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Low temperature limits cambial activity and determines secondary growth at the alpine treeline

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Temperature is the driving factor behind the formation of natural high elevation treelines, directly affecting xylogenesis. The low temperature limitation of meristematic processes is thus key to understand treeline formation. Here, we studied xylogenesis in Pinus uncinata during the growing season by sequential microcoring at the Swiss treeline. To assess temperature sensitivity of xylogenesis in situ, we applied controlled Peltier-mediated cooling and warming ($\pm$3 K relative to ambient temperatures) to branch segments in P. uncinata, commencing 12 days after snowmelt. Surprisingly, xylogenesis in aboveground tissues started one week before snowmelt, and the cambial zone was fully developed by the time the cooling and warming treatment started. Although not significantly, experimental cooling of branches reduced the number of cells produced per season, likely due to the slower rate of cell production in the cambial zone during the short remaining period of cambial activity, whereas warming extended the production of earlywood into the late season. We conclude that temperatures early in the season determine the width of the cambial zone and thereby strongly control the number of tracheids produced during the forthcoming season. Temperatures later in the season largely determine the earlywood-latewood ratio, rather than affecting the number of tracheids produced per season. These data provide an empirical basis for the mechanistic understanding of tree growth at treeline in response to temperature.