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Direct and indirect effects of environmental limitations on white spruce xylem anatomy at treeline

Timo Pampuch[1], Mario Trouillier[1], Alba Anadon-Rosell[1], Jelena Lange[1,2], and Martin Wilmking[1]
[1]Institute of Botany and Landscape Ecology, University Greifswald, Greifswald, Germany
[2]Department of Physical Geography and Geoecology, Charles University in Prague, Prague, Czechia

Treeline ecosystems are of great scientific interest to study the direct and indirect influence of limiting environmental conditions on tree growth. However, tree growth is complex and multidimensional, and its responses to the environment depend on a large number of abiotic and biotic factors and their interactions.

In this study, we analyze the growth and xylem anatomy of white spruce trees (*Picea glauca* [Moench] Voss) from three treelines in Alaska (one warm and drought-limited, and two cold and temperature-limited treelines). We hypothesized (1) no difference between the treelines regarding the relationship between tree DBH and height, yet in general (2) faster growing trees at the warmer site. Additionally, we expected to find differences in xylem anatomical traits with trees from the drought-limited site having adapted to drought conditions by (3) forming smaller lumen diameter due to water deficit but (4) a higher xylem anatomical density due to higher temperatures and a longer vegetation period.

Regarding growth in height and diameter, trees at the drought-limited treeline grew relatively (1) taller and (2) faster compared to trees at the temperature-limited treelines. Raw xylem anatomical measurements showed (3) smaller lumen diameters and (4) higher density in trees at the drought-limited treeline. However, using linear mixed-effect models, we found that (i) traits related to water transport like lumen diameter were not significantly correlated with the actual amount of precipitation during the vegetation period but with tree height. We also found that (ii) traits related to mechanical support like density were mainly positively influenced by the mean temperature during the vegetation period.

The differences in lumen diameter found in the raw data can be explained by differences in the growth rates of the trees, since lumen diameter at the lower part of the tree stem needs to increase over time with increasing tree height. The greater wood density at the drought-limited treeline is probably caused by the higher temperature that leads to more biomass production, and potentially longer vegetation periods.

Our study shows that xylem anatomical traits in white spruce can be directly and indirectly controlled by environmental conditions. While lumen diameter is not directly influenced by environmental conditions but indirectly through tree height, other traits like anatomical density

show a direct correlation with environmental conditions. Our results highlight the importance of approaching tree growth in a multidimensional way and considering direct and indirect effects of environmental forcing.