COMPARATIVE HIGH MOUNTAIN RESEARCH ON THE TREELINE ECOTONE UNDER HUMAN IMPACT*

CARL TROLL’S “Asymmetrical Zonation of the Humid Vegetation Types of the World” of 1948 reconsidered

With 5 figures and 7 photos

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Summary: 50 to 40 years after C. TROLL’S concepts on the ‘Asymmetrical Zonation of the Humid Vegetation Types’ and the ‘Tropical Mountains’ it has become evident that quasi natural and heavily human-interfered treelines had been amalgamated. Isolated fruiting and regenerating trees in zonal habitats of a quasi-alpine environment above the present upper forest border witness the potential natural presence of forest. The high-altitude grassland of the Paramo or equivalent dwarf-shrub formations up to at least 4,100 m a. s. l. are supposed to be a replacement vegetation induced and maintained by fire used by man to obtain open pastures or for hunting purposes. Thus, the inner tropical treeline is lowered artificially by 500 to 600 m. In TROLL’S figure of 1948 the treelines of mountains of the northern hemisphere are drawn 800 to 1,300 m too high and those of the southern hemisphere 500 to 800 m too low. TROLL’S concept to classify forests of subtropical mountains as altitudinal equivalent of high latitude vegetation formation is misleading, because the dominant treeline species are differing Larix, Pinus and Fexa of high latitude versus Juniperus and Abies as subtropical upper treeline constituents. The presence of epiphytes suggests the classification as cloud forests.

Considerations upon the structure of a treeline ecotone without human interference are highly hypothetical, because nearly all accessible treelines are influenced by man-induced fire, grazing or wood-cutting. Few examples from possibly natural sites show a disintegration from closed forests into isolated stands of single trees in a completely closed cover of evergreen shrubs. Most treeline constituents show transitions from tree to dwarf-shrub under natural conditions as well as in disturbed sites. In arid environments it is even more difficult to estimate the potential natural structure of the treeline ecotone, because open dwarf-forests had been widely destroyed.

1 Introduction: what to compare?

The quest for the potential natural treeline

As early as any attempts were made to compare altitudinal belts and vegetation structures in high mountain environments of different latitudes, the treeline ecotone attracted particular interest. This is especially the case with Comparative High Mountain Research in Germany initiated and inspired by CARL TROLL. His illustrative concepts first published in 1948 with the diagram of the “Asymmetrical Zonation of the Humid Vegetation Types of the World” (Fig. 1) and “The Tropical Mountains” of 1959 became increasingly accepted in the last 50 to 40 years. In the light of more recent progress of Comparative High Mountain Research the surprisingly unchanged state of the art will be reconsidered here in respect to the treeline ecotone.

* Dedicated to CARL TROLL on the occasion of his 100th birthday
Fig. 1: The timberlines in the asymmetrical vegetation belts of the world, from Troll (1948) (changed).

Three issues characterize Troll's concept:

- the vegetation zones of the northern hemisphere do not correspond to any vegetation type of the southern hemisphere and the run of the treeline's altitude on both hemispheres is strikingly different.

- the upper forest limit of inner tropical mountains (10°N to 10°S) at 3,500 m a.s.l. is 1,300 m lower than the upper limit of forests of northern subtropical mountains of Eastern Tibet (30°-32°N) as well as of Andean Polylepis groves under the Tropic of Capricorn.

- within tropical-alpine grass- and shrublands isolated tree groves can be found up to 1,400 m beyond the upper limit of forests.

The study of Troll's concepts led to minor corrections and principle considerations on the origin of the structure and dynamics of the forest ecotone in high mountain environment which will be communicated here. As the diagram of "the Asymmetrical Zonation of the Humid Vegetation Types of the World" is the most repeatedly cited graph in issues of Comparative High Mountain Research it may be justified to comment on the pronounced asymmetry of the forest belts: It is evident that the real upper limits of the north-hemispheric boreal forests are mostly 800 to 1,300 m lower than shown in the original diagram given in Figure 1 (e.g. Central European Alps 46°N, 3,300 m in the diagram versus 1,800 to 2,200 m in reality). In contrast, the real south-hemispheric treelines are 500 to 800 m higher. Even though the main issue is maintained with these corrections, the real extent of the forest belts is slightly less eye-catching and illustrative as repeatedly cited.

The more serious question is if it is meaningful in Comparative High Mountain Research to amalgamate forest patterns of different origin, i.e. natural forest boundaries of mountains without any marked human interference (if there are any) and those forest structures under human impact which are part of cultural landscapes. Troll's concepts did not reflect the possibility that forest patterns of natural and cultural origin were blended. This is even more surprising because High Mountain Research started in the European Alps with a treeline which is well-known to be heavily influenced by man and his cattle. It is therefore a substantial precondition of Comparative High Mountain Research to consider the origin of the upper treeline in different latitudes: the comparison of treelines is only meaningful if climatically induced vegetation limits are considered. It is certainly misleading to discuss the worldwide run of the treeline if man-made and natural forest limits are mixed. This leads to the quest for the potential natural treeline, which delimitates a hypothetical forest area after the cease of human impact. Unfortunately, the decisive physiological causes of the upper treeline are still under consideration (Stevens a. Fox 1991; Korner 1998; 1999), making any reconstruction of climatically induced, potential natural treelines by means of modelling difficult.

In this paper a more inductive approach is made: if isolated fruiting and regenerating trees or groves in zonal habitats (i.e. without water-surplus, micro- or mesoclimatic or edaphically favourable conditions) are found above the present upper forest border, it is concluded that the surrounding shrubby or herbaceous vegetation replaces natural forests which were removed by human impact. The uppermost isolated trees or groves thus should indicate the minimum altitude of...
the potential natural treeline. This will be demonstrated with examples from the Andes and from East African Mountains.

The structures of such natural treelines are obviously not homogenous and self-evidently influenced by the relief (YOUNG 1993); the variety of treeline patterns is shown by closed Nothofagus forests of the New Zealand’s Alps reaching their upper limit in a clear-cut line of a low dense thicket (NORTON a. SCHONENBERGER 1984), by Pinus cembra groves in the European Alps and ribbon forests with Picea engelmannii or Abies lasiocarpa in the Rocky Mountains (HOLTMEIER 1986; 1999), or closed Abies densa forest gradually disintegrating into isolated trees within closed Rhododendron-thickets of the Himalaya, and closed Erica dwarf forests disintegrating into isolated globular multi-stemmed trees or bushes within closed Alchemilla-scrub in tropical East Africa. Thus the conclusion from isolated groves to a potentially higher elevated forest belt first refers to the growing conditions of trees in general. The investigation of structural types of the treeline ecotone is a second step. Moreover we have to consider that the different actual structures of the treeline ecotone are not necessarily in accordance with the present climatic conditions but reflect climatic changes of several hundreds of years in the tree’s lifetime.

2 Forest relics in the fire-climax of tropical high altitude grasslands

Equatorial mountains are widely covered by closed tussock-grasslands down to 3,500 m a. s. l. or even lower. This Páramo grassland is known from New Guinea, from some of the East African Mountains and the northern Andes. Yet, it is well known that isolated groves of trees are scattered in this tropical high-altitude grassland up to 1,400 m above the present upper forest border. Providing the forest belt is limited by climatic constraints such as lack of warmth, naturally isolated tree growth above the forest belt can only be explained by extrazonal habitat conditions.

2.1 Polylepis groves in the Andean Páramo

The phenomenon of isolated stands of trees within the tropical high-altitude grasslands was perceived as an open scientific problem in the Andes first: tree groves of Polylepis scattered in the Andean Highlands far above the upper limit of the forest belt of the outer Andean declivities were interpreted as relics of a forest belt cleared by humans (ELLENBERG 1958; 1996) or as natural stands confined to special edaphic or microclimatic conditions: TROLL (1959) and WALTER a. MEDINA (1969) asserted the opinion that coarse boulder accumulations often covered with Polylepis groves provide more favourable and warmer growing conditions; this was widely accepted. In-depth research in the Páramos of Ecuador undertaken by LAEGAARD (1992) and by KESSLER (1995) on Polylepis in Bolivia however, revealed that these Polylepis groves are neither confined to certain soil conditions nor to any other natural ecological habitat factor. The same distribution pattern obviously refers to Gynoxis sp. in the Páramos of Chimborazo (SKLENAR, pers. comm. 14/12/1998). Finally, short-term soil temperature measurements failed to find evidence that boulder fields are extrazonally warmer habitats (KESSLER a. HOHNWALD 1998). Man-induced fire, wood-cutting and grazing have destroyed a forest belt of Polylepis so that only a few isolated groves survived. The tropical grassland of the Páramo turns out to be widely a fire-climax under human impact. This is possibly supported by zoological research: after STURM (1978), the fauna of the Páramo is not significantly different from the fauna of the neighbouring forests; and REIG (1986) concludes from the higher number of small mammals in the Puna that the Páramo is younger in age. In Bolivia the relics of Polylepis forests cover c. 500,000 ha, which is expected to be 10% of the potential natural forest cover (KESSLER 1995). If the Bolivian Highlands (Altiplano) are at least partly considered to be potentially forested, the open dwarf-forests of Polylepis tarapacana of the volcanoes of the western Cordillera would integrate into a forest belt with the world’s highest forests in c. 5,000 m a. s. l. on the Co. Sajama (18°30’S). The treatment of the respective Polylepis stands as forests remains a matter of opinion, though (see below). With reference to Figure 1 it is, however, evident that the world’s highest treelines are not located in the north-hemispheric, subtropical mountains of Eastern Tibet but in the southern hemisphere.

2.2 Erica groves in the Afroalpine belt

In contrast to the Andean grasslands and their manmade relic groves, fire is a widely accepted ecological factor in the forest-grassland ecotone of the east African mountains (HEDBERG 1951; 1964; SCHMITT 1991; LANGE et al. 1997). Yet, the occurrence of isolated Erica-, Stoebe- and Hypericum-groves surrounded by tussock-grassland or Helichrysum dwarf-shrubland did not stimulate much considerations upon the potential natural extent of the forest belt, except HEDBERG (1951). Comparing the ericaceous and Afroalpine belt
Thus, evidence from different sources reveal that the upper limit of tropical forests as shown in the diagram of TROLL (1948) refers to human-altered borderlines not suitable to be compared with natural treelines. Under natural conditions the upper limit of the forest belt is at least 500 m higher than in TROLL's diagram. If Dendrosenecio and Lobelia are regarded as trees, the treeline even climbs higher.

3 Structural types of the treeline ecotone

The transition zone between forests and treeless alpine plant formations is highly diverse in structure, dynamics and terminological delimitation. Altitudes between the upper limit of (closed) forests and the highest stands of isolated and often crippled trees are called “subalpine” (see LOVE 1970); this is taken here as equivalent to 'treeline ecotone'. Using the revised UNESCO Plant Formation Classification (MUELLER-DOMBOIS a. ELLENBERG 1974) of the Working Group of High Mountain Ecology (MIEHE et al. in prep.) trees are erect-growing single- or multi-stemmed woody perennials of at least 2 m height. Trees covering more than 50% are classified as forests (50-75%: light forests / 75-100% dense forests. Trees covering less than 50% are classified as woodlands (50-25% dense woodlands, 25-10% sparse woodland). Clear definitions of 'tree' respectively 'forest', however, are blurred by the fact that many of the phanerophytic species of the world's mountain treeline ecotones show all transitions from tree to dwarf-shrub (e.g. *Polexipis tarapacana*, *Erica* spp., *Nothofagus* spp., *Betula* spp., *Juniperus* spp. and some of the *Picea* spp.) under natural conditions and after regeneration from fire or under grazing impact. The following attempt to classify some of the world's mountain treeline ecotones comprises examples from human-interfered forests and from possibly untouched sites.

3.1 Clear-cut borders of a closed forest belt or disintegration in the treeline ecotone of tropical mountains?

Both structures are well known from tropical mountains, but "the timberline is normally abrupt" and "climbs higher in valleys ... than on exposed ridges" (TROLL 1973, pp. A8-A10). Field evidence for clear-cut and treelines under natural conditions are very limited and restricted to abrupt ecophytic changes: under the perhumid climate of the Ruwenzori Mts. (9°20′N / 29°55′E) the treeline ecotone shows an irregular patchy structure of *Erica*-stands clearly divided from surrounding...
Areas without continuous ericaceous vegetation comprising all types of dwarf forest, thickets and shrublands with edaphic grassland and man-modified Helichrysum heath and herbaceous pasture.

Isolated Erica shrubs or small Erica groves within shrublands.

Swamps on permanently or seasonally waterlogged ground which is naturally devoid of woody vegetation.

Erica stands on deep rocky slopes.

Ericaceous belt shrub forest between the upper limit of ZsWcö-Dickicht and the upper limit of continuous Erica vegetation comprising dwarf forest, thickets and shrublands.

Erica dwarf forest and shrubs at bare floor with edaphic grassland in seasonally waterlogged depressions.

Shrublands of regularly scattered Erica individuals on dry rocky plains (rock grassland shrublands).

Fig 2: Actual extend of the upper montane forests and the fire-replacement successions of the ericaceous belt in the Bale Mts. of South Ethiopia. Fire relics of Erica in the midst of afroalpine pastures indicate the character of a cultural landscape with a man-interfered upper treeline. 

After MIEHE, a. MIEHE 1994, changed.
ing Afroalpine dwarf-shrubs: only very shallow and well drained substrates on rock cliffs are suitable for *Erica* trees (Photo 1), whereas neighbouring zonal, deeply weathered soils are permanently water-logged and covered with Afroalpine dwarf-shrubs and *Carex run-sornsensit-*tussocks. Similar clear-cut borders are found in semi-humid climates of other East African Mountains, but there the shallow soils of rock ledges or cliffs dry out for a longer period and are devoid of trees (Fig. 4). Moreover clear-cut borders occur at the edge of swamps and permanently boggy ground of tongue-basins. All other clear-cut forest borders examined so far in tropical mountains are influenced by man-made fire (MIEHE a. MIEHE 1994 a) and definitely not suitable to be amalgamated with natural treelines. In most cases the fire-clearing lines follow the topography: moist and moss-covered forests in gullies and gorges are not hit by fire as easy as seasonally dried out forests on open slopes. The reason why this is a common pattern of tropical mountains is that the forest climbs higher up in valleys. Under the effect of cooling and desiccating trade winds, however, this pattern may also occur naturally.

Except for the treeline ecotone of the perhumid Ruwenzori Mts, which is believed to be widely undisturbed, there are not many sites on East African Mountains, which allow to get an impression of the natural structure of the treeline ecotone. Nearly everywhere, the dynamics of regeneration after fire govern the structure of the ericaceous belt. Considerations on the potential natural structure of the ericaceous treeline ecotone should take into account upon:
- the richness of endemic plant species in the Afroalpine vegetation (HEDBERG 1969; WESCHE 2000) indicating the temporal continuity of treeless tropical-alpine habitats;
- the presence of endemic small mammals depending on habitats provided only by a diversely structured grassland with scattered shrubs (GUTTINGER et al. 1998; CLAUSNITZER 2000);
the natural environmental impact of large herbivores (buffalos, elephants) on the destruction of woody vegetation even on the higher slopes of the East African Mountains (WESCHE 2000);
- the volcanic origin of relief and soil patterns with a small-scale pattern of deeply weathered volcanic soils with peat in hypsozonal habitats and rock ledges, cliffs, boulder fields and cemented ash layers. This edaphic pattern causes a patchy vegetation structure of forest islands, shrublands, tall grassland and short grassland.

The extent of an ericaceous ecotone with a decreasing presence and height of ericas ranges higher up than 4,000 m a. s. l. Erica shrubs were found as high as at 4,370 m a. s. l. on Mt. Bwahit of the Simen Mts., at 4,200 m a. s. l. in the Bale Mts., and at 4,210 m a. s. l. on Mt. Elgon (pers. comm. K. WESCHE, 1999). The highest specimens in the Simen and Bale Mts. were found in wind-sheltered sites, whereas the highest Erica on Mt. Elgon grew on an open scree slope. All shrubs showed partly dead branch tips. Between the highest relics of Erica forest and the highest records of Erica shrubs the distribution and number of Erica records largely depend on the relief and the occurrence of rocks as fire-shelter. In the Afroalpine tussock grassland of Simen Mts. above 4,000 m, Erica seedlings and individuals, not growing higher than the tussocks, were widespread up to 4,200 m a. s. l. in 1996. If we compare this situation with the evidence of regenerating Erica formations from repeated photography documentation in other parts of Simen, it is highly probable that the status of 1996 is an early succession leading to erica-covered slopes (compare KAEPPELI 1998, Figs. 76 and 77; NIEVERGELT 1998). In the Bale Mts., Erica seedlings and smaller shrubs obviously younger in age were absent from the Afroalpine Helichrysum splendens pastures, and the same refers to the tussock grasslands of Mt. Elgon. Comparing Mt. Bwahit in the Simen Mts. and Mt. Elgon, it seems plausible to explain the presence or absence with the fire frequency, because the grasslands of Mt. Bwahit were not set on fire since long (pers. comm. H. HURNI 1999), whereas Mt. Elgon and the Bale Mts. are burnt regularly. The lack of seedlings and younger ericas in the Afroalpine belt of the Bale Mts. is not understood yet.

It is evident, however, that there is an upslope transition from dwarf Erica trees of 2–3 m height to small Erica shrubs of 30 cm. From less disturbed areas in the Bale Mts., it can be concluded that the Erica forest grades into low thicket towards its upper limit. This is symbolized in Figure 4. The horizontal distances are shortened, and the limits drawn between the different formation types do not fully show that they are in fact...
Fig. 4: Clear-cut treelines (a) under semihumid climate of the Bale Mts.: Rock ledges are unsuitable for trees because they are water-logged during the rainy season and drying out in the dry season. Under undisturbed conditions (b) a one-storeyed Erica-forest is presumed to follow above the Hagenia-forest.

In tropisch wechselfeuchten Gebirgen (Bale Mts.) können flachgründige Felsstandorte Baumfrei sein, da sie während der Regenzeit staunass sind, aber in der Trockenzeit völlig austrocknen. Unter homogenen Substratbedingungen folgt oberhalb des Hagenia-Waldes wahrscheinlich ein einstöckiger Erica-Wald.

transitions. Where the upper treeline is to be drawn is a matter of controversy; thus, a major part of the discussions about highest treelines depends on what is regarded a tree, what a shrub, what forest and scrub, respectively. According to the above-mentioned concept, Erica individuals that are at least 2 m tall, rarely single-stemmed but mostly with several stems, can still be called trees. On the contrary, the typical shrubby life form has numerous branches ascending from the base. Even though these shrubs may be up to 3 m tall, they form thickets that are difficult to penetrate. It largely depends on the topography and microclimate if these thickets form narrow hedges only around the uppermost trees or a wider zone. The thickets certainly interlock with lower Afroalpine grassy or shrubby formations in dependence of the micro-relief. Above the upper limit...
Photo 2: Probably undisturbed Erica thicket disintegrates into isolated spherical individuals. The soil is completely covered with 30 to 50 cm low scrambling thicket of Alchemilla haumannii. The Erica shrubs have a larger photosynthetically active surface compared with the closed Erica thickets in the background. The temperatures of the soil surface in the shade of closed Erica thickets and in the shade of Alchemilla thickets is expected to be similar.

Photos G. Miehe (Bale Mts., Wasama, 6°55'N / 39°46'E, 4,080 m a. s. l., 11/1/1990)

Erica-Waldgrenzökoton in den Bale Mts.: Unter homogenen Relief- und Bodenbedingungen löst sich das geschlossene Erica-Dickicht hangaufwärts in solitäre Kugelbüschel auf, deren assimilierende Oberfläche größer ist als in dichtem Bestand. Die Bodenoberfläche ist hier von geschlossenen 30-50 cm hohen Alchemilla haumannii beschattet, wie im geschlossenen Erica-Dickicht of thickets, isolated outposts of ericas, not much taller than the Afroalpine scrub, occur in the lower Afroalpine belt. Tuft trees of Lobelia rhynchopetalum are part of these Afroalpine formations. Even in the Bale Mts., there are very few sites in the ericaceous ecotone without any human interference (Photo 2): here a closed Erica thicket disintegrates into isolated spherical individuals of 1.5 to 0.8 m height. Ericas grow between Helichrysum splendidum dwarf-shrubs and semi-frutescent scrambling Alchemilla haumannii covering the soil completely with a 30 to 50 cm low thicket. The Erica individuals in the disintegration zone have a larger photosynthetically active surface in contrast to the situation in thickets where only roughly one third of the shrub has green foliage. The temperatures of the soil surface in the shade of the closed Erica thickets and in the shade of the Alchemilla thicket in the disintegration zone have not yet been measured but are expected to be similar. From this fact – disintegration of Erica scrub into isolated individuals with a continuously shaded soil surface – a cautious suggestion could be derived: with a decrease of air temperature the unfavourable conditions in Erica thickets can only be compensated through the extension of the photosynthetically active surface and an unimpeded insolation in isolated stands. The closed stand of Ericas has become too cold. If these arguments are right, the conclusion should be that the upper limit of tree growth (and related life forms of woody perennials) is in the last consequence governed by the air temperature. It is an open question how this consideration fits into Körner’s findings (1998; 1999) on the importance of the subsoil temperatures.

However, the structure of the forest-grassland ecotone of the East African Mountains would look alike without the interference of man, it is clear that the potential natural upper limit of the forest belt is built of Erica trees, growing as high up as 4,000 to 4,100 m a. s. l. From the conclusions (which only can be proved by eco-physiology) and derived from very few undisturbed sites – several arguments from animal habitat requirements and impacts and – determining properties of edaphic structures, it is highly probable that the ericaceous ecotone would naturally not be a completely closed thicket but a
diversely structured habitat with grasslands, dwarf-shrubs, Erica-shrubs and other phanerophytes.

3.2 Disintegration in the Himalayan cloud forest treeline ecotone

Under subtropical latitudes of the forest covered declivities of High Asia the upper treeline reaches altitudes between 3,900 and 4,800 m a.s.l. The forests were classified as an high altitude extension of the boreal forest belt (see Fig 1; SCHROEDER 1998), but the following structural and floristic reasons do not support this classification:

- the upper montane forests of the Himalayas and of the eastern declivity of the Tibetan Highlands emerge from evergreen broad-leaved lauraceous forests and rhododendrons as typical elements of the south-east Asian mountain vegetation. Evergreen broad-leaved phanerophytes are dominant constituents of these forests and the treeline ecotone;
- the trees and shrubs are covered with epiphytes and can therefore be classified as cloud forests being a specific humid mountain vegetation formation;
- the majority of tree species of the upper montane forests belong to the same genera which are the main constituents of the boreal forests (Larix, Picea, Betula, Sorbus), but the wide distribution of juniper forests as 'Tethys elements' (MEUSEL a. SCHUBERT 1971) show

the specific character of this subtropical altitudinal zonations.

The highest confirmed tree stands are Juniperus tibetica in moderately humid Inner Valleys of South-Eastern Tibet (30°03'N / 93°35'E) and Eastern Tibet (31°05'N / 96°58'E) reaching 4,720 m a.s.l. In the dry Inner Valleys of the Himalayas Juniperus indica, a closely related species, climbs as high as 4,300 m (28°43'N / 83°45'E, MIEHE 1982).

In more humid Inner Valleys and in the southern declivity, Juniperus recurva dominates the treeline ecotone in the whole Himalayan arc together with Abies spectabilis and Abies densa (east of 89°E). Juniperus recurva attains the highest records of trees in the Himalayas in 4,440 m a.s.l. in the Khumbu Himal (South of Mt. Everest, 27°52'N / 86°48'E, MIEHE 1991). In the Black Mountains of Central Bhutan (27°23'N / 90°42'E), the highest fir-stands reach 4,250 m a.s.l.; records from Nepal in heavily disturbed sites are slightly lower. Larix is only of minor importance and occurs in scattered stands on open soils of landslide areas (Photo 4), but is certainly a tree which climbs as high as the treeline ecotone. Betula utilis is the only one of the High Asian birches reaching the treeline. The domaine is strictly Himalayan. Betula is a main constituent of the treeline ecotone. Highest stands are found at 4,200 m a.s.l. in the rain shadow of the High Himalayas, forming pure
stands of a dense dwarf forest strictly confined to the shady slopes (MIEHE 1982). In contrast to Betula utilis, Sorbus spp. do not form pure stands but are commonly found in the treeline ecotone with multi-stemmed isolated dwarf trees towering evergreen closed rhododendron thickets reaching 4,450 m a.s.l. (Photo 5, 6).

In wide parts of the Himalayas and the eastern declivity of High Asia, differences of aspect is a conspicuous vegetation pattern in the treeline ecotone: forests are widely restricted to the shady slopes leaving the sunny slopes covered with pastures rich in mostly thorny shrubs (Rosa spp., Berberis spp., Caragana spp., Cotoneaster spp., Lonicera spp., Potentilla fruticosa and dwarf-shrub Rhododendron spp.). A general assumption was, that the sunny slopes are exposed to frost and drought during the dry winter season, thus being unsuitable for tree growth (HAFFNER 1981; v. WIßMANN 1960/61), while the forests of the shady slope remain in the shelter of a snow cover. However, the assertion that his pattern of a subtropical summer rainfall forest ecotone is natural (TROLL 1971), is easily falsified as soon as isolated juniper trees or groves are found, which grow within pastures under normal conditions, not differing from those of the surrounding herbaceous and shrubby formations. Similar to the isolated Gynoxys-, Polylepis- or Erica-trees in the Andean or Afroalpine grassland, the fact that these isolated trees are vital and seedlings and younger trees are present proves that this aspect-depending ecotone is man-induced. Pastoralists and livestock breeding farmers have cleared the pristine forests of the sunny slopes by fire in order to obtain open pastures especially for winter grazing, when the distant alpine summer grazing grounds are snow-covered. The vegetation patterns on these winter pastures are largely similar in both eastern Inner Valleys of the Himalaya and the eastern declivity of the Tibetan Highlands. Only in very limited and little known parts of the south-eastern Himalayas, this widespread pattern of the treeline ecotone is missing; here both aspects are covered with coniferous forests. In remote parts of the Black Mountains of Central Bhutan, both aspects are covered with Abies densa forests, whereas in rain shadow areas of south-eastern Tibet (Kongbo 30°03’N / 93°59’E), Abies georgei (Atlas of Tibet 1990) forms closed forests on the shady slope with evergreen rhododendrons in the understorey, in
Photo 5: Above the uppermost Betula utilis forests, multi-stemmed Sorbus microphylla (arrows) dominate a closed Rhododendron andropogon dwarf-scrub of the shady slope. The rowan grows up to 4,300 m a.s.l. 
Photo: G. MIEHE (Langtang, Central Nepal 28°12’N / 85°39’E, 4,120 m a. s. l., 11/10/1986)

Nordexponierter Hang im gemäßigten Regenschatten des Zentralen Himalaya. Oberhalb der höchsten Birkenwälder wachsen einzelnstehende vielstämmige Ebereschen-Zwergbäume in einer geschlossenen Flur aus immergrünen nieder-alpinen Zwergstrauch-Rhododendren. Die höchsten Sorbus microphylla stehen in 4300 m NN

Photo 6: Multi-stemmed dwarf trees of Sorbus microphylla with Lonicera obovata, Rhododendron campanulatum and dwarf-scrub rhododendrons in the treeline ecotone of a shady slope 
Photo: G. MIEHE (Upper Trisuli catchment, Tibet, China, 28°32’N / 85°16’E, 4,300 m a. s. l., 24/8/1993)

Vielseitnägige Ebereschen-Zwergbäume im Waldgrenzokoton eines zentral-himalayischen Schatthangs, umgeben von Sträuchern des Waldgrenzokoton (Lonicera obovata, Rhododendron campanulatum) und niederalpinen Zwergstrauch-Rhododendren
contrast to open dwarf-forests of *Juniperus tibetica* on sunny slopes. Up to now, the authors did not manage to reach untouched high altitude forests and totally undisturbed treeline ecotones, but it is evident that in forests with little human interference differences of aspect are inconspicuous.

On all slopes with very little or possibly no human disturbance encountered so far, the structure was similar: under homogeneous relief and soil conditions the highest layer of phanerophytes in a multi-storeyed forest disintegrates upslope from a closed stand into isolated individuals, overtopping the next lower and closed storey. On undisturbed slopes of south-east Himalayan *Abies densa* forests, the closed rounded tree crowns increasingly disintegrate upslope until the fir trees overtop well isolated from each other the closed evergreen broad-leaved rhododendron thickets (Photo 3). In the Central Himalayas as well *Abies spectabilis* disintegrates into a closed *Betula utilis* forest. Approaching their upper limit, the birches as well grow isolated in a closed thicket of evergreen broad-leaved *Rhododendron campa-

### 3.3 Treeline ecotones of open forests in arid environments

Open forests of arid high mountain environments are widely built of *Juniperus* spp. Climatic data are scarce, both for the lower limit of forests and for the upper treeline ecotone as well. In winter-rainfall regions of south-western North America, the Mediterranean mountains, the Armenian, and the Iranian Highlands, precipitation of 200 to 300 mm/a or possibly less is believed to delimitate the forest zone (FREITAG 1971; 1972; HENNING 1994; TROLL 1972). Further east, summer rainfall increases but the threshold of 200 to 300 mm/a seems to remain valid: climatic data of the CAK research scheme from the eastern Hindukush and western Karakoram of Pakistan, show values below
South facing open Cupressaceae-forest between 3,300 and 3,500 m a.s.l., 12 km north of Jomosom (Central Nepal, 28°54'N / 83°46'E). Annual rainfall is expected not to exceed 300 mm. The forest is one of the least disturbed forests in the dry borderlands north of the Himalayas (MLEHE et al. 1996) and in the rainshadow of the High Himalayas of Central Nepal, spring- and summer-rainfall between 258 and 210 mm/a is suitable for Cupressaceae-forests (MIEHE et al. 2000). In the summer rainfall region of Southern Tibet, which was commonly regarded as a treeless high cold steppe (ZHANG 1988; LAUER et al. 1996), isolated open forests grow in areas of more or less 300 mm/a (Fig. 5).

In vast areas of Eurasia, the open juniper forests are widely extinct and considerations upon their potential natural domain are highly speculative. Especially the (drought determined) lower treeline ecotone is heavily influenced by man, because the junipers of the lower treeline are usually the timber and firewood resources nearest to the settlements. Undisturbed lower treeline ecotones of open juniper forests had not been encountered so far in Eurasia, but from the treeline ecotone of the La Sal Mts. of Utah (38°20'-35°N / 109°05'-20°W, HENNING 1975), we may extrapolate that the trees grow more and more stunted and decrease in height down to two metres or even less, while the distance between the trees increases. A possibly similar situation is shown on Photo 7 from a remote south-facing slope in the Tibetan Himalaya of Nepal.

In most cases not only the lower treeline ecotone, but the whole forest belt is severely influenced by extraction of construction wood. Erect growing stems are cut favourably and the junipers then regenerate by resprouting from the base growing as a shrub-like multi-stemmed tree. In a few sites, however, where logging was prohibited by religious beliefs (MIEHE et al. 2000), there is a more or less continuous decrease of growth height and higher percentage of multi-stemmed individuals approaching the upper treeline ecotone. Juniperus turkestanica, which dominates the upper treeline ecotone in the Karakoram, keeps its scapose growth form upslope with an erect solid trunk, but reduces gradually its height until it attains a few decimetres. Juniperus indica and J. tibetica of the arid Himalayas and South Tibet, tend to grow increasingly as caespitose shrubs or multi-stemmed trees, with the tendency to grow with upwards curved shoots. With increasing altitude, the leading shoot shows more and more dead parts and several younger but repeatedly damaged side shoots. The percentage of dead wood is usually highest in the treeline ecotone except in those localities where an obvious actual rise of the treeline leads to a high number of young trees in the ecotone.
All junipers are confined to open rocky and well drained substrates; humic moist soils are left out. Episodically long-lasting snow cover in the winter-precipitation areas lead to heavy damages, possibly by snow-mould. In heavily grazed sites, the trampling effect of livestock may lead to a higher portion of younger trees and seedlings in rock fissures and rock outcrops, which are off the trampling interference. Especially on rocks of mountain ridges or other exposed rocky parts of slopes, juniper trees are clustered. It has to be proved by future biogeographical investigations if this pattern depends on the resting habits of birds, especially jackdaw, which distribute juniper seeds. Moreover, the storing habits of small mammals can not be excluded for this obvious distribution pattern.

4 Constraints and future priorities of Comparative High Mountain Research on the treeline ecotone

Despite increasing efforts in research on the high altitude treeline ecotone, the data base for comparative studies especially on the highest tree stands is still poor. Detailed and well documented descriptions from the mountains with the world's highest treelines are still missing. From the Western Andes it is well known, that *Polylepis tarapacana* climbs as high as 3,100 and 5,200 m a. s. l. [Jordan 1983; Kessler 1995], but neither detailed information about structure and species composition nor climatic data from the upper treeline ecotone are yet available. The same refers to highest tree stands in Eastern Tibet. The meritorious compilation of Chen (1987) gives information only about highest altitudes of *Abies squamata* (4,600–4,700 m), *Larix potaninii* (4,800 m) and *Sabina squamata* (5,000 m) with no further notes on locations than mentioning the catchment of the Yalongjiang river for *Larix*. Juniper forests, are not considered here and the citation of *Sabina squamata* as a tree (op. cit. p. 197) requires verification, because this species is known from the Himalayas as a dwarf-shrub only.

The worst deficit and therefore highest priority in future research is, however, in the extent of human interference even in mountains without permanent human presence. This refers especially to inner tropical humid mountains like the Ruwenzori Mts. or mountains in New Guinea [Corlett 1984; Loeffler 1979], where hunters use fire as a tool during hunting campaigns in severe dry seasons.

Apart from the European Alps and parts of the Rocky Mts., little or nothing is known about the treeline's vegetation history during the Holocene and about the extent and scale of successions of forests after fire or other human interference. This is especially the case with *juniperus*-forests on sunny slopes of the declivities of High Asia, which are increasingly supposed to belong to secondary progressive successions after fire-clearing.

Especially palynological attempts on treeline changes are challenging, because the pollen-identification of the two major tree species of the highest treelines was not yet successful: it is still not possible to distinguish between the Rosaceae genera *Polylepis* forming trees and the mat-forming *Acana* (Kessler 1995) of the Andes. In High Asia, the interpretation of pollenanalytical results is blurred by the fact, that the tree-forming species of *Juniperus* cannot be differentiated from the dwarf-shrub species of the same genus. Causes of treeline are still dubious. Clear terminology of the ecotone structure and lifeform is a precondition for this major desideratum. Recent efforts in ecophysiology with special attention to soil temperatures (Körner 1999) should be supported by interdisciplinary working groups. Seed dispersal and seed banks have not yet been studied in the treeline ecotone of mountains apart from the European Alps or the Rocky Mts. Here again interdisciplinary efforts of zoology and vegetation sciences are needed.

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References


