

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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Zusammenfassung: Studien zu natürlichen und anthropogen geprägten Strukturen an der oberen Waldgrenze – eine kritische Würdigung von CARL TROLL's Konzept der „asymmetrischen Verteilung der immerfeuchten Vegetationstypen der Erde“

C. TROLL's Konzepte der „asymmetrischen Verteilung der immerfeuchten Vegetationstypen der Erde“ von 1948 und der „Höhenstufen tropischer Gebirge in vergleichender Sicht“ von 1959 gehören zu den meistzitierten Abbildungen des vegetationsgeographischen Schrifttums. Die zweifelsohne bestehende ungleiche Verteilung der Vegetationszonen der Erde ist anschaulicher dargestellt als es der Höhenverlauf der oberen Waldgrenze hergibt. In den nordhemisphärischen Gebirgen sind die Waldgrenzen um 800–1300 m zu hoch und auf der Südhalbkugel um 500–800 m zu tief eingetragen. Die in 3500 m Meereshöhe gelegene obere Waldgrenze tropischer Gebirge ist durch anthropogen verursachtes Feuer um 500–600 m erniedrigt worden, womit naturnahe und mutmaßlich klimainduzierte Höhengrenzen mit solchen verglichen wurden, die feuerverursachte Kulturlandschaftsstrukturen sind. Das innertropische Höhen Grasland des Páramo ist eine durch Menschen geschaffene und durch wiederholtes Brennen erhaltene Feuerklimax. Isolierte Waldvorkommen in Normalstandorten umgeben von tropischem Höhen Grasland oder vergleichbaren Zwergstrauchformationen bezeugen die Waldfähigkeit. Die natürliche Struktur des Waldgrenzökotons ist nur schwer greifbar, da in den meisten Gebirgen Menschen zur Schaffung und Erhaltung von Hochweiden oder auch nur zu Jagdzwecken die Wälder und ihre Höhengrenzen verändert haben. Wenige Beispiele aus entlegenen Bergregionen Afrikas und des Himalaya deuten darauf hin, daß sich der Wald gegen seine Obergrenze in einzelnstehende und niedriger wachsende Bäume auflöst, die in humiden Gebirgen in einem geschlossenen immergrünen Strauchbestand stehen.

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 Páramo 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 innertropical 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 *Picea* 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

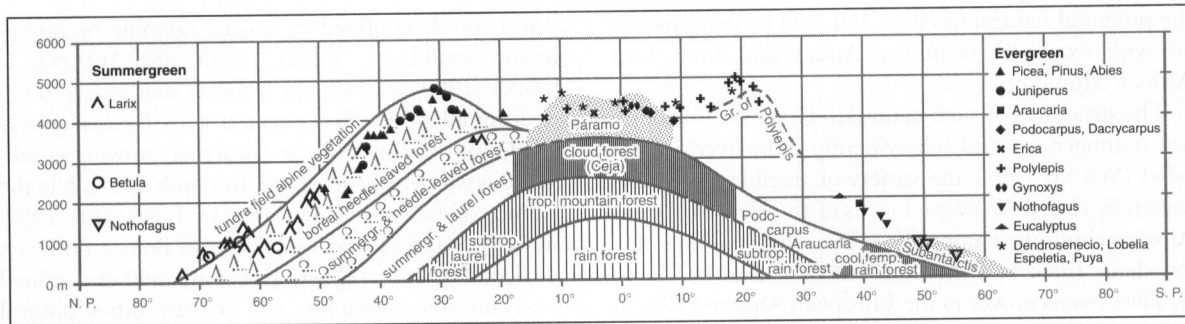


Fig. 1: The timberlines in the asymmetrical vegetation belts of the world, from TROLL (1948) (changed)

Sources: after TROLL 1948; BYKOV 1978; CHEN 1987; ELLENBERG 1996; FINSTERWALDER a. JORDAN 1987; GORCHAKOVSKY a. SHIYATOV 1978; HERMES 1955; HERZOG 1931; HILDEBRAND-VOGEL a. VOGEL 1995; HOLTMEIER 1995; JORDAN 1978; KESSLER 1995; KLÖTZLI 1975; LAEGAARD 1992; LAUER a. KLAUS 1975; G. MIEHE 1991; MIEHE et al. 1996; S. a. G. MIEHE 1994; PÉREZ 1994; RUTHSATZ 1977; P. SKLENÁR, pers. comm. 14.12.1998; TROLL 1939; WALTER a. BRECKLE 1994; WALTER a. Medina 1969; WALTER 1974; WARDLE 1974; WERDECKER 1955

Die (potentielle natürliche) obere Waldgrenze im asymmetrischen Vegetationsaufbau der Erde, nach TROLL (1948) (verändert)

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 innertropical 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-hemispherical 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; KÖRNER 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. SCHÖNENBERGER 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 micro-climatic 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 (SKLENÁR, 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 man-made 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

of the Simen Mts. (13°10'–25°N / 38°10'E), the Bale Mts. (7°10'N / 40°E) and Mt. Elgon (0°54'–1°25'N / 34°14'–45°E) between 3,200 and 4,300 m a. s. l., it is evident that fire is the overruling determinant for the forest distribution, despite differences in climate, soils and human interference (see HURNI 1982; KAEPPELI 1998; MIEHE a. MIEHE 1994 b; NIEVERGELT et al. 1998; WESCHE et al. 1999). The permanent presence of live-stock and herders in all three mountain areas has only ceased on Mt. Elgon through nature conservation policies, but fire as a tool to improve grazing conditions, to extinguish groves as hiding-places of hyenas etc. and for hunting purposes is still present. The actual distribution of isolated stands of *Erica*-, *Stoebe*- or *Hypericum*-thickets depends largely on the occurrence of fire-breaking rock-outcrops, cliffs or boulder fields bare of inflammable vegetation. On homogenous open slopes, groves or thickets only survive in an irregular pattern if the fire frequency is low, allowing the slow-growing woody perennials to regenerate from a xylopod-like base (*Erica*) or from root-suckers (*Hypericum*). The surrounding vegetation may consist of caespitose individuals of the same species as the tree-forming ones of the groves: *Erica* spp. have the ability to regenerate as a shrub after the tree form was burnt down. Repeated fire-clearing keeps the shrubs low and allows the herders to control the grazing sites easily. If the fire-frequency is low, the ericaceous pastures may recover to reform thickets and finally to multi-stemmed dwarf forests. If the scrub is burnt more frequently, *Erica* and other potentially tree-forming species disappear and give way to grassland (Simen Mts., Mt. Elgon) or dwarf-shrublands of *Helichrysum splendens* (Bale Mts.). The altitude of the highest tree-forming outposts depends on the accidental presence of fire-breaking rocks or the frequency and accidental run of the fires. Around Mt. Bwahit (Simen) the highest trees (definition see below) were found in 4,000 m a. s. l., in Bale at 4,100 m a. s. l. and on Mt. Elgon at 4,160 m a. s. l. The extent of the fire-replacement thickets forming the ericaceous belt of the Bale Mts. is shown in Figure 2. The status of 1989/90 according to field evidence was supplemented by interpretation of air photos of 1967 and 1972. The irregular run of the border between *Erica*-thickets and Afroalpine open dwarf-shrublands is a typical fire-pattern. Figure 3 shows the potential natural extent after a (hypothetical) cease of human interference. In the Simen Mts., however, *Erica* forests and thickets did already regenerate in the way it is presumed for the Bale Mts. Repeated photography between 1976 and 1997 gives clear evidence of the extent of a forest belt formed of *Erica arborea* (KAEPPELI 1998; NIEVERGELT et al. 1998).

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 LÖVE 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 ecotone show all transitions from tree to dwarf-shrub (e.g. *Polylepis 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 edaphic changes: under the perhumid climate of the Ruwenzori Mts. (0°20'N / 29°55'E) the treeline ecotone shows an irregular patchy structure of *Erica*-stands clearly divided from surround-

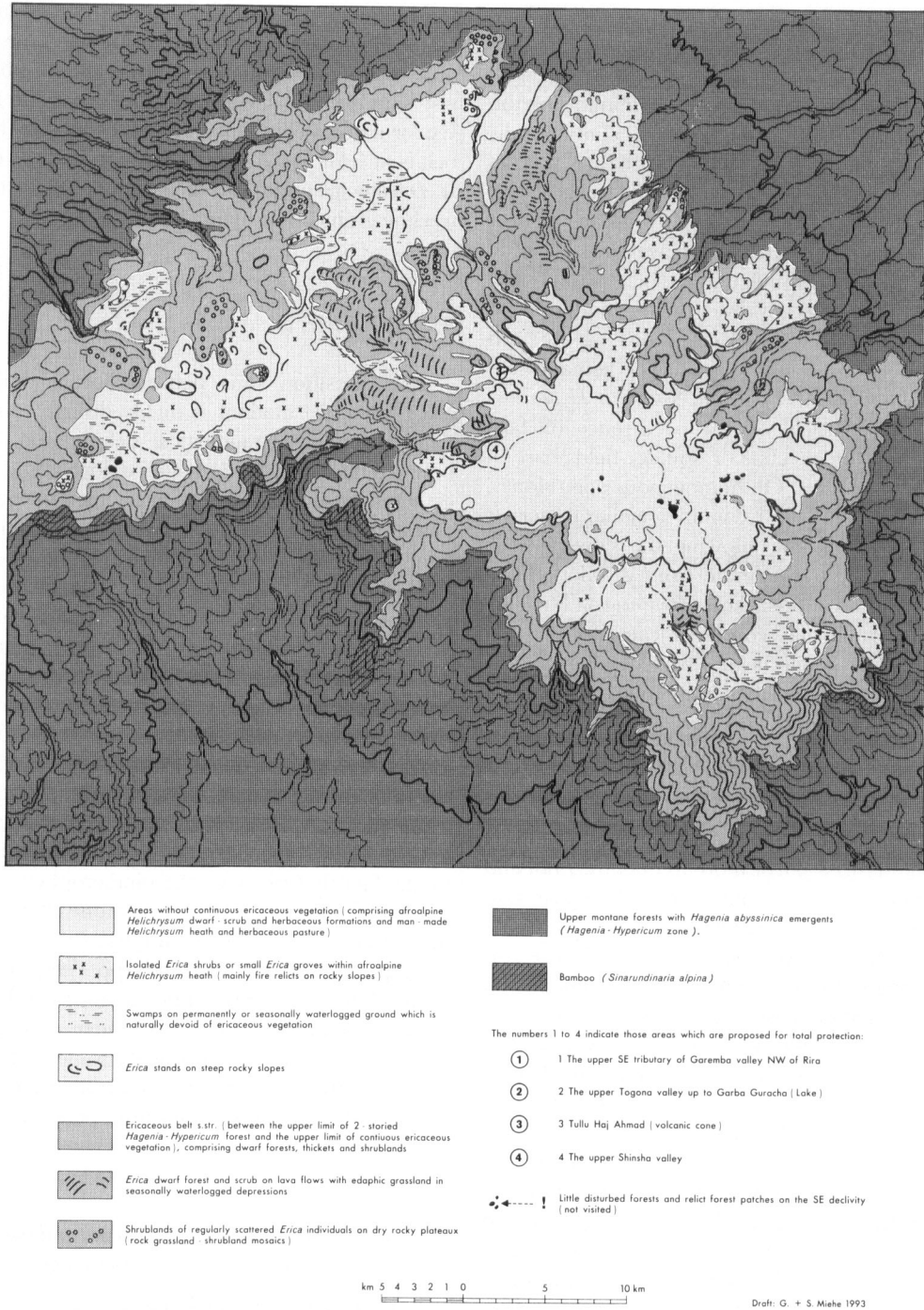


Fig. 2: Actual extend of the upper montane forests and the fire-replacement successions of the ericaceous belt in the Bale Mts. of South Ethiopia. Fire-relicts of *Erica* in the midst of afroalpine pastures indicate the character of a cultural landscape with a man-interfered upper treeline

After MIEHE, a. MIEHE 1994, changed

Aktuelle Verbreitung von *Erica*-Wäldern im Hochweidegebiet der Bale Mts. in Süd-Äthiopien. Der unregelmäßige Grenzverlauf zwischen *Erica*-Dickicht und *Helichrysum*-Heiden ist typisch für Weidpflege mittels Feuer

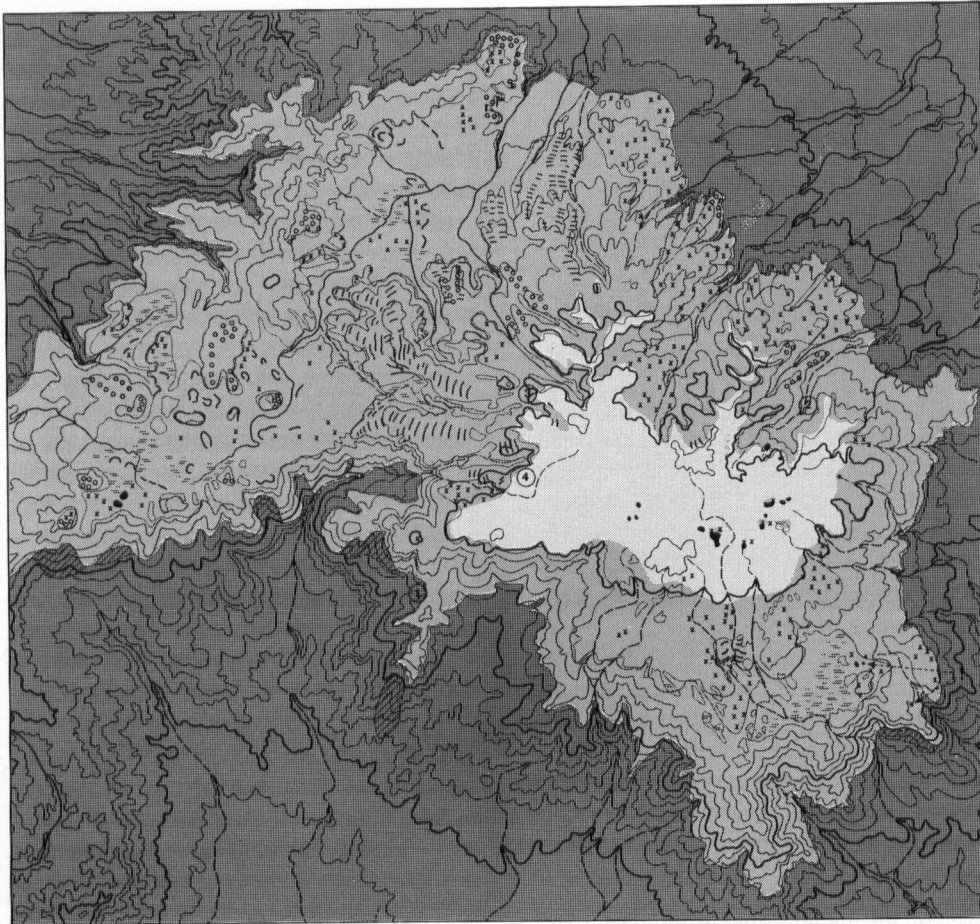


Fig. 3: Potential natural extent of ericaceous and Afroalpine vegetation
Potentielle natürliche Ausdehnung des *Erica*-Waldes

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 runsoroensis*-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 tree-line 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 (GÜTTINGER et al. 1998; CLAUSNITZER 2000);



Photo 1: Clear cut treelines under perhumid climate of the Ruwenzori Mts.: water-logged zonal habitats are not suitable for tree-growth. *Erica* can grow only on irregular distributed shallow well-drained rock cliffs

Photo: G. MIEHE (Ruwenzori Mts., Bujuku Valley, 0°25' N / 29°28' E, 3,400 m a. s. l., 28/2/1997)

Die Struktur des Waldgrenzenökotons kann in perhumiden Gebirgen durch Substratwechsel bedingt sein; nur flachgründige Felsklippen ohne Wasserstau tragen *Erica*-Bäume; hypsozonale Standorte sind zu naß für diese Baumarten. Die obere Waldgrenze kann hier eine Nässegrenze sein

– 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 4,240 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

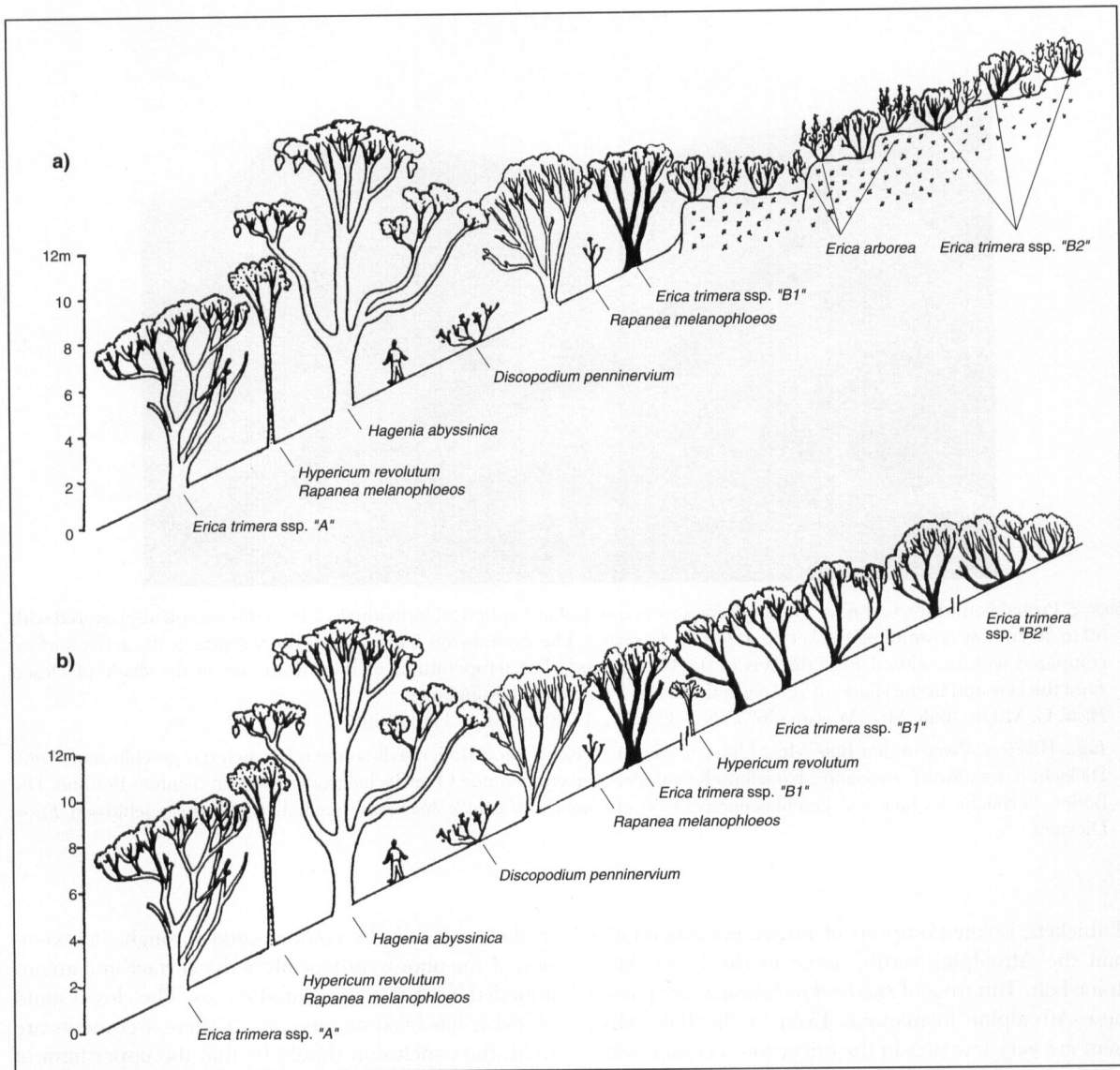


Fig. 4: Clear-cut treelines (a) under semihumid climate of the Bale Mts.: Rock ledges are unsuitable for trees because they are water-logged during the rainy season and drying out in the dry season. Under undisturbed conditions (b) a one-storeyed *Erica*-forest is presumed to follow above the *Hagenia*-forest
After MIEHE a. MIEHE 1993, changed

In tropisch wechselfeuchten Gebirgen (Bale Mts.) können flachgründige Felsstandorte baumfrei sein, da sie während der Regenzeit staunäß 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

Photo: 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 Kugelbüsche 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 rynchopetalum* 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 ecophysiology) 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

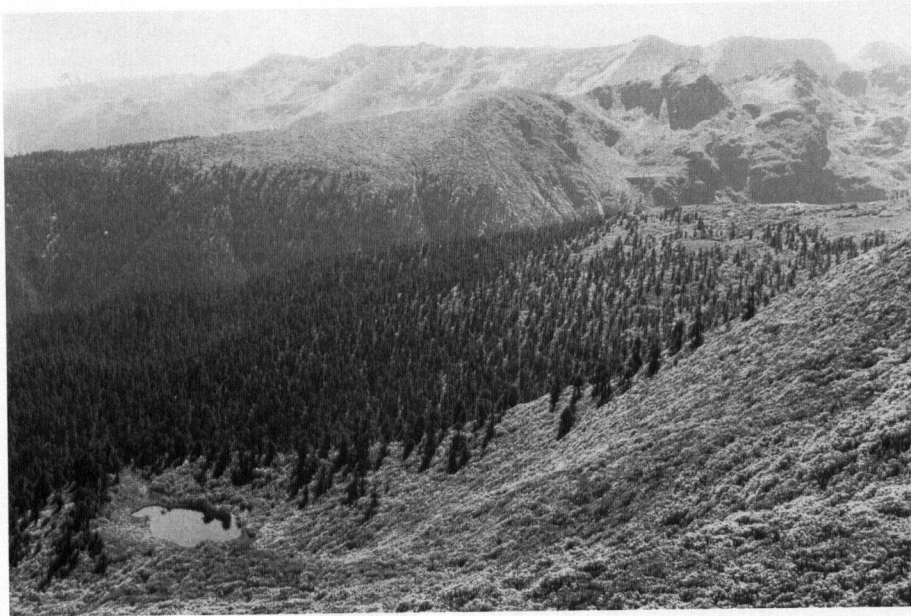


Photo 3: Probably undisturbed treeline ecotone of the south-eastern Himalaya: Closed forests of *Abies densa* disintegrate in the treeline ecotone into isolated trees towering a closed evergreen broadleaved rhododendron thicket.

Photo: G. MIEHE (Black Mountains, Central Bhutan, 27°23'N / 90°42'E, 4,250 m a. s. l., 16/10/1998)

Obere Waldgrenze im Südost-Himalaya: Der geschlossene *Abies densa*-Wald lichtet sich in ca. 4000 m; einzelne Tannen stehen in geschlossenem, zwei bis drei Meter hohem immergrünen Rhododendron-Dickicht

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°59'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°45' 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



Photo 4: Undisturbed treeline ecotone of Central Himalayan Inner Valleys: north facing slope with successions of *Larix himalaica* (1) after repeated landslides in open stands. Beyond mostly multi-stemmed *Betula utilis* and *Sorbus* (arrows) spp. grow in *Rhododendron setosum* dwarf-scrub

Photo: G. MIEHE (Langtang, Central Nepal, 28°12'N / 85°29'E, 4,020 m a. s. l., 6/6/1986)

Waldgrenzökoton im Zentralen Himalaya: Rutschungsflächen werden von *Larix himalaica* besiedelt. Darüber folgen vielstämmige Birken- und Ebereschen-Zwergbäume in geschlossener Flur niederalpiner immergrüner Zwergstrauch-Rhododendren

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

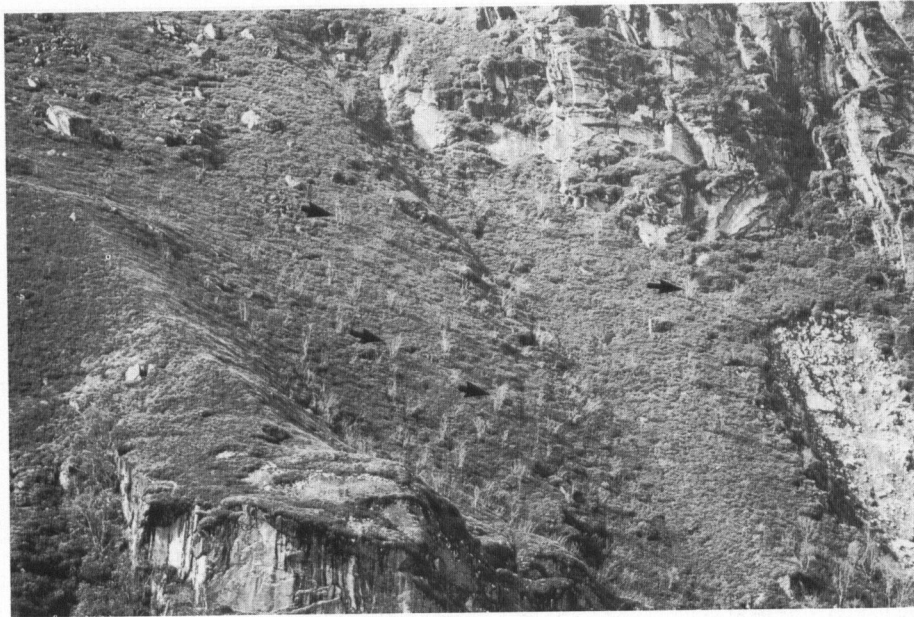


Photo 5: Above the uppermost *Betula utilis* forests, multi-stemmed *Sorbus microphylla* (arrows) dominate a closed *Rhododendron anthopogon* dwarf-scrub of the shady slope. The rowan grows up to 4,300 m a. s. l.

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 einzelstehende 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)

Vielstämmige Ebereschen-Zwergbäume im Waldgrenzökoton eines zentral-himalayischen Schatthangs, umgeben von Sträuchern des Waldgrenzökotons (*Lonicera obovata*, *Rhododendron campanulatum*) und niederalpinen Zwergstrauch-Rhododendren

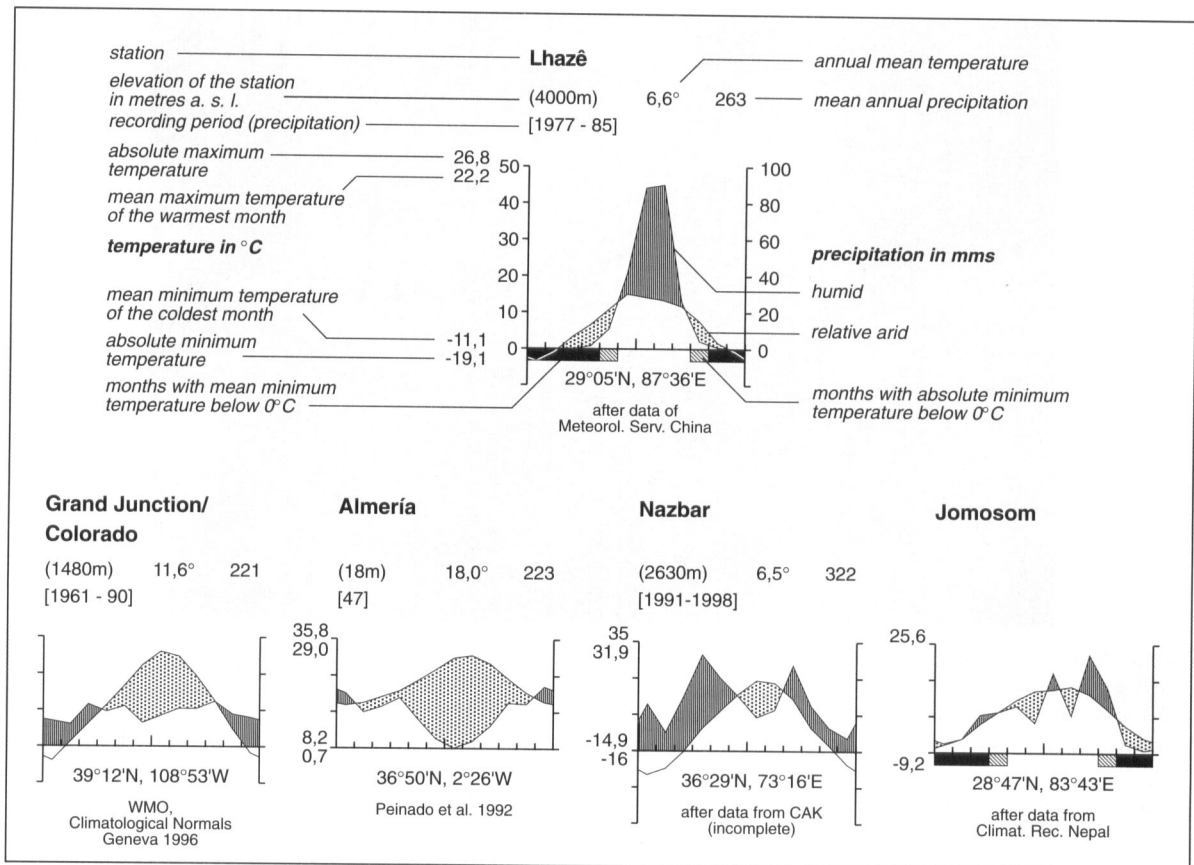


Fig. 5: Climatic diagrams (after WALTER 1955) from areas of open juniper forests
Klimadiagramme (nach WALTER 1955) aus Wacholder-Offenwaldgebieten

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-*

nulatum. Beyond the highest *Betula* trees multi-stemmed dwarf trees of *Sorbus* spp. continue (Photo 4–6). This refers to structures of the shady slope only, however. It is yet unknown how the treeline ecotone of the sunny slope would look like in its untouched state.

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

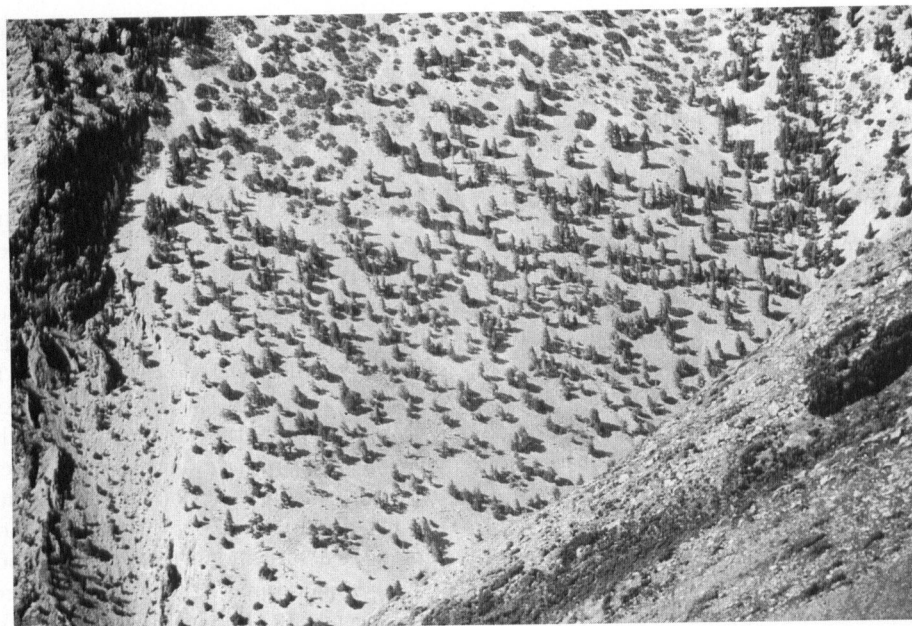


Photo 7: South facing open Cupressaceae-forest between 3,300 and 3,500 m a.s.l., 12 km north of Jomosom (Central Nepal, 28°54'N / 83°46'E). Annual rainfall is expected not to exceed 300 mm. The forest is one of the least disturbed forests in the dry borderlands north of the Himalayas

Photo: G. MIEHE (26/7/1977)

Südexponierter *Cupressus*- und *Juniperus*-Offenwald zwischen 3300 und 3500 m NN, 12 km nördlich von Jomosom (Zentralnepal, 28°54'N) im Trockengebiet des Tibetischen Himalaya Nordnepals. Die Jahressumme des Niederschlags ist wahrscheinlich nicht höher als 300 mm. Der Bestand ist einer der wenigen kaum gestörten Offenwaldrelikte im Tibetischen Himalaya

300 mm/a (MIEHE 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 decacentimetres. *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 5,100 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 perhumid mountains like the Ruwenzori Mts. or mountains in New Guinea (CORLETT 1984; LÖFFLER 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 *Acaena* (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

- ATLAS OF TIBET PLATEAU. Ed. by Institute of Geography, Chinese Academy of Sciences. Beijing 1990.
- BEUG, H.-J. a. MIEHE, G. (1999): Vegetation history and human impact in the Eastern Central Himalayas (Helambu, Langtang/Nepal). *Dissertationes Botanicae* 318, Stuttgart.
- CHEN, C. (1987): Standortliche, vegetationskundliche und waldbauliche Analyse chinesischer Gebirgsnadelwälder und Anwendung alpiner Gebirgswaldbau-Methoden im chinesischen fichtenreichen Gebirgsnadelwald. *Dissertation Univ. Bodenkultur* 30, Wien.
- CLAUSNITZER, V. (2000): Rodents of Mt. Elgon (Uganda). Ecology, biogeography and the significance of fire.. Ph.D. thesis University of Marburg.
- CHORLETT, R. T. (1984): Human impact on the subalpine vegetation of Mt. Wilhelm, Papua New Guinea. In: *J. Ecol.* 72, 841–854.
- ELLENBERG, H. (1958): Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. In: *Umschau*, (21) 645–648; (22) 679–681.
- (1996): Páramos und Punas der Hochanden Südamerikas, heute größtenteils als potentielle Wälder anerkannt. In: *Verhand. Ges. Ökologie* 25, 13–23.
- FREITAG, H. (1971): Die natürliche Vegetation Afghanistans. In: *Vegetatio* 22, 285–344.
- (1972): Die natürliche Vegetation des südostspanischen Trockengebietes. In: *Bot. Jb.* 91, 147–308.
- GÜTTINGER, R.; LEUMANN, L.; GETAHUN, M.; SIMMEN, J. a. WÜST, M. (1998): The actual situation of several small mammal species in the park area. In: *NIEVERGELT, B.; GOOD, S. a. GÜTTINGER, R. (Eds.): A survey on the flora and fauna of the Simen Mountains National Park Ethiopia.* Zürich, 64–73.
- HAFFNER, W. (1981): Geo-ecological observations in Khumbu. In: *LIU DONGSHEN (Ed.): Proceed. Symp. Qinghai-Xizang (Tibet) Plateau.* Beijing, 1977–1986.
- HEDBERG, O. (1969): Evolution and speciation in a tropical high mountain flora. In: *Biol. J. Linn. Soc.* 1, 135–148.
- HENNING, I. (1975): Die La Sal Mountains, Utah. Ein Beitrag zur Geoökologie der Colorado-Plateau-Provinz und zur vergleichenden Hochgebirgsgeographie. *Akad. Wiss. Lit., Math.-Naturwiss. Kl. Mainz* 1975, 2. Wiesbaden.
- (1994): Hydroklima und Klimavegetation der Kontinente. *Münstersche Geographische Arbeiten* 37, Münster.
- HOLTMEIER, K. F. (1986): Über Bauminseln (Kollektive) an der klimatischen Waldgrenze – unter besonderer Berücksichtigung von Beobachtungen in verschiedenen Hochgebirgen Nordamerikas. In: *Wetter und Leben* 38, 121–139.
- (1999): Ablegerbildung im Hochlagenwald und an der oberen Waldgrenze in der Front Range, Colorado. In: *Mitt. Deutsch. Dendrol. Ges.* 84, 39–61.
- JORDAN, E. (1983): Die Verbreitung von *Polylepis*-Beständen in der Westkordillere Boliviens. In: *Tuexenia* 3, 101–116.
- KAEPPEL, M. (1998): Regeneration and age structure of relict ericaceous forests. A dendrochronological study near the timberline in the Simen Mountains, Ethiopia. M.Sc. thesis, unpubl. Institute of Geography, Berne.
- KESSLER, M. (1995): *Polylepis*-Wälder Boliviens: Taxa, Ökologie, Verbreitung und Geschichte. *Dissertationes Botanicae* 246, Stuttgart.
- KESSLER, M. u. HOHNWALD, S. (1998): Bodentemperaturen innerhalb und außerhalb bewaldeter und unbewaldeter Blockhalden in den Bolivianischen Hochanden. Ein Test der Hypothese von Walter und Medina 1969. In: *Erdkunde* 52, 54–62.
- KÖRNER, C. (1998): A re-assessment of high elevation tree-line positions and their explanation. In: *Oecologia* 115, 445–459.
- (1999): Alpine plant life. Functional plant ecology of high mountain ecosystems. Berlin.
- LAEGAARD, S. (1992): Influence of fire in the grass páramo vegetation of Ecuador. In: *BALSLEV, H. a. LUTEYN, J. L. (Eds.): Páramo. An Andean ecosystem under human influence.* London, 151–170.
- LANGE, S.; BUSSMANN, R. a. BECK, E. (1997): Stand structure and regeneration of the subalpine *Hagenia abyssinica* forests of Mt. Kenya. In: *Bot. Acta* 110, 473–480.
- LAUER, W.; RAFIQPOOR, D. u. FRANKENBERG, P. (1996): Die Klimate der Erde. Eine Klassifikation auf ökophysiologischer Grundlage der realen Vegetation. In: *Erdkunde* 50, 275–300.
- LÖFFLER, E. (1979): Ursprung und Verbreitung der Páramo-Grasländer in Ostneuguinea. In: *Erdkunde* 33, 226–236.
- LÖVE, D. (1970): Subarctic and subalpine. Where and what? In: *Arctic Alpine Res.* 2, 63–73.
- MEUSEL, H. u. SCHUBERT, R. (1971): Beiträge zur Pflanzengeographie des Westhimalajas, 3. Teil. In: *Flora* 160, 573–606.
- MIEHE, G. (1982): Vegetationsgeographische Untersuchungen im Dhaulagiri- und Annapurna-Himalaya. *Dissertationes Botanicae* 66, 1, 2, Vaduz.
- (1990): Langtang Himal. Flora und Vegetation als Klima-zeiger und -zeugen im Himalaya. A prodromus of the vegetation ecology of the Himalayas. Mit einer kommentierten Flechtenliste von JOSEF POELT. *Dissertationes Botanicae* 158, Stuttgart.
- (1991): Die Vegetationskarte des Khumbu Himal (Mt. Everest Südabdachung) 1:50 000. Gefügemuster der Vegetation und Probleme der Kartierung. In: *Erdkunde* 45, 81–94.
- MIEHE, G. a. MIEHE, S. (1993): On the physiognomic and floristic differentiation of ericaceous vegetation in the Bale Mountains, SE-Ethiopia. In: *Opera Botanica* 121, 85–117.
- (1994): Zur oberen Waldgrenze in tropischen Gebirgen. In: *Phytocoenologia*, 24, 53–110.

- MIEHE, G.; MIEHE, S.; HUANG JIAN u. OTSU TSEWANG (1998): Forschungsdefizite und -perspektiven zur Frage der potentiellen natürlichen Bewaldung in Tibet. In: Petermanns Geographische Mitteilungen 142, 153–162.
- MIEHE, G. a. MIEHE, S. (in prep.): A checklist of high mountain vegetation formation.
- MIEHE, S. a. MIEHE, G. (1994): Ericaceous forests and heathlands in the Bale mountains of south Ethiopia. Ecology and man's impact. Hamburg.
- MIEHE, S.; CRAMER, T.; JACOBSEN, J.-P. a. WINIGER, M. (1996): Humidity conditions in the western Karakorum as indicated by climatic data and corresponding distribution patterns of montane and alpine vegetation. In: Erdkunde 50, 190–204.
- MIEHE, S.; MIEHE, G.; HUANG JIAN; OTSU TSEWANG; TUNTSU TSEREN a. TU YANLI (2000): Sacred forests of South-Central Xizang and their importance for the restoration of forest resources. In: Marburger Geographische Schriften 135 (in press).
- MUELLER-DOMBOIS, D. a. ELLENBERG, H. (1974): Aims and methods of vegetation ecology. New York.
- NIEVERGELT, B. (1998): Long-term changes in the landscapes and ecosystems of the Simen Mountains National Park. In: NIEVERGELT, B.; GOOD, S. a. GÜTTINGER, R. (Eds.): A survey on the flora and fauna of the Simen Mountains National Park Ethiopia. Zürich, 8–23.
- NORTON, D. A. a. SCHÖNENBERGER, W. (1984): The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. In: Arctic Alpine Res. 16, 361–370.
- SCHMITT, K. (1991): The vegetation of the Aberdare National Park Kenya. Hochgebirgsforschung 8, Innsbruck.
- SCHROEDER, F. G. (1998): Lehrbuch der Pflanzengeographie. Wiesbaden.
- STEVENS, G. C. a. FOX, J. F. (1991): The causes of treeline. In: Annu. Rev. Ecol. Syst. 22, 177–191.
- TROLL, C. (1948): Der asymmetrische Vegetations- und Landschaftsbau der Nord- und Südhalbkugel. In: Göttinger Geographische Abhandlungen 1, 11–27.
- (1959): Die tropischen Gebirge. Bonner Geographische Abhandlungen 25, Bonn.
- (1972): The upper limit of aridity and the arid core of High Asia. In: C. TROLL (Ed.): Geoecology of the high mountain regions of Eurasia. Erdwiss. Forsch. 4, Wiesbaden, 237–243.
- (1973): The upper timberlines in different climatic zones. In: Arctic Alpine Res. 5, A3–A18.
- WALTER, H. (1955): Die Klimadiagramme als Mittel zur Beurteilung der Klimaverhältnisse für ökologische, vegetationskundliche und landwirtschaftliche Zwecke. In: Ber. Deutsch. Bot. Ges. 68, 331–344.
- WALTER, H. u. MEDINA, E. (1969): Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas (vorläufige Mitteilung). In: Berichte Deutsche Botanische Gesellschaft 82, 275–281.
- WESCHE, K. (2000): The high-altitude environment von Mt. Elgon (Uganda/Kenia). Climate, vegetation and the impact of fire. Ph.D. thesis University of Marburg.
- WESCHE, K.; CLAUSNITZER, V.; MIEHE, S. a. MIEHE, G. (1999): Habitat conditions in afroalpine communities – examples from Uganda and Ethiopia. In: BRECKLE, S.-W.; SCHWEIZER, B. a. ARNDT, V. (Eds.): Results of worldwide ecological studies – Proceed. 1st Sympos. A. F. W. Schimper Foundation of H. a. E. WALTER, Hohenheim, Oktober 1998. Stuttgart.
- WISSMANN, H. v. (1960/61): Stufen und Gürtel der Vegetation und des Klimas in Hochasien und seinen Randgebieten. In: Erdkunde 14, 249–272; 15, 19–44.
- YOUNG, K. R. (1993): Changes in forest structure and regeneration between two Peruvian timberline margins. In: Arctic Alpine Res. 25, 167–174.
- ZHANG JINGWEI (Ed., 1988): The vegetation of Xizang. Beijing (in chin.).