The Timberline Ecotone in the Himalayan Region: An Ecological Review

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The Himalayan region has the highest and most diverse treeline in the world. Lying between montane forests and alpine vegetation, the alpine timberline is a particularly conspicuous boundary and has attracted the interest of researchers for many decades. However, the timberline in the Himalayas has been much less studied than its European counterparts due to remoteness of these mountains. This review describes the floristic features and distribution pattern of the timberline in the Himalayan region, the climatic factors that influence the distribution, the carbon and nutrient supply mechanism for treeline formation, and treeline shift and recruitment under climate change scenarios. The Himalayan region presents the highest timberlines and treelines in the world and the most diverse in terms of treeline tree species of Abies, Picea, Larix, Juniperus and Betula. Temperature is the principal determinant of timberline position and distribution. Worldwide treelines are formed where the growing season soil temperature is ca. 7°C. Supplies of water, nutrients, and carbon do not limit treelines on the global scale, but they are modulators of treeline position at the local scale. A response of timberlines to global warming has been observed in the form of increasing tree recruitment and tree growth rather than timberline advance, especially in the eastern Himalayas. A clearer mechanistic understanding of the timberline is needed in order to be able to predict the potential impacts of human activity and related global change in this sensitive region.

Keywords: carbon and nutrient relationship; climate change; floristic and species composition; timberline; timberline shift; timberline ecotone

Introduction

In a broad sense, the alpine timberlines represent is the upper limit of forest on a mountain (Wardle 1974). Above the timberline, the dense and close forests give way abruptly or gradually to shrubs and/or meadows. The life and growth form of trees change sharply; trees become stunted and deformed by the severe climate. A zone called the krummholz often lies above the timberline, in which case the tree limit can be taken as the level at which krummholz with tall flagged trees is replaced by krummholz with low tree species. The timberline is often regarded as the ecotone or ecosystem interface between montane and alpine communities. The areas below the timberline, including forests and their ecotones, are referred to as the sub-alpine zone, and the area of low-growing vegetation above it as the alpine zone. The species composition changes greatly from the sub-alpine to the alpine or arctic region due to the high habitat heterogeneity.

The timberline is not an abrupt physical line, rather it is a boundary or transition zone, but viewed from a distance, the ecotonal transition looks quite abrupt and is customarily regarded as a line. The upper limit of natural forests with a steep gradient and increasing stand fragmentation and stuntedness is sometimes called the treeline ecotone (Körner 1998a), or more commonly, as here, the timberline ecotone. Körner defines a tree (1998a) as an upright woody plant with a dominant above-ground stem that reaches a height of at least 3 m, with its crown closely coupled to prevailing atmospheric conditions. Therefore, the treeline is defined here as the altitude above which any trees are lower than 3 m (Körner 2012b). The timberline ecotone is the broad area of 50 to 100 m below the treeline to the line bounding the full forest – the timberline. Since the timberline and treeline are coupled boundaries, the fundamental mechanisms causing their general position should be similar (Körner 1998b).

The Himalayan region, including the Tibetan Plateau, is a unique physiogeographical region with an average elevation above 4,000 masl. The monsoon and westerlies strongly influence the climate (Zheng et al. 1981). The topographic configuration and atmospheric circulation determine the horizontal differentiation of the natural vegetation. From southeast to northwest, the vegetation changes successively with decreasing moisture from montane forest, through high-altitude shrub, alpine meadow, and alpine steppe, to alpine deserts. Spruce fir is the dominant forest type and stands are widely distributed across the Himalayas. The upper limit of the forests – the timberline – varies with topography and climatic conditions The timberlines of the spruce fir forests on the Tibetan Plateau are at the highest elevations in the world as a result of the comprehensive effect of uplifting and the heating effect of the vast mass of the plateau, called the 'mass elevation effect' (or in German 'Massenerhebungseffekt') (Schweinfurth 1957). The higher than normal temperature at this elevation in the growing season facilitates the upward movement of the timberline.

Many studies have been carried out on the vertical vegetation zonation and spruce-fir forests of China and the Tibetan Plateau over the last 30 years (Liu and Zhong 1980; Wu 1980; Kuan 1982; Li et al. 1985; Liu 1985; Zheng and Yang 1985; Zhang et al. 1988). However, the vegetation surveys mainly focused on typical forests or the vegetation zone, and there are few studies of the timberline. Li and Chou (1984) estimated the distribution of spruce-fir forests in China and modelled the three-dimensional distribution of spruce forests. They concluded that a decrease of one degree latitude correlated to a 103 m increase in the elevation of the timberline. Zheng (1995) examined the correlation between coniferous forest vegetation and climatic factors such as temperature and moisture in the southeastern Tibetan Plateau (Zheng 1995). However, little is known about the spatial distribution of the timberline and its relation to climate across the Tibetan Plateau. There is still some debate on the physiological mechanism of treeline formation, notwithstanding research over the last ten years (Körner 2012a).

The main objective of this review is to describe the floristic pattern of timberline species and their spatial distribution in the Himalayan region, especially the Tibetan Plateau, identify the relationship between the timberline and climatic conditions, and review the mechanisms of timberline formation and the response of tree growth and regeneration to climate change.

Floristic Features of Timberline Species in the Himalayan Region

Floristic patterns of tree species

Spruce-fir forests are mainly distributed across the southeastern part of the Tibetan Plateau, between 85–105°E and 26–38°N. The coniferous species in the sub-alpine belt of the southeastern part of the Tibetan Plateau (i.e., Hengduan mountain range) and the southern slopes of the Himalayan range are highly diverse, with 16 species of *Abies*, 16 species of *Picea*, six species of *Larix*, and 11 species of *Juniperus* (*Sabina*) reported on the Tibetan Plateau. However, only 14 species of *Abies*, five of *Picea*, five of *Juniperus*, and four of *Larix* can reach the climatic forest limit and become timberline species. In addition, sclerophyllous *Quercus* and deciduous broad-leaved trees such as *Betula* can also form forest limit vegetation in the western Himalayas, southeastern Tibetan Plateau, and northern Hengduan Mountains. For example, *Betula utilis* is a timberline species in Uttarakhand, India. The Hengduan Mountains are a species differentiation centre for fir trees (*Abies* spp.), with nine species reported, of which seven (*Abies ferreana*, *A. squamata*, *A. nukiangensis*, *A. delavayi*, *A. georgei*, *A. georgei var. smithii*, and *A. forrestii*) constitute timberline vegetation. The area around Kangding County, in western Sichuan Province, is a species differentiation centre for the genus *Picea* (spruce) with more than ten species dominant in the sub-alpine belt. Of these, however, only *Picea balfouriana*, *P. purpurea*, *P. likiangensis*, and *P. crassifolia* can reach the forest limit and become timberline species, with *P. balfouriana* the most common and widely distributed along the timberline in the eastern Tibetan Plateau. *Larix* is a forest limit genus on sunny slopes. In western Sichuan, *L. potaninii* is a widespread timberline species and can extend to the Bailongjiang (Bailong river) watershed in southern Gansu Province. *L. potanini var. marcrocarpa* is widely distributed in southwestern Sichuan, northwestern Yunnan, and northeastern Tibet Autonomous Region (TAR). Fir trees can form the forest limit at an elevation of 3,800–4,300 masl, but *Sabina* (now *Juniperus*), which includes a few typical alpine species, can constitute the highest forest limit in the world. *S. convallium*, *S. Sultuaria*, and *S. tibetica* are representative timberline species on sunny slopes in the Tibetan Plateau (e.g., in western Sichuan and eastern TAR). *S. przewalskii* and *S. komarovii* are dominant in the timberline on sunny slopes in eastern Qinghai, southern Gansu, and northwestern Sichuan.

Juniperus indica, *J. recurva*, *Abies spectabilis*, *A. densa*, *A. Pindrow*, and *Betula utilis* are all found in timberlines on the southern slopes of the Himalayas (Schweinfurth 1957; Stainton 1972; Rawal and Pangtey 1994). *Quercus aquifolioides* and *Q. semecarpifolia* can not only extend into the timberline on sunny slopes in the western Himalayas, they can also be part of the timberline in the Hengduan Mountains, for example in western Sichuan and northwestern Yunnan. Timberline species in northwestern Yunnan also include *Abies geogei*, *A. delavayi*, *Picea likiangensis*, and *P. likiangensis var. balfouriana*. The timberline elevation ranges from 3,600 masl in the southeastern Himalayas to 4,200 masl in the eastern TAR.

Distribution patterns of the timberline on the Tibetan Plateau

The height of the mountains in the southeastern part of the Tibetan Plateau increases gradually from east to west and the timberline rises from around 3,600 masl to 4,300 masl. At the eastern edge of the southern part of the Tibetan Plateau, towards the western border of the Sichuan basin from Tianquan and Baoxing Counties to Jiuzhaigou County, *Abies faxoniana*, *A. Fabri*, and *Picea purpurea* grow at elevations from 3,500 masl up to the timberline at around 3,800 masl. The elevation of the timberline increases gradually with decreasing latitude in the eastern part of the Tibetan Plateau, to its highest position at latitude 30°N (Li and Chou 1984), the natural boundary of spruce-fir species differentiation and distribution. Here in the northern section of the Hengduan Mountains, in the southeastern corner of TAR, *Picea balfouriana*, *Abies squamata*, and *A. georgei var. smithii* form the highest timberline in the world at altitudes of 4,300 masl or more. *Abies squamata* and *Picea balfouriana* extend north of latitude 30°N up to the southern tip of Qinghai Province. Further to the north, up to 35°N, these timberline species are replaced by *Picea crassifolia*, *P. purpurea*, *Sabina tibetica*, and *S. przewalskii* and the timberline descends to below 3,500 masl. South of latitude 30°N, towards the northwestern part of Yunnan Province, the timberline decreases to 3,800 masl and lower, and contains *Abies gerogei*, *A. gerogei var. smithii*, and *Picea likiangensis*.

The height of the timberline is also closely correlated with longitude as a result of the 'Massenerhebungseffekt' (Schweinfurth 1957). Spruce-fir forests extend across a wide range on the Tibetan Plateau from the more westerly part at 85°E to the most easterly section at 105°E. From 85°E to 96°E, the timberlines on the south slopes of the Himalayas lie at around 4,000 masl and are formed by *Abies densa*, *A. spectabilis*, *A. delavayi*, *A.delavayi var. motuoensis*, and *A. chayuensis*. Further to the east, from 95°E to 105°E, the timberline elevation decreases gradually with increasing longitude, to as low as 3,400 to 3,600 masl in the eastern Qilian Mountains in the northeast part of the Tibetan Plateau. Timberline species such as *Pieca balfouriana* and *Abies squamata* are replaced by *A. faxoniana*, *P. purpurea*, *A. forrestii*, and others from west to east.

Climatic Factors Affecting the Position of the Timberline

Temperature is a well-recognized predictor of timberline position and distribution at the global scale. However, there are few weather stations established near the timberline in the Himalayan region and temperatures had to be extrapolated from lower or nearby weather stations to estimate climatic conditions at timberlines. The results are subject to some uncertainty compounded by the lack of information on the topographical and vegetation status at these sites. It is generally accepted that the 10°C warmest month isotherm represents the geographical location of the timberline across the world. Wang et al. (2004) extrapolated this thermal condition to the timberline in China. He found that the limit of the eastern Himalayan timberline is set by an air temperature of 8.2°C during the growing season and annual biotemperature (ABT) of 3.5°C (Wang et al. 2004). This is similar to the extrapolation on the Tibetan Plateau (Shi 1999).

Schickhoff (2005) extrapolated the temperature at the timberline in the Himalayan region and identified marked differences in the mean temperatures. As a result of the raised temperatures resulting from the mass elevation effect, the mean temperature of 10 to 13°C in the warmest month in the northwestern Himalayas and Karakoram was higher than in the more humid and monsoon-influenced eastern regions and markedly higher than the range of around 10°C usually observed in northern hemisphere continental mountains (Schickhoff 2005). This is the effect of extensive mountain massifs acting as elevated heating surfaces which leads to positive thermal anomalies compared with the marginal ranges or free air. The upper timberline in the Tibetan Plateau and eastern Himalayas develops at much lower mean temperatures and the altitude of the timberline is also lower.

The air temperature at the timberline shows considerable variation in different regions. Holtmeier and Broll (2007) argue that mean temperatures differ so much that air temperature is not a suitable indicator of thermal conditions and isotherms of air temperature should not be considered as the causal factor for the upper timberline.

On-site observations indicate that the average growing season mean ground temperature at a depth of 10 cm of soil along the treeline is around 6.5°C, with very little site-to-site variation. This seasonal mean is a better predictor of timberline position than the warmest month temperatures or a suite of thermal sums tested (Körner and Paulsen 2004). The soil temperature was measured at 10 cm depth at treelines in ten monitoring sites in the eastern Himalayas using the automatic sensor TIDBIT; the results indicated an average growing season temperature of 7.1°C, consistent with previous observations in the eastern Tibetan Plateau (Shi et al. 2008) and quite similar to the worldwide average of 6.7°C (Körner and Paulsen 2004). The slightly higher value than the world average might be due to the elevation mass effect, which increases the elevation of the timberline and its thermal threshold. The growing season soil temperature is proving to be the most stable thermal parameter for the timberline, compared to measurements such as air temperature, accumulated temperature, and length of growing season, and is now a common thermal threshold for forest growth at high elevations at the global scale.

Although soil temperature plays a profound role in seedling establishment, and tree growth and survival, there are very few measurements of soil temperature at timberlines in the Himalayan region. More studies need to be conducted to investigate the relationship between timberline tree growth and soil temperature.

Water, Nutrient, and Carbon Supply in the Timberline Ecotone

Körner (2012c) argues that there are no reasons to assume that water is a limiting factor at the treeline because the water supply is extremely variable across the globe (Körner 2012a), but treelines still usually reach the highest elevation. For example, *Polylepsis* grows to 5,200 masl in Bolivia and junipers to 4,800 m in southern TAR (Hoch and Körner 2005; Miehe et al. 2007). Thus, it seems that water is not the limiting factor controlling the height of treelines.

It is often assumed that nutrients become limited at high-altitude treelines because nutrient availability is constrained by low temperature. But there are two facts that argue against this assumption. First, the nutrient contents, especially nitrogen, in organisms at treelines are at the same level as those in closed forest at lower altitudes (Birmann and Korner 2009). Second, treeline positions are no higher in nutrient-accumulative areas and do not reach higher elevations in areas rich in nutrients (Körner 2012c). Furthermore, fertilization manipulation did not lead to raising of treelines. Growth is more limited by temperature than by nutrient uptake (Tranquillini 1979), and low temperature is the key limiting factor for treeline formation.

The debate over the mechanistic factors that limit the altitudinal treeline has continued for more than a century (Tranquillini 1979). Environmental effects on both photosynthetic carbon gain and respiratory-driven growth processes have been used to evaluate limitations at the alpine treeline. Most of the earlier studies focused on correlations between treeline altitudes worldwide and associated mean minimum annual temperatures. According to these more traditional ideas, trees are unable to assimilate enough carbon for survival above certain altitudes. However, Körner proposed that low soil temperatures coupled with physiological drought stress inhibit the carbon processing abilities at the treeline, not the ability to gain carbon via photosynthesis (Körner 1998a; Körner 2003). Körner's hypothesis suggests that the limit at high elevations is not due to photosynthetic carbon gain as such, but rather to the processing of fixed carbon into growth via respiratory physiology. This is also indicated by more recent studies which suggest that an increase in non-structural carbon pools without significant growth is caused by carbon source availability exceeding demand (Körner 2003). Shi et al. (2008) indicated that the highest treelines in the eastern Himalayas actually have significantly higher non-structural carbohydrate (NSC) at treelines than in the lower closed forests. Thus it seems that NSC is not a limiting factor in tree growth at the treeline. This is further supported by the observation of a linear increase in NSC in woody plants with increase of altitude in Wolong Nature Reserve, Sichuan (Shi et al. 2006). Although a carbon limitation phenomenon has been observed in the Gongga Mountains in the eastern Tibetan Plateau, this temporary depletion of carbon occurred during bud burst in early spring (Li et al. 2008).

Impact of Global Warming on Treelines

The Himalayas experienced warming of 1.5°C between 1982 and 2006, an average rate of 0.06°C yr^{-1}, with the greatest average increase in winter (0.07°C yr^{-1}), and lowest in summer (0.03°C yr^{-1}) (Shrestha et al. 2012). Treelines are sensitive to climate warming and may respond by advancing beyond their current position or enhancing growth. It is usually assumed that the timberline ecotone will undergo significant change in terms of structure and position and it is expected to shift in response to global warming. There is abundant evidence of tree growth enhancement and/or treeline shift in the Himalayas over the past decades.

Treeline shift response to climate change can be monitored using images from remote sensing satellites, which helps to overcome the difficulties posed to direct observation by the poorly accessible Himalayan terrain (Rawat 2012). Panigrahy et al. (2010) mapped the treeline using nearly 20 years of satellite images. Imagery of Nanda Devi Biosphere Reserve in the central Indian Himalayas from 2004 revealed a dramatic increase in vegetation cover and drastic reduction of snow cover in areas that had been glaciated in 1986. Alpine plant species have been found to shift to higher elevations, although the shifting rate varies with species and their sensitivity to climate. Various studies indicate that the ecosystems in the Himalayas have experienced significant changes since 1960 (Panigrahy et al. 2010; Sushma et al. 2010). However, treeline dynamics appear to be more related to changes in snow precipitation than to global warming (Negi 2012). Remote sensing investigations by Singh et al. (2012) indicated that the treeline shifted 388 ± 80 m upwards in the Uttarakhand Himalayas between 1970 and 2006. A study using repeat photography and supplementary measurements in the eastern Himalayas (northwest Yunnan) also indicated glacier recession and an advance in the treeline (Baker and Moseley 2007).

There are very few actual field observations of treeline dynamics in the Himalayas due to the remoteness and poor accessibility, and high cost of expeditions. However, one study indicated that treelines in the Sygera Mountains in eastern TAR had shifted in the past 400 years, whereas others carried out in the eastern Himalayas showed no indications of treeline shift. Most treeline vegetation change is growth and regeneration enhancement rather than actual shift. There was an abrupt recruitment of Smith fir trees in the eastern TAR in the 1970s, but no significant upward movement of the treeline position (Liang et al. 2011). Recruitment of juveniles and seedlings was mostly close to juvenile firs and *Rhododendron* mats and over moss-lichen and organic matter substrates, indicating the importance of availability of microsites for successful Smith fir recruitment (Wang et al. 2012).

The increased warming has significantly extended the length of the growing season. However, the longer growing season has had little effect on tree ring growth. For example, modelling using results from a weather station record at the timberline in the Sygera Mountains of eastern TAR (4,390 m) indicates that the growing season has extended significantly – by 21.2 days – mostly as a result of a delayed end (by 14.6 days) rather than earlier onset (by 6.6 days). Nevertheless, there was no increase in radial growth of Smith firs at the timberline (Liu et al. 2013).

In summary, the timberlines of the Himalayan region are among the highest in the world due to the marked mass elevation effect of the Tibetan Plateau. This area also has the most diverse timberline species and geomorphology, and the tree species diversity results in abundant timberline forms and growth forms. The air temperature isotherms are not good predictors of timberline elevation, in contrast, the growing season mean soil temperature at a soil depth of 10 cm has a close to constant value at the timberline of nearly 7°C around the world. Low temperature appears to be the most important factor controlling formation of the timberline. The trees in the timberline ecotone are not physiologically inferior to other trees; the low temperature appears to limit the carbon sink ability rather than the carbon source at the timberline. In other words, the timberline is the threshold for limitation of growth caused by low temperature. Water and nutrients do not appear to be key factors for determining the timberline position; at most they are modulating factors in the local environment. With increased global warming, the timberline would be expected to advance to higher altitudes, but as yet the changes observed have been limited to increasing tree recruitment and tree growth rather than timberline advance.

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