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Opinion

Treeline-Quo Vadis? An Ecophysiological Approach

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Abstract: At high elevation or latitude, the margin of the life-form tree is set by low temperature, with trees defined as upright woody species taller than 2–3 m. Globally, the temperature limit of the life-form tree occurs whenever the growing season mean soil temperature declines to 6.7 ± 0.8 °C. Disturbance and human land use, however, can cause trees to be absent from the climatic treeline. After addressing definitions and concepts related to treeline ecophysiology and examining treeline structure and dynamics, the focus will be on future treeline developments with respect to climate, competition and land use change. Finally, changes in economic structure and land use within the treeline ecotone are outlined with respect to net ecosystem production and year-round evapotranspiration.

Keywords: treeline ecotone; ecophysiological-based treeline concept; global change; climate warming; land use change; competition

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Citation: Gruber, A.; Oberhuber, W.; Wieser, G. Treeline-Quo Vadis? An Ecophysiological Approach. *Forests* **2022**, *13*, 857. https://doi.org/10.3390/f13060857

Academic Editors: Jesús Julio Camarero, Yafeng Wang, Jinniu Wang and Yang Yang

Received: 25 April 2022
Accepted: 27 May 2022
Published: 30 May 2022

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1. Introduction

In various parts of the globe trees have limits to their distribution [1–3], which demarcates boundaries and endpoints in adaptation to a changing environment [4]. Alpine and polar treelines represent boundaries for treelife [5], which are set by low temperature at high elevation or high latitude, respectively [5–7]. Margins can also become visible between two biomes (vegetation types) such as the treeline ecotone, which forms a transition zone (interface) between the closed montane forest below and the treeless alpine zone above [5–8].

In the existing literature, however, the term treeline is often used as a synonym for the treeline ecotone [9–12]. From an ecophysiological point of view, such a generalisation is ambiguous and may provoke misinterpretations. Additionally, even the definition of the term treeline varies considerably among studies. While some define the treeline as a line connecting the uppermost trees of a certain size within the treeline ecotone [11–13], others also include the presence of krummholz (distorted and stunted tree specimens) [14]. Thus, it is necessary to distinguish between the general limit of the life-form tree, set by thermal growth constraints, (fundamental niche) and the actual local tree limit set by disturbances (realized niche) [15]. Therefore, in this paper, we first address definitions and concepts related to treeline ecophysiology. Moreover, after focusing on treeline structure, treeline developments with respect to climate, competition and land use change are examined.

2. Alpine Treeline: Definitions and Concepts

The entire transition zone between the uppermost closed montane forests and the treeless alpine zone is termed the treeline ecotone [5,6,16]. Along the altitude up through the treeline ecotone (for definitions see Table 1), there are two other boundaries: the treeline and the tree species limit. The treeline, i.e., the low-temperature range limit of the life-form tree at high elevation or high latitude [15], is defined as the upper limit of upright stemmed trees taller than 2–3 m [5,6,17,18]. Such a tree height ensures that the crowns protrude above the snow cover during the winter and are aerodynamically well coupled to the free atmosphere. This definition of the life form tree excludes seedlings,

distorted dwarfed tree specimen (so-called krummholz) and scrub-like individuals. While the term krummholz designates environmentally dwarfed forms of tree specimens that become upright at favourable sites, the term scrub should only be applied to those treeline specimens whose shrubby form is of genetic origin [5,7,16], for example, *Pinus mugo*. Above the treeline, all these structures experience microclimatic conditions similar to low-stature alpine vegetation such as grassland, meadows and dwarf-shrub communities.

Table 1. Definitions and nomenclature used in discussing the nature of the alpine treeline. Compiled and modified after [4–8,15,17].

Term	Definition
Treeline ecotone	The transition zone between the closed montane forest and the treeless alpine zone
Treeline	The low temperature range limit of the life-form tree at high elevation or high latitude
Life-form tree	Upright stemmed woody plant of at least 2–3 m in height which is well coupled to the atmosphere
Krummholz	environmentally distorted dwarfed forms of tree specimem that become upright at favourable sites
Scrub	treeline specimem whose shrubby form is of genetic origin
Tree species line	The elevational limit of tree species (seedlings, and crippled individuals)
Fundamental niche	The range of environmental conditions where a taxon is able to live, survive and grow. E.g., physiological boundary of the life-form tree
Realized niche	The space where a taxon actually lives set by disturbances, etc. The local limit of the life form, which is always smaller than the corresponding fundamental niche
Limes divergence	A diffuse boundary zone in which one major habitat type changes gradually into another
Limes convergence	A well-defined boundary zone between two fairly uniform major habitat types

With respect to treeline position, at high elevation a differentiation has to be made between the border of the fundamental and the realized niche [15]. The fundamental niche represents the physiological temperature driven distribution boundary of the life-form tree (see below). The realized niche by contrast denotes the local tree limit set by disturbances (biotic interaction, pastoral land use, logging, fire, avalanches, pests, etc.). Consequently, the realized niche is always smaller than the corresponding fundamental niche, which indicates that actual presence of trees is often a poor indicator of the line at which the life form tree reaches its natural low-temperature-driven physiological limit. Realized niche boundaries caused by human disturbances are often termed actual-anthropogenic treelines [19], suggesting that treelines have been depressed [20] by removing trees from their upper distribution limit, although humans cannot affect the low temperature-limit of the life form tree, but they may have removed trees from there [17].

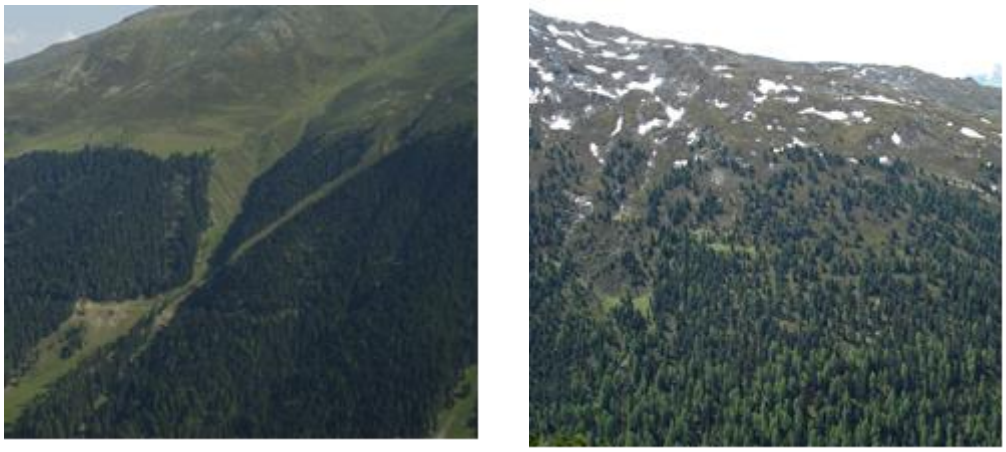
3. Treeline Position

A global survey demonstrated that the altitudinal position of the treeline is closely related to soil and air temperature. A growing season mean soil temperature of 6.7 ± 0.8 °C in 10 cm soil depth and a growing season mean air temperature ranging from 5.5 to 7.0 °C matches the upper elevational limit of the life form tree [17,21,22] and constrains tree growth in temperature limited ecosystems [18,23], respectively. Remarkably, these treeline temperatures match the thermal limit of wood formation [24,25] and are close to the temperature threshold for root growth [6,26–29]. Nevertheless, thermal growth constraints hold for all cold-adapted plants and are not tree specific [30]. Besides a tight coupling of their crowns to the free atmosphere in the harsh alpine climate, tree canopies experience the full strength of the ambient air temperature, when compared to low stature plants nearby. Trees also negatively influence their root zone temperatures by self-shading. Thus, due to an interaction between tree architecture and climate, trees co-determine their distribution limit at high elevation [5–10,15–18].

4. Treeline Structure and Dynamics

The shape of the climate driven low temperature limit of the life-form tree at high elevation (the treeline) can vary [6,7,31] as to whether it is abrupt, when the montane

forest will continue as a closed stand up to the treeline, forming a sharp boundary to the treeless alpine belt (limes convergence), or whether it is diffuse, when the montane forest gradually opens merging with low-stature vegetation up to the tree limit (limes divergence). According to Tranquillini [7] a gradual opening of the forest up to treeline provides more light and warming of the rooting zone by solar radiation, ensuring a greater productivity of isolated trees than in a closed stand, but also more winter damage. Conversely, closed stands generate a more favorable internal climate for tree survival, which considerably contrasts with the climatic conditions in the low stature vegetation nearby. Nevertheless, sharp, (Figure 1a) and diffuse (Figure 1b) treelines represent two stages of the same treeline ecotone [7,17], reflecting natural stand dynamics including regeneration and mortality [32] and past disturbances [19]. Thus, in the course of a few decades, a recent sharp treeline may become fragmented, whereas a previously diffuse treeline may close up to a sharp border line.



(**a**) (**b**)

Figure 1. Sharp (**a**) versus diffuse (**b**) treeline in the Tyrolean Alps at 2100–2200 m a.s.l. The sharp treeline formed by *Pinus cembra* in the Radurschltal shows only little signs of opening towards their upper limit, whereas the diffuse treeline composed of *Pinus cembra* and *Larix decidua* in the Tuxer Alps is gradually opened by avalanches and due to century long pastoral use.

There are also other attempts at classifying treeline types [13,16,33]. These forms include abrupt forest limits due to unstable debris or steep rock walls, anthropogenic forest limits located at the upper rim of steep trough walls and the krummholz belt [10]. These latter treeline structures, however, do not match an ecophysiological-based treeline concept based on the low temperature induced upper limit of the life-form tree [6,7,17,34].

5. Treeline Quo Vadis?

Given that high elevation treeline ecotones are temperature-limited systems [5,6,16], climate warming is likely to stimulate treeline advancements and to generate growth enhancements within the treeline ecotone [13,30,35,36]. A global meta-analysis of treeline responses to climate warming revealed treeline advances in only 52% of the analysed sites [35], suggesting that treelines do not respond similar to climate warming at a global scale. Even so, a shortcoming of the review [35] is that almost all advances do not match an ecophysiological treeline concept, as the authors focused on krummholz, saplings and seedlings rather than the upper margin of the life-form tree set by low temperature (see above). Even so, while sharp treelines showed almost no advances, some diffuse treelines showed advances, which, however, may be related to gap-filling [37,38] due to changes in land-use management and decreasing grazing pressure [34,37].

As shown in a case study, diffuse (open) and sharp (closed) treelines also differ with respect to tree growth (Figure 2). In an open treeline recent climate warming triggered an enhancement in basal area increment of solitary mature *Pinus cembra* L. and *Larix decidua*

Mill. trees. In contrary, in a closed stand nearby, an adequate growth response was almost lacking. This suggests that at treeline, due to competition for light, soil water availability and nutrients [39–42], the positive effect of climate warming on individual tree growth is counteracted by dense canopies.

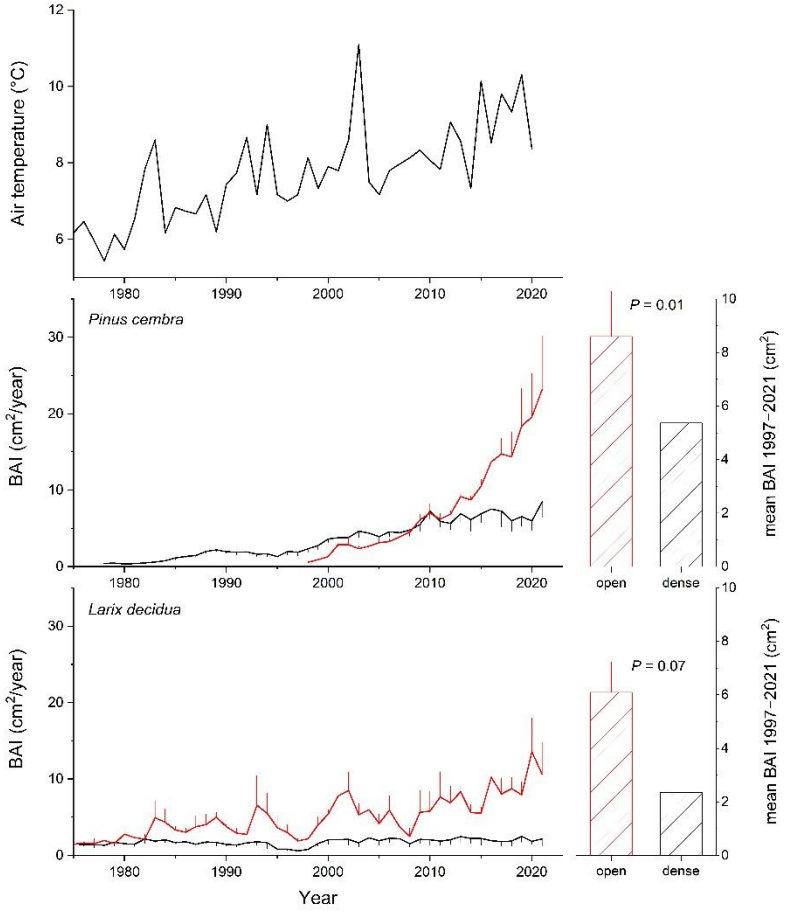


Figure 2. Temporal variation in seasonal mean summer (June–August) air temperature (top) and (left) basal area increment (BAI) and (right) annual mean BAI for the period 1997–2021 of mature *Pinus cembra* (middle) and *Larix decidua* (bottom) trees growing in open (red) and dense (black) stands at treeline on Mt. Patscherkofel, Central Tyrolean Alps (47°12′33″ N; 11°27′40″ E). BAI values estimated according to [41,42] are the mean ± SE of 3 trees. $p < 0.10$ was regarded as significant according to recommendations of [43] for small sample sizes. Authors unpublished observations.

Aside from low temperatures, low nutrient availability [7,44] and competition for nutrients with understory vegetation [45] are also known to restrict tree growth at treeline. At treeline in the Austrian Alps, three years of understory removal significantly increased radial growth of solitary adult *Pinus cembra* trees by 17 ± 4% above the level of control trees [46]. Additionally, there is evidence, that seedling and tree establishment above the current treeline are favoured by the absence of a dense understory vegetation [36,47–51].

Treeline ecotones are also affected by changing land use practices which are likely to surpass potential effects of climate warming. Due to reductions in land management and land abandonment, the N_2-fixing tall shrub green alder (*Alnus alnobetula* (Ehrh.) K. Koch) is currently invading alpine pastures in the Austrian, French, Italian and Swiss Alps [38,52–55]). *Alnus* primarily allocates carbon into root suckers and adventitious shoots and thus is forming extremely dense coppices [55,56]. After *Alnus* has taken over, a dense canopy prevents seedling and tree recruitment across the treeline ecotone [38,56,57].

6. Global Change Perspectives

Besides climate warming, changes in economic structure and land use are, major driving forces for ecosystem functioning and dynamics [58] and influence biogeochemical cycles [59]. For example, within the treeline ecotone of the central European Alps, year-round evapotranspiration and net ecosystem production tend to decline from the uppermost closed forest towards dwarf shrubs and grasslands (Table 2). Water loss of solitary trees within the treeline ecotone matches the values of forests, dwarf shrub communities and grassland ecosystems. The invasion of formerly high elevation pastures by *Alnus alnobetula* enhances water loss through evapotranspiration including interception losses, as compared to grassland communities [54,58]. *Alnus* also increases nitrate leaching [53] and N_2O emissions [56,57].

Table 2. Year-round evapotranspiration (ET) and net ecosystem production (NEP) of various vegetation types within the treeline ecotone of the Central Tyrolean Alps. Compiled after [60–68].

Vegetation	ET (mm y^{-1})	NEP (g C m^{-2} y^{-1})
Uppermost closed forest	480	360
Dwarf shrubs	350	210–250
Grassland and pastures	210–280	60–140
Trees at treeline	278–350	
Krummholz	250	
Alnus alnobetula	300	

In conclusion, as the climate driven limit of the life-form tree at high elevation is set by low temperature, climate warming will cause treelines to move upwards [5,6,30,34]. Nevertheless, treeline advancements will lag considerably behind climate warming, as good seed years may not match with good follow up seedling establishment years [6,34]. Furthermore, strong competition for belowground resources between dense alpine vegetation and trees is decisive for seedling establishment and tree survival at treeline [69]. In conclusion, one has to be aware that treelines might be more susceptible to human impacts such as management practices and land use change than to climate warming [34]. On the other hand, a warming-induced limitation of soil water availability is likely to limit tree growth, suggesting no treeline advance in a warmer world, as shown for the southern Andes [70] and the Tibetan plateau [71]. Nevertheless, it is temperature which sets the definitive biological limit to the life form tree at high elevation [17,34].

Author Contributions: G.W., W.O. and A.G. contributed equally to the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: Open Access Funding by the Austrian Science Fund (FWF), P 34706-B. For the purpose of open access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript version arising from this submission.

Data Availability Statement: The basal area and ring width data presented in this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.6587736 (accessed on 1 April 2022).

Acknowledgments: We would like to thank three anonymous reviewers for their comments on an earlier version of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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