

CLIMATIC TREELINES: CONVENTIONS, GLOBAL PATTERNS, CAUSES

With 7 figures

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Zusammenfassung: Klimatische Baumgrenzen: Konventionen, globale Muster, Ursachen

Das Phänomen der alpinen Waldgrenze wird aus globaler Perspektive betrachtet. Sieht man von lokalen/regionalen (inklusive anthropogenen) Gründen ab, die das Fehlen von Bäumen mitverantworten, findet sich die alpine Waldgrenze weltweit auf Höhenlinien mit erstaunlich uniformen Temperaturen während der Wachstumsperiode. Dagegen haben andere Limitierungsfaktoren (inkl. die Temperatur des wärmsten Monats) keine globale Gültigkeit, sondern führen zu lokaler Modifizierung des globalen Musters. Die abrupte Verbreitungsgrenze von Bäumen erklärt sich aus der engen aerodynamischen Kopplung zwischen Baumkronen und atmosphärischen Bedingungen. Die Position der Baumgrenze ist daher anhand der einheitlichen Temperaturschwelle gut voraussagbar, was sie zu einer idealen biogeographischen Referenzlinie für Modelle macht, wie z.B. zur Abschätzung der potentiellen globalen Bergwaldbedeckung.

Summary: The high altitude treeline phenomenon is discussed with a global perspective. If one disregards local/regional (including anthropogenic) reasons for the absence of trees, the high elevation treeline is found at surprisingly uniform growing season temperatures worldwide, while other types of thresholds (including the warmest month temperature) do not work on a global scale. This phenomenon is explained by the close aerodynamic coupling between tree crowns and atmospheric conditions. It is shown that the treeline position can be predicted well by thermal thresholds alone, which makes it an ideal biogeographic reference line in modelling, for instance to estimate the global mountain forest area.

Introduction

The high elevation treeline issue re-visited here is a classical case where a lack of definition and missing agreement on conventions paved the way to a multitude of interpretations, which at first sight seem to hopelessly trap the community concerned in academic debate and misunderstanding. In this contribution I will try to develop a logical concept that potentially hosts all the various ideas which had been evolving over the years, but still offers a pathway towards ecological theory, which permits the formulation of scientific hypotheses and their testing. Otherwise this science is at risk of remaining descriptive and phenomenological. A treeline concept which implies lack of understanding (everything matters) does not seem to advance this field of science. Neither in the treeline debate nor in any other scientific debate does progress come from emphasizing that things are complex and multi-factorial, a popular escape route from theory-based, mechanism-oriented understanding of life phenomena.

1 A practical treeline convention

A lot of misunderstanding is rooted in terms which have different meanings to different people. In essence, the globe's terrestrial land cover types fall into a hand-

ful of major biota such as grassland, shrubland, forests and mosaics among them. Each of these "formations" has boundaries for particular reasons. Forests or woodlands may find limits in dry, wet or cold conditions. Other reasons for the lack of tree growth are disturbances. Recurrent natural fires and follow-up browsing/grazing pressure (self-sustained grassland systems in parts of the savanna and prairie), avalanches, rockfall or very loose substrate may prevent trees from establishing and growing. Topography-induced extreme wind speed, such as near coastal plains, mountain tops or ridges can prevent tree growth as well. On top of these natural disturbances, human influences are most obvious reasons for the lack of trees in certain areas, irrespective of whether the terrain is mountainous or flat.

Except for one of the above-mentioned factors (low temperature) all other factors can prevent tree growth at any point on the globe which could potentially support trees (Fig. 5), hence none of these factors has *a priori* anything to do with mountains. If we are ever to arrive at a scientifically sound high elevation treeline theory, a first step is to acknowledge that there are these two categories of factors (Fig. 1), one category intrinsically tied to the very nature of mountains, i.e. operative at all mountains globally, and the other group of factors which may come into play anywhere on the globe, including mountains. Because this "other group" of

factors represents a near-endless list of local/regional peculiarities, these “azonal” drivers – as significant they may be locally – are not helpful for a global concept.

2 Why should we aim for a global concept?

Acknowledged for as long as we know, trees find an upper limit in all mountains around the globe which are high enough. This trivial fact by itself calls for a set of drivers of high elevation treeline formation that is independent of local peculiarities, but these local peculiarities may interfere with such a global driver. The fact that tree limits are reached at different elevations across latitudes, ranging from close to sea level at polar latitudes and reaching elevations >4,000 m at subtropical and tropical mountains, has long attracted ecologists, given the obvious need for a physical explanation of such a latitude-associated change (e.g., TROLL 1973; HOLTMEIER 2000, 2003). It seems that nobody really questions that low temperature is the only factor that can exert such an overarching global influence. The question to be resolved is how precise this driver operates across the globe and how its action upon trees may be modified by other physical conditions. There are only very few other physical factors which change with elevation in a consistent way across the globe. These are atmospheric pressure and clear (!) sky radiation regime (reduced turbidity, higher fraction of short wave radiation at high altitude). None of the other climatic factors shows worldwide consistent elevational gradients (KÖRNER 2003, 2007). Actual solar radiation may change in any direction depending on cloudiness (e.g., declining to 1/3 of the lowland dose at the treeline in New Guinea). Precipitation may either decrease or increase, wind speed is well known to be lower in the interior parts of mountain systems than on summits or exposed crests and are generally less in rough landscapes than in coastal plains. The close association of

treeline with physics-driven phenomena (the altitudinal snow line) was first documented by HERMES (1955). However, because “latitude” encapsulates broad spectra of actual local climate, correlations as those developed by HERMES remain very noisy, and latitude is in fact a poor proxy for mountain climate (JOBAGY a. JACKSON 2000). Yet, these correlations, as coarse as they might be, call for a more careful examination of the climatic drivers behind. At the least, they confirm that we are dealing with a global phenomenon with a physical basis.

3 What is a tree, a forest? What is a line?

Before entering a more careful evaluation of the actual drivers behind HERMES’ correlations, agreement is needed on the very nature of the object under debate. This is not a scientific issue, but simply a need in terms of communication. In agreement with earlier suggestions, it seems useful to adopt a tree concept which separates clearly emerging stature from any prostrate stature tree species may adopt. As long as individuals of a tree-forming species are nested in a shrub or grass layer, they have not reached a size to which some of the major attributes of the life form tree applies, namely emergence above shrub/grass vegetation, high degree of aerodynamic coupling to the atmosphere, protruding potential snow cover, competitive superiority in terms of light capture, etc. In most cases a height of 3 m is sufficient to meet these criteria, but applying a somewhat greater height would not change the debate, whereas including size classes below ca. 1 m would confuse the issue for most locations (shrub size).

Once agreed on the emergent nature of what we call a “tree” irrespective of taxonomic affiliation, the next convention needed relates to the question of whether single trees, groups of trees or full ground cover by trees is made a criterion. Again, the debate would not differ with any of these three criteria adopted, because they are largely running in parallel. We simply need to agree on a convention. In my opinion, isolated trees provide too noisy a signal. They may be remnants of destroyed forests or occupy peculiar microhabitats (“outposts”). A more consistent picture is achieved if groups of trees, i.e. patches of uppermost undisturbed forest, are connected with a line (Fig. 2). Connecting the uppermost lobes of closed forest commonly comes very close to the above definition, hence the rather meaningful synonymous term “forest line” adopted by many authors. Whether the trees contributing to such a virtual line have “timber” size (timberline), seems of less biological relevance.

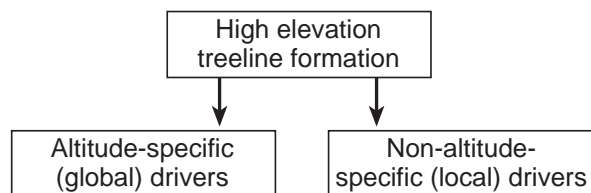


Fig. 1: Treelines are controlled by global and regional drivers
Baumgrenzen werden durch global gültige und regionale Faktoren bestimmt

As is obvious from the above, the term “line” is another convention, because, in reality, forests or patches of forests never “line up”. What might be an obvious line from great distance offers a rather gradual, fragmented picture in situ. Hence, the issue becomes a question of scale. Whoever looks for precision better than 50 m in elevation or 100 m distance on a slope, overlooks “the nature of the ecotone”. The debate becomes fruitless if greater precision is attempted. 50 m elevation corresponds to ca. 0.3 K difference in temperature, which is for too small to permit a meaningful biological interpretation. So when the term “line” is used in communication, this does not imply a physical line, but rather refers to a boundary or obvious transition zone at the above level of precision. Agreement on such a convention is needed before entering a meaningful debate on mechanisms.

4 Life form versus species

Another convention is that of a “life form” limit. The treeline marks a boundary for upright, emergent tree stature, irrespective of species. For a treeline to be

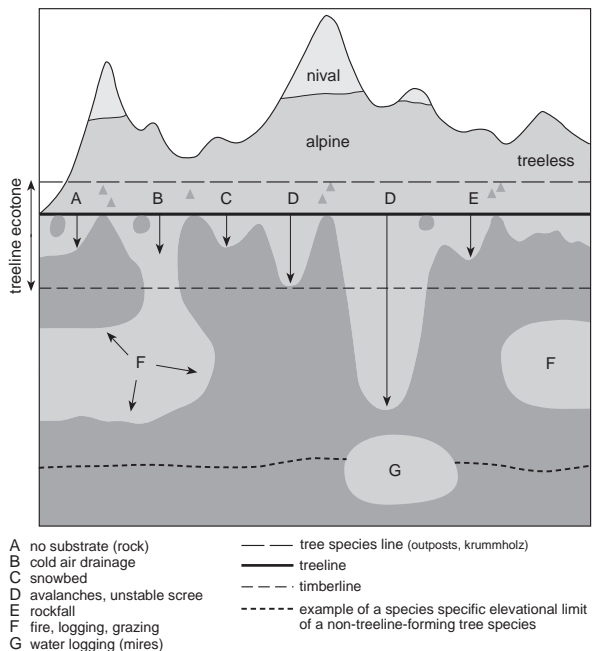


Fig. 2: A schematic illustration of various factors that may modulate the forest and tree limit at a local scale compared to the limit set globally by thermal conditions alone

Schematische Darstellung der Baum- und Waldgrenze unter dem Einfluss unterschiedlicher, nur lokal wirksamer Faktoren im Vergleich zu jener Grenzlinie, die weltweit allein durch die Temperatur bestimmt wird

formed it thus requires taxa that are able to live at the life form limit. This is indeed a delicate issue, because how does one know where the absolute limit of the life form would be? There are only a few families worldwide which evolved genera which, reach the treeline as for instance Asteraceae, Betulaceae, Cupressaceae, Ericaceae, Myrtaceae, Pinaceae and Rosaceae.

When such taxa are regionally not available for whatever reasons, any species could become a treeline species at its species-specific upper elevational limit. Here two examples: the isolated Hawaiian Archipelago lacks treeline taxa so that one tree-stature Myrtaceae (*Metrosideros polymorpha*) and one legume (*Sophora chrysophylla*) reach an upper limit, several hundred metres above which one can find mighty planted specimen of *Picea abies* (Norway spruce), other conifer taxa and even Mediterranean eucalypts (Fig. 3). The same in New Zealand, where *Nothofagus* forms an elevational tree species line, several hundred meters above which *Pinus contorta* does very well, in fact so well that this species became a conservation issue (WARDLE 1985a, b). If one aims at arriving at a global picture, such species- or region-specific elevational limits must be clearly separated from the life form limit. However, most parts of the globe have treeline taxa which form the backbone of a general high elevation treeline theory. If there were not such a common life form (species-independent) limit, it would be hard to imagine how the global patterns of treeline elevation could have developed.

5 Global patterns

Historically, the two major constraints of the treeline debate (beyond the confusion on conventions) was often the focus on certain temperate zone treelines rather than a global vision, and the lack of meteorological data from places where forests reach an upper limit for reasons other than disturbance or because of factors not related to general mountain phenomena. One result of the regional bias was the often quoted 10 °C warmest month isotherm as a treeline proxy, which does indeed hold for parts of the Alps and parts of the Rocky Mountains, but fails nearly everywhere else (KÖPPEN 1936). It may reach 13 °C in Hokaido and 6 °C on some equatorial mountains (KÖRNER 1998). Second, scaling low elevation meteorological station data to treeline elevations bears a lot of uncertainty. Adopting the above conventions for what is a tree, a treeline, a tree-forming taxon and strictly avoiding situations in which not generally mountain-specific factors come into play (such as a lack of moisture or disturbances), the growing season mean temperatures found

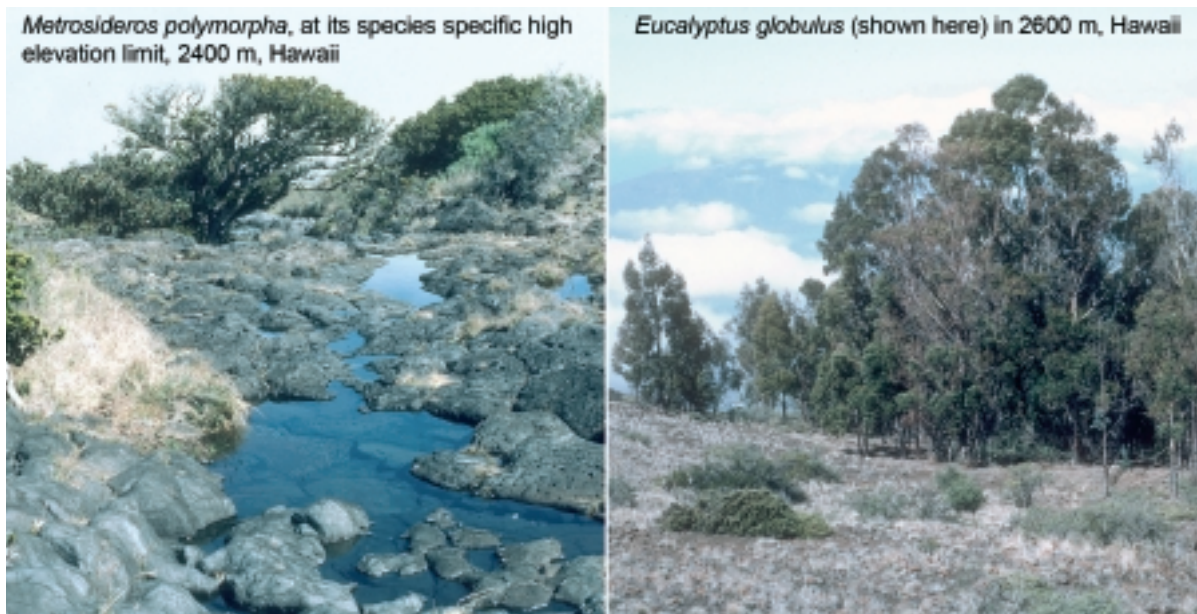


Fig. 3: The distinction between a local tree species line (here exemplified by *Metrosideros polymorpha* on Haleakala, Hawaii) and treeline, a life form boundary irrespective of tree taxa. Tall specimen of planted *Picea abies* grow vigorously on Haleakala at 300 m higher elevation than *Metrosideros*. Similarly, *Eucalyptus* species (example shown here) and various pine species grow above the altitudinal *Metrosideros* tree species line on the slopes of Mauna Kea, Hawaii

Unterscheidung zwischen lokaler Baumartengrenze (am Beispiel von *Metrosideros polymorpha* am Haleakala, Hawaii) und der Baumgrenze, einer Baumart-unabhängigen Lebensformbarriere. Große Exemplare angepflanzter Fichten (*Picea abies*) finden 300 m oberhalb der *Metrosideros*-Baumgrenze üppiges Wachstum. Ähnlich wachsen *Eucalyptus*-Arten (hier gezeigtes Beispiel) und verschiedene Föhrenarten oberhalb der *Metrosideros*-Baumgrenze an den Hängen des Mauna Kea in Hawaii

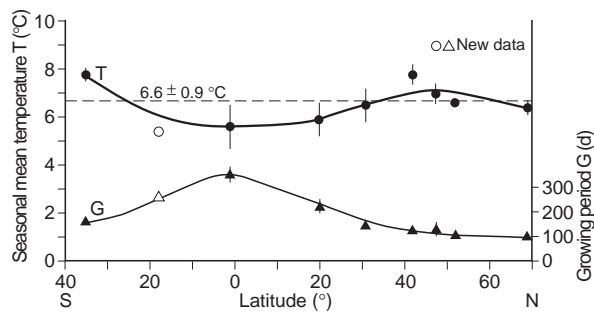


Fig. 4: The global pattern of seasonal mean ground temperature (–10 cm depth) at treeline elevations. Data originally published by KÖRNER and PAULSEN (2004). Supplemented by new data for Kilimanjaro, Sajama (4,800 m, Bolivia) and Eastern Tibet (4,500 m). For definition of “season” see the text

Globales Muster der durchschnittlichen saisonalen Bodentemperatur an verschiedenen Baumgrenzhöhen (–10 cm Tiefe). Originaldaten publiziert in KÖRNER and PAULSEN (2004). Ergänzt durch neue Daten für Kilimanjaro, Sajama (4.800 m, Bolivien) und Ostt Tibet (4.500 m). Definition der Wachstumsperiode siehe Text

at treeline are covering a surprisingly narrow range of 5 to 8 °C, mostly between 6 and 7 °C, with a global mean of 6.7 ± 0.8 °C for 30 locations (Fig. 4, KÖRNER a. PAULSEN 2004).

Given that these data cover all non-polar latitudes, very different taxa and a suite of topographical and soil conditions, the signal is much less noisy than one could expect. It is of particular interest that season length seems to play such a minor role. There is a tendency towards a lower (ca. 5.5 °C) threshold near the equator, values are between 7 and 7.5 °C in the temperate zone, and again a lower threshold applies at higher latitudes, perhaps because of the longer day length. The lower threshold near the equator reflects perhaps a slight compensatory effect of a full year growing season, but the mean growing season temperature at 700 m elevation in the arctic north (*Betula* treeline) is also quite low, namely 6.2 °C, and it is 5.6 °C in equatorial New Guinea at 3,800 m. Once forests are closed and shade the ground, ground temperatures hardly differ with slope exposure (KÖRNER a. PAULSEN 2004). Another so far unexplained observation is that it does not seem to

be the thermal sum (e.g., day degrees) which matters. We calculated sums above 0 °C, above 5 °C and above 7 °C, none of which predicts nearly as well treeline position as the seasonal mean temperature, which awaits mechanistic biological explanation.

These calculations of relevant site temperature adopt a globally consistent convention on season length. The growing season is defined as the period between the first week (after a cool period) when the mean air temperature is >0 °C and the first week at the end of a warm period when the mean air temperature is below 0 °C. For practical reasons, we infer these atmospheric thresholds from the closest correlate with –10 cm soil temperature, which is 3.2 °C. This soil signal is also somewhat buffered against short-term climatic excursions above ground and thus integrates over a few days. Soil temperature at a mean air temperature of 0 °C represents a rather robust threshold which matches phenological observations well and is also suitable in the tropics (KÖRNER a. PAULSEN 2004). Any deviation from this threshold would be of a systematic nature across the globe and would not affect the basic message that natural climatic treelines occur at a common threshold temperature.

6 Towards a global climatic envelope for tree growth

Based on the above rationale a common low temperature limit to tree growth offers a reference line against

which other biogeographic zones can be defined. However, for a general global boundary of forests it needs a moisture threshold as well. Using a world climate database which accounts for actual elevation per 30" pixel (www.worldclim.org) an algorithm was applied, which assumes a certain soil capacity to hold plant available moisture (following www.daac.ornl.gov, and an assumed 100 mm pool for areas with no data) and fills/depletes this pool on a daily basis, depending on precipitation and evapotranspiration (the latter modelled, using conventional meteorological theory, and expressed in mm, KÖRNER a. PAULSEN, unpubl.). Together with the thermal thresholds for tree growth reported above, this leads to a "potential forest" map of the world of 83 Mio km², almost twice as large (plus 45%) as the actual forest covered area according to various statistics (Fig. 5). In other words, 45% of the terrestrial area that could potentially carry forest for climate reasons only, is not forested, for natural (fire, grazing, lack of substrate, fresh-water areas) or anthropogenic reasons. Of the potential global forest area 9.4% are (statistically) on steep terrain (a 'steep' pixel is defined here by a minimum altitudinal difference of 250 m between anyone pair among this and its 8 neighbour pixels), which is approximating the world's mountain forest area by ca. 5 Mio km². The analysis, which roots in the thermal limits derived from high elevation treeline research also depicts the polar treeline quite well, hence underlining a more general meaning of the routines initially developed for climatic treelines in mountains.

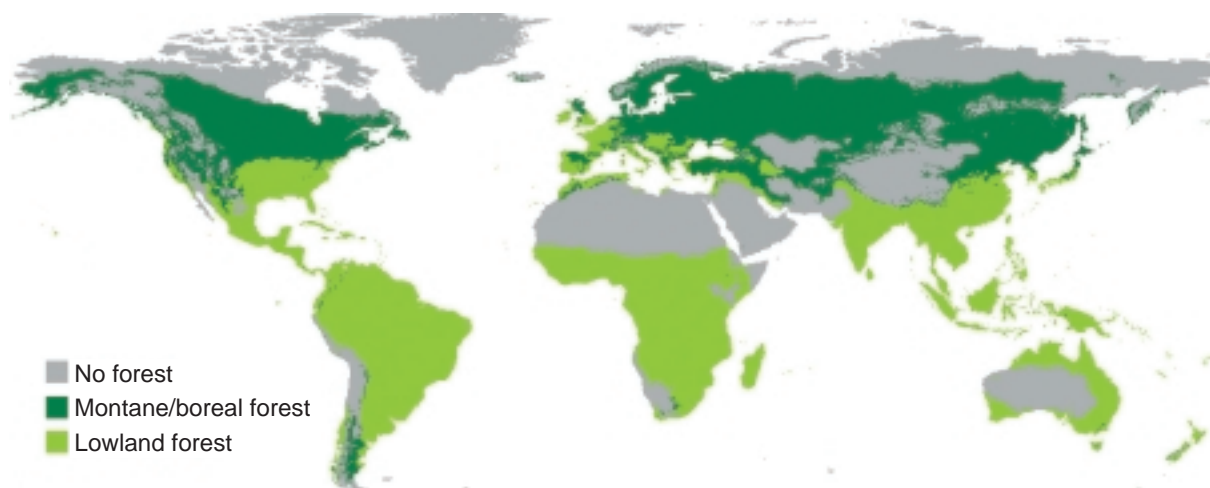


Fig. 5: The global distribution of potentially forested area, as derived from a minimum moisture requirement for tree growth and the cold limit of tree distribution obtained from treeline ecology (Fig. 6)

Das globale Vorkommen von potentiell bewaldetem Gebiet, abgeleitet aus den für das Baumwachstum minimal notwendigen Niederschlägen und der Kältengrenze der Baumverbreitung gemäss Baumgrenzökologie (Abb. 6)

This global digital database of potential tree occurrence also offers a new approach to HERMES' (1955) global treeline vs. altitude assessment. Because each pixel of our database carries an elevation stamp, we can plot a latitude profile of the potential treeline position. At the same time this line marks the lower edge of the alpine belt, which by definition contains no trees (Fig. 6). Although such a database can never depict every local detail or topography and climate, the overall picture we arrive at seems to match observations well. The model clearly depicts the equatorial depression of treeline (higher cloudiness, and thus reduced temperature).

7 What causes the global climate treeline phenomenon?

The above analysis clearly underpins a global pattern of thermal limits of trees, which is to be seen as an envelope of options. Whether trees occur at a given point within this envelope will depend on many other things, as discussed in the introductory sections. Here we ask what might cause this thermal delineation of tree distribution. Are trees physiologically inferior to other life forms when temperatures get cold? Why should they be less adapted to run their basic metabolism at low temperature than grasses, herbs and shrubs which still thrive at 800–1,500 m above treeline?

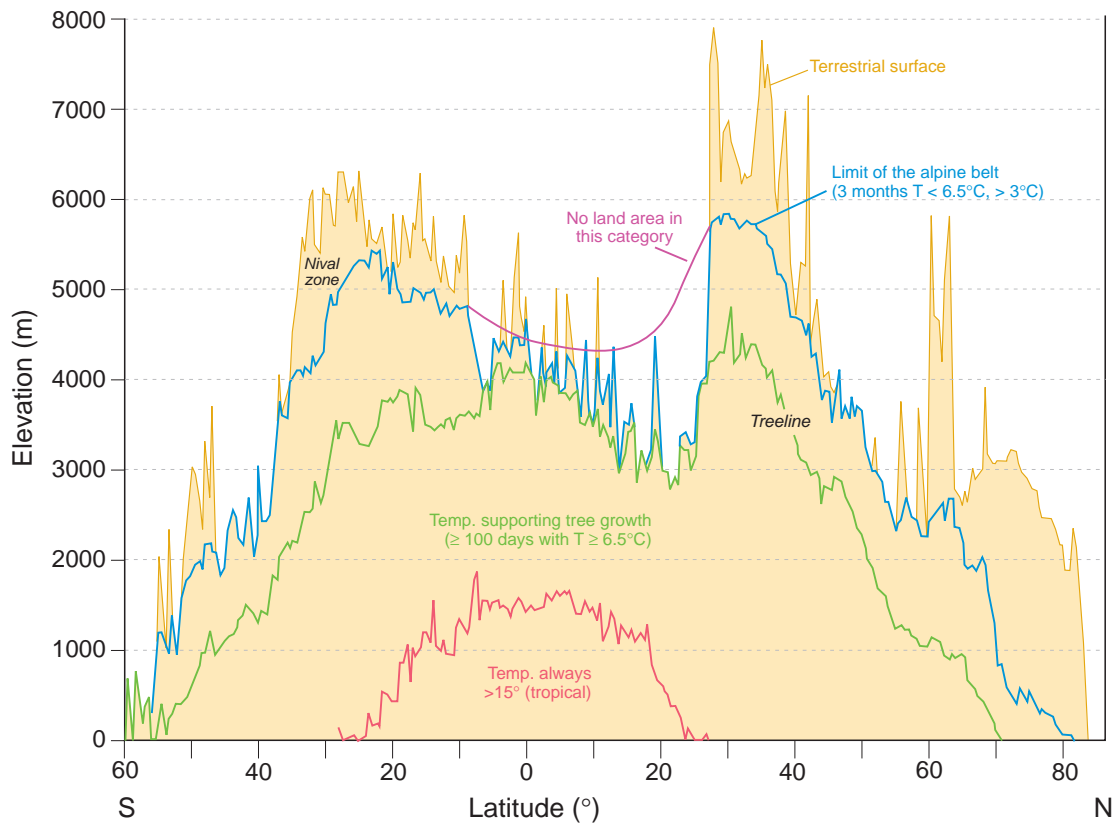


Fig. 6: The latitudinal distribution of maximum elevation of land area, modelled altitudinal position of treeline and the upper limit of the alpine belt (with the nival belt above). For comparison, the elevation of the year-round absolute monthly minimum 15 °C isotherm is shown, which delineates the boundary of low elevation tropical forests. The dotted line is for equatorial latitudes which lack sufficient terrestrial land area with a nival belt. At this resolution, very local excursions of treeline conditions to extremely high elevation such as in Bolivia (4,810 m, HOCH a. KÖRNER 2005) cannot be seen

Latitudinale Verteilung der maximalen Höhe der Landfläche, der modellierten Baumgrenzhöhe und der Obergrenze der alpinen Zone (darüber liegt die nivale Zone). Zum Vergleich ist die Höhe der Isotherme für das absolute Monatsminimum der Luft pro Jahr von +15 °C eingezeichnet, welche die Grenze der tiefgelegenen tropischen Wälder beschreibt. Die punktierte Linie bezeichnet äquatoriale Breiten, die nicht genügend oder keine Landflächen mit einer nivaler Zone aufweisen. Bei dieser Auflösung sind sehr lokale Abweichungen der Baumgrenze in extreme Höhen nicht sichtbar (z.B. in Bolivien, 4.810 m, HOCH a. KÖRNER 2005)

The likely answer is that there is no physiological difference, and treeline trees are well adapted to where they grow (e.g., TRANQUILLINI 1979; KÖRNER 2003). However, trees are exposed to a harsher climate, because of their stature. Trees, protruding through the shrub layer, become exposed to free atmospheric convection and thus operate at close to air temperature for most of the time. By contrast, low stature plants profit from aerodynamic decoupling which leads to a warmer microclimate (KÖRNER et al. 2003). This can be nicely illustrated by modern thermal imagery technology (Fig. 7). Trees emerge as “cold fingers” compared to the warm matrix of low stature heathland, in which plants “air-condition” their micro-environment so that these thermal constraints rarely come into action. Stature is the only common trait that unifies trees of genera such as *Polylepis*, *Erica*, *Leptospermum*, *Juniperus*, *Pinus* and *Eucalyptus*, which otherwise differ in their whole evolutionary history and in many specific traits. Thus, the high elevation climatic treeline appears as a result of an architecture-related phenomenon that operates across taxa and latitudes. In other words, the treeline phenomenon as defined here is related to the same basic physiological constraints that limit growth and development of all cold-adapted plants, including winter wheat and winter rape, and we need to address a much more basic question, namely what is the general cause of growth limitation in cold-adapted angiosperms between 5 and 7°C.

In this context, trees do not represent a special case, and the answers may well come from research with cold-adapted lines of *Arabidopsis thaliana*. Among the potential mechanisms, I refer the reader to earlier assessments, particularly to chapter 14 in KÖRNER (2003). From all what we know today, the most likely limitation is associated with the metabolism of growing tissues. There is no evidence that treeline trees are carbon-limited (HOCH a. KÖRNER 2003, 2005), and it rather seems like the carbon charging of trees increases as one approaches their upper distributional limit. There is no plausible reason why above- or below-ground meristems should differ in their thermal requirements, hence it is irrelevant whether the constraints operate primarily via apical meristems of shoots or roots or the cambial meristems. We have shown that a cool root zone alone (ca. 6°C) suffices to cripple trees otherwise experiencing mild above-ground conditions (KÖRNER a. HOCH 2006). Another issue to be resolved is the nature of the thermal limit itself. A mean temperature does not seem to account for the well known non-linearity of metabolic responses to increasing temperature, but still provides the closest proxy in this case. Unpublished experiments with temperatures either steady or oscillat-

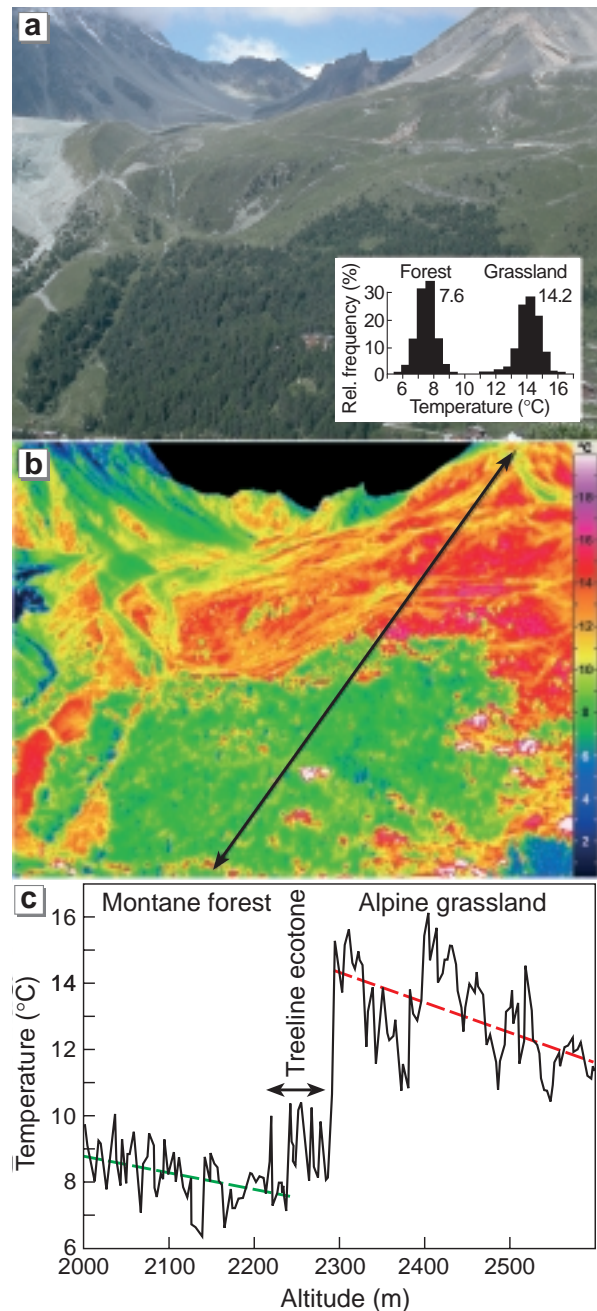


Fig. 7: Land surface (vegetation) temperature across an elevational transect in the Central Alps (near Arolla, Swiss Alps). Note the sharp transition (warming) as one moves from the forest belt into the alpine heathland

Oberflächentemperaturen der Vegetation entlang eines Höhentransektes in den Zentralalpen (nahe Arolla, Schweiz). Man beachte den scharfen Wechsel in der Temperatur (Erwärmung) zwischen Waldgürtel und alpiner Heide

ing around 6 °C seem to support that temperatures in excess of 6 °C do not compensate for periods with temperatures below 6 °C in a more than arithmetic way, for which we have no plausible explanation (G. HOCH, pers. comm.). These thermal thresholds for growth are similar to those observed by other authors for various growth-related phenomena (e.g., HAVRANEK 1972; VAPAAVUORI et al. 1992; ALVAREZ-URIA a. KÖRNER 2007; JAMES et al. 1994).

8 Conclusions

The treeline debate will only make progress if we adopt common criteria and conventions and separate local peculiarities from global patterns. Thermal conditions certainly envelope the potential for tree growth at a narrow range of low threshold temperatures. Whether trees do occur at a given place within this thermal envelope relates to influences which are not generally altitude-specific (see the assessment e.g. by HOLTMEIER 2000, 2003). The relevant temperatures are those during which plants grow and develop, hence annual means, which include the dormant period, seem unsuitable for making any inferences. The causes of the limit of tree taxa of different evolutionary history at similar growing season temperatures appear to lie in their emergent stature (architecture), and there is no reason to assume a physiological inferiority of trees compared to cold-adapted representatives of other life forms. Most likely, the treeline is only a special case of a general limitation of plant growth by low temperatures. The relative abruptness of the life form boundary (PAULSEN et al. 2000) suggests a biological threshold phenomenon which materializes in treeline trees because of their close coupling to atmospheric conditions. The mechanisms responsible for the abrupt decline in tree vigour near the climatic treeline are most likely associated with processes related to tissue formation (meristem activity, cell differentiation), as was already suspected by DÄNIKER (1923). A multitude of other influences may depress forests from their climate-driven uppermost position, but by definition and convention, such depressed forest boundaries do not deserve the term treeline, because such boundaries can occur anywhere. It is of great interest to understand the causes of local/regional forest depressions below the thermal treeline. A consistent treeline theory as proposed here provides the required biogeographic reference. The great advantage of this theory-based treeline definition is that potential treeline position can be predicted with high confidence by a simple mathematical model.

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