time of Japanese cherries. Other climatic variables may also influence the timing of phenophases to some extent. Saavedra et al. (2003) and Molau et al. (2005) noted that the timing of snowmelt can be an important variable for early spring phenophases in northern alpine climates. While snowmelt is strongly influenced by temperature, it is also influenced by the amount of precipitation and other factors.

In the year of late bud break, the development of leaves was quicker than in the year of early bud break, in line with a strategy of high-altitude plants for overcoming the short growing period. Delayed bud break has been suggested to be a potentially defensive characteristic for deciduous trees against early-feeding lepidopteran larvae. Delayed leaf growth can thus be seen as a potentially valuable characteristic that helps defend deciduous trees against insects (Haukioja et al. 1985). Equally, early budbreak or meristem dehardening increases the risk of frost damage to meristems or young leaves (Linkosalo et al. 2000). Braate (1995) reported that warm conditions early in spring followed by frost appeared to cause extensive damage to birch in northeastern North America.

Leaf fall in *Betula utilis* was associated with the drop in temperature during autumn. A long rainy season leads to a prolonged growth period, which is beneficial for perennial deciduous plants to maximize leaf life span. A longer leaf life span is associated with potentially higher carbon gain by the plant (Kikuzawa 1994) and more efficient nutrient use (Eckstein et al. 1999). Leaf emergence in deciduous species is closer to summer, and the light conditions are more favourable for photosynthesis at the start of the growing season than at the end. Thus, it is probably more favourable for plants to grow and expand their leaves earlier in spring rather than to prolong the photosynthetic season into the autumn (Karlsson 1989; Myneni et al. 1997). In a study twenty years ago in Pindari and Sundardhunga region in the Western Himalaya, Rawal et al. (1991) reported sprouting of *Betula utilis* at elevations of 3,300 and 3,450 masl by 10 May. In the present study, the mean day of bud break at 3,300 and 3,450 masl was recorded as 102±11.5 and 104±10.5 JD, or 12 and 14 April, 26–28 days earlier than in the previous study. This could indicate differences in the climatic conditions of the different locations or a shift in the phenology, it will be necessary to revisit the same locations to confirm which of these is the case.
The process of leaf development in *Betula utilis* depends strongly on the temperature after bud development. Late spring frost in March and April delays this process, and extreme climatic events such as snowfall in April/May after exposure of the soil to extreme frost in February/March lead to retarded development of leaves and shoots. The combination of low winter temperature, sufficient soil moisture after snowmelt, and higher air temperature lead to the greater production of leaves with more leaf area. As a pioneer species, *Betula utilis* has the shortest leaf life span and growing period of all the timberline tree species.

In 2010, the year with the lowest air temperatures, the growth rate of *Betula utilis* after bud break was accelerated and the duration of bud swelling to bud break was lowest. This indicates that a low temperature may trigger growth in the entire growing season. The production of leaves per shoot was also the highest and the average leaf area was 50% greater than in the lowest growth year. The production of one extra leaf per shoot was not statistically significant, but had considerable importance for enhancing the photosynthetic efficiency of the species. An experimental study by Xu et al. (2011) indicated that warming markedly altered structural/functional leaf traits and enhanced the photosynthetic capacity of treeline birch saplings. Such positive responses in treeline birch would be favourable for the growth of the species under future warmer climate scenarios.

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