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interaction between plants and pathogens. It connects the dynamics of the processes mediating the assembly of soil and plant-associated microbiomes (the causes, i.e., microbiome make-up) and how changes on these processes and in the local environment ultimately affect the dynamics of disease outcome (the consequences, i.e., microbiome functioning).

Acknowledgments

I thank M.J.L. Brossi, R. Masteling, and F.D. Andreote for their critical reading of the manuscript. I also thank the three anonymous reviewers for their careful review and constructive suggestions.

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https://doi.org/10.1016/j.tplants.2020.01.007

References

1. Yang, J. *et al.* (2009) Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci.* 14, 1–4
2. Pineda, A. *et al.* (2010) Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends Plant Sci.* 15, 507–514
3. Atkinson, G.F. (1892) *Some Diseases of Cotton*. Agricultural Experiment Station of the Agricultural and Mechanical College, Auburn, Alabama, Bulletin, No. 41
4. Henry, A. (1931) The natural microflora of the soil in relation to the foot-rot problem of wheat. *Can. J. Res.* 4, 69–77
5. Mazzola, M. (2002) Mechanisms of natural soil suppressiveness to soilborne diseases. *Antonie Van Leeuwenhoek* 81, 557–564
6. Kloepper, J.W. *et al.* (1980) *Pseudomonas* siderophores: a mechanism explaining disease-suppressive soils. *Curr. Microbiol.* 4, 317–320
7. Expósito, R.G. *et al.* (2017) Current insights into the role of rhizosphere bacteria in disease suppressive soils. *Front. Microbiol.* 8, 2529
8. Van Elsas, J.D. *et al.* (2012) Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proc. Natl. Acad. Sci. U. S. A.* 109, 1159–1164
9. Mallon, C.A. *et al.* (2018) The impact of failure: unsuccessful bacterial invasions steer the soil microbial community away from the invader's niche. *ISME J.* 12, 728–741
10. Rillig, M.C. *et al.* (2015) Interchange of entire communities: microbial community coalescence. *Trends Ecol. Evol.* 30, 470–476
11. Carrión, V.J. *et al.* (2019) Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome. *Science* 366, 606–612
12. Grainger, T.N. *et al.* (2019) Applying modern coexistence theory to priority effects. *Proc. Natl. Acad. Sci. U. S. A.* 116, 6205–6210

Forum

New Evidence of Thermally Constrained Plant Cell Wall Lignification

Alan Crivellaro[1,*] and Ulf Büntgen[1,2,3,4]

Lignin enhances the mechanical strength of plants and enables their intrinsic water transport. Dendrochronological, wood anatomical, and plant physiological evidence now suggests that the degree of lignin deposition is constrained by low temperature. Placing these findings in an ecological context implies rethinking of the global treeline position.

More than 200 years ago, Alexander von Humboldt provided the first global argument for a thermal threshold of the altitudinal and latitudinal limits of upright tree growth [1] (Figure 1A). Although it has been suggested that cell wall lignification might be a factor in determining the global treeline position [2] (Figure 1B), a firm explanation of how low temperatures mechanically, physiologically, and/or chemically limit the upright growth of trees is still missing.

The Role of Cell Wall Lignification

Unlike other components of secondary cell walls that are polysaccharide in nature (holocellulose), lignin is a heteropolymer derived from amino acids [3]. Being hydrophobic, lignin constrains the hydration of cellulose, which is stronger under dry than wet conditions. The strengthening role of lignin is essential for most plant lifeforms, as it enables individuals to cope with mechanical stress and to undertake root-to-leaf water transport. Water-conducting cells require waterproofed and rigid walls to facilitate water uplift and to resist strong negative pressure in their conduits. In response to the mechanical demands associated with their sheer body size, self-supporting plants rely on lignin to stand upright and manage static and dynamic stressors. Lignin deposition is the final step of plant cell wall biosynthesis [3], which establishes functionally mature cells before their genetically programmed death. While the study of lignin has a long tradition in papermaking and related industrial processes, its consideration and interpretation in plant ecology and biomechanics remain marginal.

To better understand the formation of wood tissues at the cold limit of plant growth, a recent paper by Körner *et al.* [4] describes the phenology and physiology of the snowbell, *Soldanella pusilla* (Primulaceae), at around 2450 m a.s.l. (meters above sea level) in the central Swiss Alps. *Soldanella* is a snowbed-adapted clonal herb that enters winter conditions without visible aboveground flowering shoots. This fascinating study shows that flower-bearing shoots can grow horizontally in the transition zone between soil and snow, even when temperatures during an extended cold season are persistently around 0°C. Such extremes slow substantially but do not stop entirely the structural investment in new cells that are responsible for the elongation of flowering shoots. At this stage in life, the almost nonlignified cell walls of *Soldanella* lack the important polymerized hardening structure needed to grow upright (Figure 1C). However, once their flower stalk is exposed to warmer temperatures after snowmelt, the thermally induced process of cell wall lignification rapidly starts. Only at this point can the flowers of *Soldanella* stand upright 60 mm above the ground.

The Ecological Relevance of Cell Wall Lignification

Although not explicitly mentioned, Körner *et al.* [4] provide important

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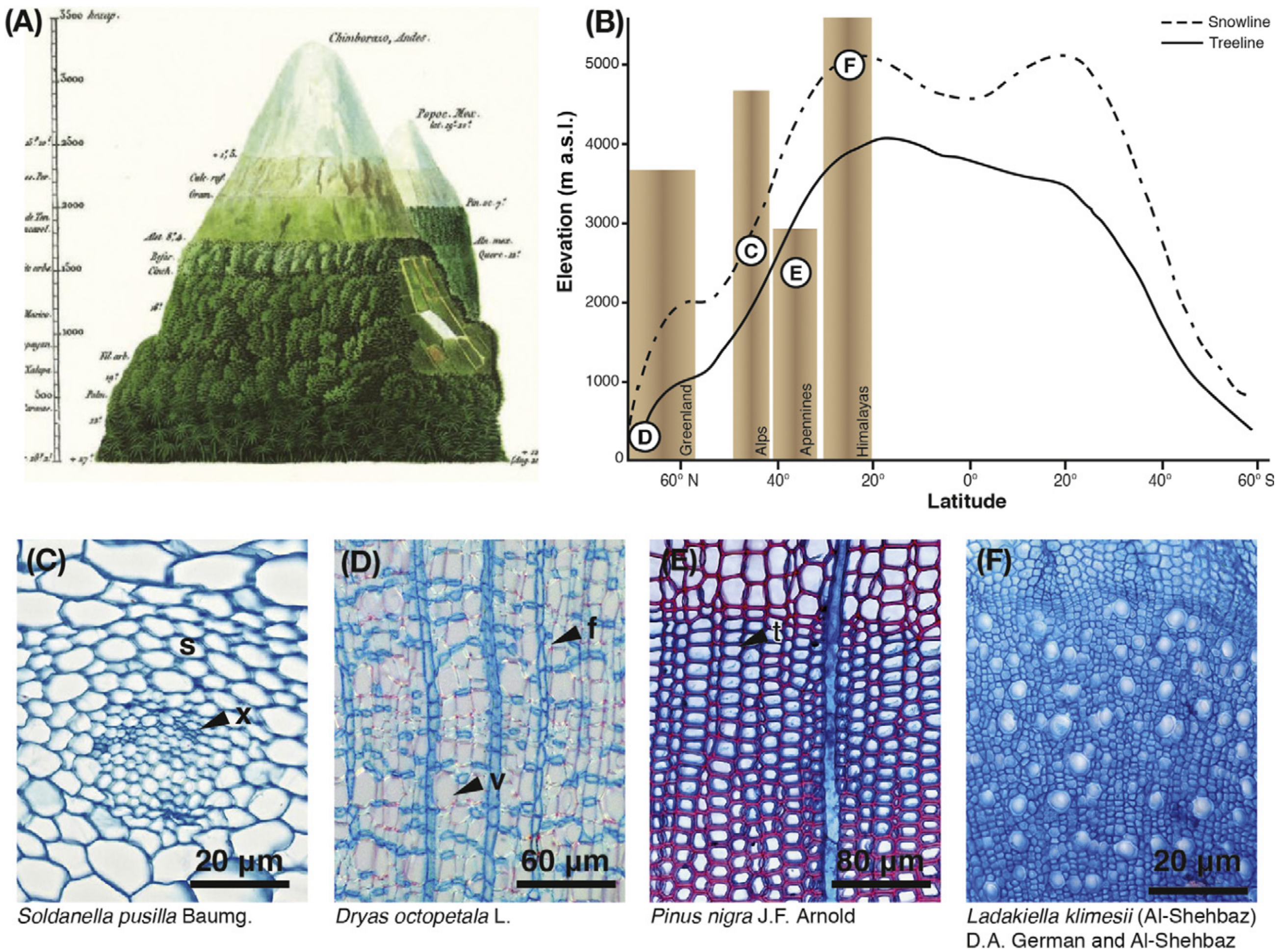

Figure 1. The Thermal Limit of Cell Wall Lignification. (A) Humboldt's illustration of Chimborazo volcano with vegetation belts driven by decreasing temperatures with increasing elevation [1]. (B) Snowline and treeline elevation changes from the Northern to the Southern Hemisphere [2]. (C) Double-stained thin section of *Soldanella pusilla* Baumg. (Primulaceae) flower stalk freshly excavated from snow in late spring shows almost no lignin (blue-stained cell walls) in sclerenchyma (s) and xylem vessels (x) [4]. (D) Double-stained thin section of *Dryas octopetala* L. (Rosaceae) stem wood from eastern Greenland reveals almost completely nonlignified (only slightly red) xylem vessels (v) and fibers (f). (E) *Pinus nigra* J.F. Arnold (Pinaceae) wood thin section from >1800 m a.s.l. (meters above sea level) in the central Italian Apennines. The so-called 'Blue Ring' refers to a lack of lignin in latewood cell walls (t) in 2009, when severe atmospheric cooling lasted for a few days at the end of the growing season [9]. (F) Stem section of *Ladakiella klimesii* (Al-Shehbaz) D.A. German and Al-Shehbaz (Brassicaceae) from 6200 m a.s.l. in the Himalayan Ladakh shows an almost completely nonlignified xylem (blue).

insights into the plant physiological limits of the development and lignification of cell walls at the cold distribution limit. Acknowledging the biological value of their work, which certainly opens a window towards understanding the low-temperature limits of plant growth in general, we argue for a stronger emphasis on the ecological relevance of cell wall lignification in a wide range of species and at larger spatial scales. Nevertheless, we agree that the short stature of most alpine and arctic plants creates advantages (i.e., a warmer microclimate). This lifeform strategy underpins the 'small by design' concept stating that small plants 'engineer' their microclimate by adopting a short stature to enhance heat accumulation near the ground during extremely short growing seasons [5]. A thermal limitation of cell wall lignification, however, ultimately hinders alpine and arctic plants in growing tall. This concept of 'small by constraint' relates to the fact that low temperatures prevent the lignification of any newly formed cell wall. The resulting short stature of plants in extremely cold environments not only prevents them from size-dependent mechanical and hydraulic stresses, but also facilitates their decoupling from ambient temperatures in favor of warmer growing conditions. Although it might be argued that small plants in cold environments do not require lignified stems due to their short stature, many short plants in warm climates are rich in lignin [6].

Suggesting a thermal limit for cell wall lignification, the recent findings are in line with previous evidence from experimental and observational studies. Trees growing under controlled soil temperatures below 7°C exhibit low mechanical strength due to the failure of cell wall lignification [7]. Stem thin sections from *Dryas octopetala* L. that grew at 70° N in coastal east Greenland lack lignification in the cell walls of their vessels and fibers [8] (Figure 1D). Furthermore, so-called 'Blue Rings' in trees at the species-specific cold distribution limits often coincide with abrupt cooling after large volcanic eruptions (unpublished), when cell wall lignification does not occur to its full extent [9] (Figure 1E). Reduced cell wall lignification has further been reported in plants at 6200 m a.s.l. in the Himalayan Ladakh [10] (Figure 1F). Bolstered by these findings, we disagree with Körner *et al.* [4] that slow metabolism restricts the growth, development, and reproduction of plants and thus weakens their long-term fitness, a statement contrary to the 'grow fast–die young' theory [11]. In fact, lacking cell wall lignification does not relate to slow metabolism but rather reflects plant growth under cold extremes.

The Importance of Interdisciplinary Research

Despite recent advances in lignin-related research in molecular genetics, biochemistry, bioenergy, and genomics, it remains unclear when, if at all, the enzyme-mediated lignification phase exactly ends [3]. Moreover, the ecological importance of lignin's intricacies of genetic and metabolic control is still underestimated. Future research at the interface of wood anatomy, plant physiology, macroecology, and biochemistry should link experimental observations at the cell level with biogeographic patterns at the global scale. We therefore call for new research to gain mechanistic understanding of how and why low temperatures determine the global treeline. Future work should also provide a biological and/or physiological explanation for the spatial distribution limit of plants towards colder (micro)climates. A more detailed anatomical assessment of wood formation under cold conditions could help understanding of the role of temperature in cell wall lignification [12]. Nevertheless, we anticipate exploration beyond the treeline paradigm and even investigations beyond the tree lifeform to unravel the dominant factors and processes of plant adaptation to cold temperatures. In our view, the global treeline represents a sharp isotherm where the mechanical and hydraulic properties of wood cell walls rapidly change. While poorly lignified trees do not exist because they could not stand, lifeforms including an overarching trend with lower lignification rates towards colder climates should indicate a general pattern. While (and contrary to [4]) polarized light microscopy does not visualize lignin, it reveals whether cellulose is in a crystalline form. Safranin and astrablue staining of anatomical stem thin sections, however, allows the quantification of more or less lignin content [13]. Plant stem anatomical analyses across the largest trees and smallest herbs [14,15] may help to elucidate the evolutionary and environmental drivers of the biosynthesis and lignin deposition of cell wall components in different cell functional types, within and between species.

Acknowledgments

Alma Piermattei and Christian Körner stimulated discussion and Fritz H. Schweingruber kindly provided the anatomical image of *Ladakiella klimesii* obtained from a thin section of a plant collected by Jiri Dolezal. Two anonymous referees kindly commented on a previous version of the manuscript. U.B. received funding from the SustES Project (CZ.02.1.01/0.0/0.0/16_019/0000797).

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https://doi.org/10.1016/j.tplants.2020.01.011

References

1. von Humboldt, A. and Bonpland, A. (1807) *Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer: Auf Beobachtungen und Messungen Gegründet, welche vom 10ten Grade Nördlicher bis zum 10ten Grade Südlicher Breite, in den Jahren 1799, 1800, 1801, 1802 und 1803 Angestellt Worden Sind*, Bey F.G. Cotta (in German)
2. Körner, C. (2012) *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*, Springer
3. Meents, M.J. *et al.* (2018) The cell biology of secondary cell wall biosynthesis. *Ann. Bot.* 121, 1107–1125
4. Körner, C. *et al.* (2019) Life at 0°C: the biology of the alpine snowbed plant *Soldanella pusilla*. *Alp. Bot.* 129, 63–80
5. Körner, C. (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*, Springer
6. Schweingruber, F.H. *et al.* (2011) *Atlas of Stem Anatomy in Herbs, Shrubs and Trees*, Vol. 1. Springer
7. Schenker, G. *et al.* (2014) Physiological minimum temperatures for root growth in seven common European broad-leaved tree species. *Tree Physiol.* 34, 302–313
8. Büntgen, U. *et al.* (2015) Temperature-induced recruitment pulses of arctic dwarf shrub communities. *J. Ecol.* 103, 489–501
9. Piermattei, A. *et al.* (2015) The "Blue Ring": anatomy and formation hypothesis of a new tree-ring anomaly in conifers. *Trees Struct. Funct.* 29, 613–620
10. Dolezal, J. *et al.* (2018) *Anatomy, Age and Ecology of High Mountain Plants in Ladakh, the Western Himalaya*, Springer
11. Büntgen, U. *et al.* (2019) Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. *Nat. Commun.* 15, 2171
12. Donaldson, L.A. (1991) Seasonal changes in lignin distribution during tracheid development in *Pinus radiata* D. Don. *Wood Sci. Technol.* 25, 15–24
13. Baldacci-Cresp, F. *et al.* (2020) A rapid and quantitative safranin-based fluorescent microscopy method to evaluate cell wall lignification. *Plant J.* Published online January 9, 2020. https://doi.org/10.1111/tpj.14675
14. Büntgen, U. *et al.* (2014) Introducing wood anatomical and dendrochronological aspects of herbaceous plants: applications of the Xylem Database to vegetation science. *J. Veg. Sci.* 25, 967–977
15. Crivellaro, A. and Schweingruber, F.H. (2015) *Stem Anatomical Features of Dicotyledons. Xylem, Phloem, Cortex and Periderm Characteristics for Ecological and Taxonomical Analyses*, Kessel