

Maximum height in a conifer is associated with conflicting requirements for xylem design

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Despite renewed interest in the nature of limitations on maximum tree height, the mechanisms governing ultimate and species-specific height limits are not yet understood, but they likely involve water transport dynamics. Tall trees experience increased risk of xylem embolism from air-seeding because tension in their water column increases with height because of path-length resistance and gravity. We used morphological measurements to estimate the hydraulic properties of the bordered pits between tracheids in Douglas-fir trees along a height gradient of 85 m. With increasing height, the xylem structural modifications that satisfied hydraulic requirements for avoidance of runaway embolism imposed increasing constraints on water transport efficiency. In the branches and trunks, the pit aperture diameter of tracheids decreases steadily with height, whereas torus diameter remains relatively constant. The resulting increase in the ratio of torus to pit aperture diameter allows the pits to withstand higher tensions before air-seeding but at the cost of reduced pit aperture conductance. Extrapolations of vertical trends for trunks and branches show that water transport across pits will approach zero at a heights of 109 m and 138 m, respectively, which is consistent with historic height records of 100–127 m for this species. Likewise, the twig water potential corresponding to the threshold for runaway embolism would be attained at a height of ≈ 107 m. Our results suggest that the maximum height of Douglas-fir trees may be limited in part by the conflicting requirements for water transport and water column safety.

air-seeding pressure | bordered pit | embolism | hydraulic architecture | *Pseudotsuga menziesii*

Recent research on determinants of maximum tree height has focused on indirect impacts of the hydrostatic (hydraulic and gravitational) limitations associated with the increased tension in the water column from soil to upper leaves on photosynthesis and growth (1–4). Here, we explore an additional hypothesis: that, as an adaptive response to the higher xylem tension in the tops of tall trees, their xylem shows structural modifications that decrease the risk of embolism but also decrease the efficiency of water transport. As tree height increases, the structural modifications needed to satisfy safety requirements eventually will reduce water transport virtually to zero. Resistance to transpiration-induced flow of water through the xylem creates a gradient of steadily increasing tension (also referred to as negative pressure) between the roots and the uppermost leaves. Gravity acting on the vertical water columns in the xylem imposes an additional 0.01 MPa increase in tension per meter increase in height. Because the water is transported under tension, the system is highly susceptible to the entry of gas bubbles, which breaks the cohesion of the water column. These air-seeded emboli can disable parts or all of the conducting system (5, 6). Xylem structural features that increase the resistance to embolism typically decrease the hydraulic conductivity (7, 8), and it has been documented that specific conductivity decreases with height in Douglas-fir (9). Thus, as tension in their xylem in-

creases with height, trees must strike a balance between limiting the risk of embolism and maintaining adequate capacity for water transport to the leaves. This tradeoff of xylem safety against efficiency may impose structural limits on tree height concomitant with reduced capacity of processes, such as photosynthesis and growth, to adjust to vertical gradients of increasing xylem tension (9, 10).

Douglas-fir tracheids are elongate dead cells ≈ 1 –4 mm long and 10–55 μm in diameter. The shared double cell walls of adjacent tracheids are traversed with bordered pits through which water moves along the pressure gradient [supporting information (SI) Fig. S1]. Because all of the water that ascends within conifer xylem must pass through the bordered pits of overlapping tracheids, pit characteristics are a major determinant of tracheid and whole xylem hydraulic conductance (11–13) and account for $>50\%$ of total xylem hydraulic resistance across a broad range of tracheid- and vessel-bearing species (14). The pit membrane of Douglas-fir and most other conifers is chemically and structurally unlike membranes in living cells: It contains the torus (a central impermeable thickening) surrounded by a thinner and porous margo that is mostly composed of encrusted cellulosic strands (Fig. S1A and B). The membrane can be deflected within the pit chamber to serve as a valve. At full deflection, the torus blocks the aperture (called pit aspiration), preventing the flow of water or gas between cells. Thus, the intertracheid spread of embolism via air-seeding is prevented if the pressure difference between an embolized tracheid (near atmospheric pressure) and an adjacent water-filled tracheid (at a negative pressure) is sufficient to cause the margo to stretch and displace, allowing the torus to seal the pit aperture (Fig. S1A).

The structure of the pit complex (the border plus the membrane, hereafter referred to as the pit) thus plays a key role in determining the balance between the hydraulic safety and efficiency of tracheids (9, 14). In the tallest conifers, as xylem tracheids become increasingly resistant to embolism, at some point they may become nearly nonconductive (9), which would increase the axial tension gradient, potentially leading to a cycle of increasing embolism resistance and diminishing conductivity. Tracheid length and diameter are quite variable in a tree, with smaller cell sizes at the tip and in branches than at the tree's base (15). Pits usually occupy much of the face of a tracheid, and they, too, are quite variable in size throughout the tree (9).

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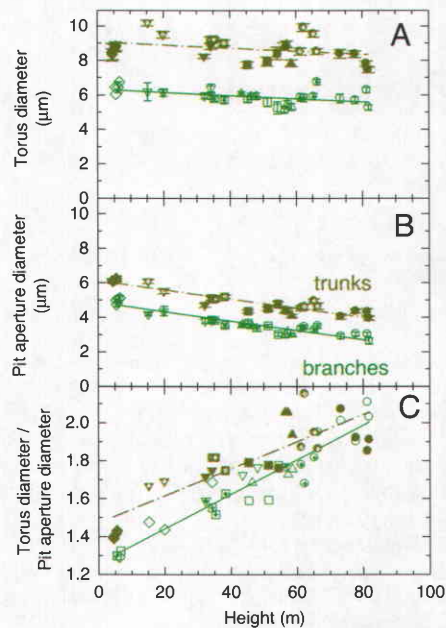


Fig. 1. Pit anatomical characteristics of tracheids as a function of height in branches and trunks. (A) Torus diameter with height in branches ($r^2 = 0.25$, $P = 0.01$) and trunks ($r^2 = 0.11$, $P = 0.10$). Values are means \pm SE. (B) Pit aperture diameter with height in branches ($r^2 = 0.87$, $P < 0.001$) and trunks ($r^2 = 0.84$, $P < 0.001$). (C) The ratio of torus to pit aperture diameter with height in branches ($r^2 = 0.91$, $P < 0.001$) and trunks ($r^2 = 0.72$, $P < 0.01$). Samples were obtained at five sites in Oregon and Washington from Douglas-fir trees ranging in height from 6 to 85.5 m. Each symbol shape represents a different site. Green open symbols and open-dotted symbols represent branches sampled at the tops of the trees and at the base of the live crown, respectively. Brown filled symbols and filled-dotted symbols represent trunks sampled at the top of the trees and at the base of the live crown, respectively.

The conifer Douglas-fir (*Pseudotsuga menziesii*) is well suited for this study, because it is one of the world's tallest tree species. The tallest living Douglas-fir tree today, in Coos County, Oregon, is reported as 100 m (16), but the historical record shows 12 Douglas-fir trees taller than 100 m, ranging up to 127 m (17). For comparison, the tallest historically reported redwood tree (*Sequoia sempervirens*) is 15 m shorter, at 112 m (16). We studied structural and functional features of bordered pits from trunk and branch wood of live Douglas-fir trees ranging in height from 6 to 85.5 m (Table S1) to determine whether the vertical trends in xylem hydraulic efficiency and safety are consistent with the reported range of maximum height for this species.

Results and Discussion

We found that pit torus diameter was relatively unchanged with height in either branches or trunks (Fig. 1A) but that pit aperture diameter decreased significantly with increasing height in both branches and trunks (Fig. 1B). As a consequence, there was a highly significant increase in the ratio of torus to pit aperture diameter with increasing height in both branch and trunk tracheids (Fig. 1C). Pit apertures were smaller in tracheids from branches than trunks, consistent with branches' narrower tracheids (15, 18).

The ratio of torus to pit aperture diameter is a measure of the torus overlap at the moment of pit aspiration. After aspiration, as the pressure difference (ΔP) between a gas-filled (embolized) tracheid and a water-filled (transporting) tracheid increases, the margo continues to stretch. At the point of air-seeding of an individual tracheid, the torus has been pulled far enough through the pit aperture to expose margo pores near the torus edge.

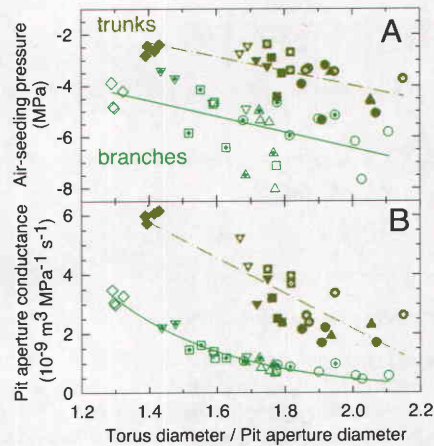


Fig. 2. Xylem safety and efficiency vs. the pit torus diameter/aperture diameter. (A) Modeled air-seeding pressure vs. torus diameter/aperture diameter in branches ($r^2 = 0.33$, $P = 0.02$) and trunks ($r^2 = 0.49$, $P < 0.01$). (B) Modeled pit aperture conductance vs. torus diameter/aperture diameter in branches ($r^2 = 0.95$, $P < 0.001$) and trunks ($r^2 = 0.76$, $P < 0.001$). Symbols are as in Fig. 1.

Predictions of models based on mechanical and morphological properties of pits and membranes are consistent with empirical studies to show that air can then be pulled through the pores into the tracheid if the ΔP is sufficient (9, 12, 19). The air-seeding pressure of an entire sample, defined as the pressure at which 50% of the maximum conductance of the xylem has been lost, is calculated by using assumptions of mechanical properties of the membrane and morphological measurements of pit and membrane characteristics (see *Materials and Methods*).

Where there is a larger overlap between the torus and aperture, the pit complex can sustain a greater ΔP before air-seeding (Fig. 2A). This greater resistance to embolism, however, occurs at the expense of a sharp decline in hydraulic efficiency (Fig. 2B), which is driven by the decrease in pit aperture diameter with height (Fig. 1B).

Air seeding pressures became substantially more negative with increasing height in both branches and trunks (Fig. 3A). The morphology of pits thus changes with height in a manner that mitigates the increased risk of embolism at height. However, the vertical increase in the hydraulic safety of Douglas-fir xylem is attained at a substantial cost in terms of water transport efficiency. The steep decline in pit aperture diameter with increasing height (Fig. 1B) caused pit aperture conductance, estimated from morphological measurements, to drop by a factor of approximately three over a height gradient of nearly 80 m (Fig. 3B). Functionally, Fig. 3B shows that the driving force necessary for moving a given amount of water through the stem is greatly increased at height because of the lower conductance there. Whole-wood xylem conductivity (conductance normalized by sample area and length) also declines with height in Douglas-fir (9, 24). Hydraulic conductivity of conifer wood is a function of both the tracheid lumen conductance and pit conductance (Fig. S2), with the latter factor as the main determinant of whole-wood xylem conductivity in conifers (20–23). Pit conductance is controlled more by aperture conductance than by membrane conductance (9, 12, 20). The pit aperture in roots, trunks, and branches of old and young Douglas-fir trees was reported to contribute $\approx 80\%$ of the total pit resistance along a height gradient of 42 m (9), which translates to the aperture having $\approx 25\%$ of the conductance of the membrane. As pit aperture conductance approaches zero, it sets an ultimate limit on xylem

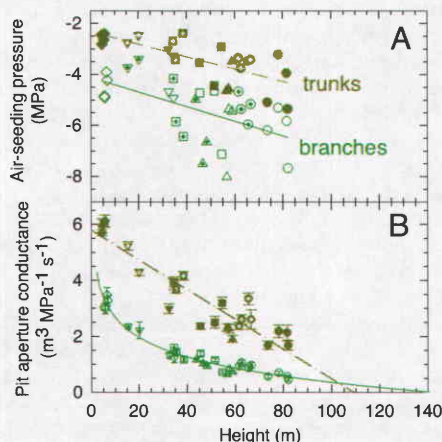


Fig. 3. Trends in xylem safety and efficiency with height and method of estimating maximum tree height from trends in pit aperture conductance with height. (A) Modeled air-seeding pressure vs. height in branches ($r^2 = 0.32$, $P = 0.02$) and trunks ($r^2 = 0.53$, $P < 0.01$). (B) Modeled pit aperture conductance vs. height in branches ($r^2 = 0.96$, $P < 0.001$) and trunks ($r^2 = 0.85$, $P < 0.01$). Values are means \pm SE. Extrapolations of the regressions were used to estimate the height at which pit aperture conductance declines to zero. This estimated height, at which xylem water transport approaches zero, was 138 m (\pm 7 m) in branches and 109 m (99–123 m) in trunks. Symbols are as in Fig. 1.

water transport even if other tracheid anatomical features such as the lumen and pit membrane pores remain conductive.

Vertical trends of different morphological traits have been used to estimate the maximum height to which trees can grow (1, 10). These extrapolations provide estimates that can be compared with observations to infer whether the trends within the data range persist beyond it. Using this approach, we made extrapolations of regressions fitted to the relationships between pit aperture conductance and height to predict the height at which pit aperture conductance would approach zero. This height was 138 m (131–145 m; 95% confidence interval) and 109 m (99–123 m; 95% confidence interval) in branches and trunks, respectively (Fig. 3B). This calculated range of maximum height for Douglas-fir, predicted on the basis of vertical trends in pit aperture conductance, is consistent with the historic record height range of 100–127 m (16, 17). All of these height estimates (including the historic ones) are approximations only and include a number of errors, and so it is remarkable the degree to which they are consistent. It should be noted, however, that most Douglas-fir trees are shorter than the theoretical maximum allowed by water transport tradeoffs because of various abiotic and biotic factors, including drought, fertility, wind, fire, insects, and pathogens that limit growth potential and induce mortality before trees reach their theoretical maximum height (25, 26).

The stronger correlations in branches than in trunks in Fig. 3B are not unexpected. The trunk is the superhighway through which the water moves, but the branches make up the distribution network and typically show more pronounced transpiration-induced fluctuations in xylem tension (5). Transient release of stored water into the transpiration stream resulting from hydraulic capacitance of sapwood is likely to exert a greater damping effect on fluctuations in xylem tension in massive trunks than in more slender branches (27–29). In addition, lower xylem specific conductivity in branches than trunks (9, 15) contributes to steeper axial tension gradients in branches.

When data from all sampling heights were combined, xylem efficiency (shown by pit aperture conductance) decreased exponentially with increasing xylem safety (shown by air-seeding pressure) (Fig. 4). The tradeoff of xylem safety against efficiency was controlled in a similar fashion in both branches and trunks,

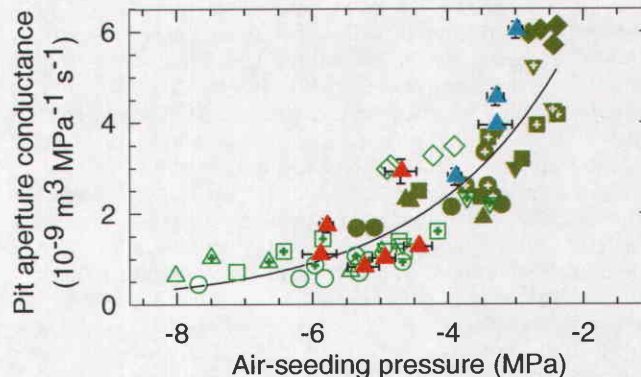


Fig. 4. Tradeoff of xylem efficiency vs. safety represented by an exponential decrease ($r^2 = 0.76$, $P = 0.02$) in modeled pit aperture conductance with increasingly negative air-seeding pressure. Green and brown symbols represent data shown in Figs. 2 and 3. Red (branch) and blue (trunk) triangles represent measured air seeding pressures obtained from vulnerability to embolism curves and calculated aperture conductances. Branch samples were collected at 6- to 56-m heights, and trunk samples were collected at 6- to 42-m heights from various locations in Oregon and Washington. Values are means \pm SE.

with branches yielding the most negative air-seeding pressures and lowest pit aperture conductances. Air-seeding pressures determined directly from xylem vulnerability curves (red and blue triangles) were consistent with those calculated on the basis of pit characteristics (green and brown symbols, Fig. 4). The samples represented by the red and blue triangles also showed a tradeoff between a different measure of xylem efficiency, whole-wood specific conductivity, and xylem safety (Fig. S2).

The air-seeding pressure is widely used as an index of xylem vulnerability to embolism (27, 32). Air-seeding pressure for branches at 56 and 34 m was -4.9 and -4.5 MPa, respectively (Fig. 5). However, vulnerability curves from which air-seeding pressures are determined are sigmoidal, and it may be more biologically relevant to consider the embolism threshold (the point at which the slope of the curve begins to increase rapidly), taken as the x -intercept of a line tangential to the midpoint of the curve. For branches at 56 and 34 m, this threshold was -3.2 and

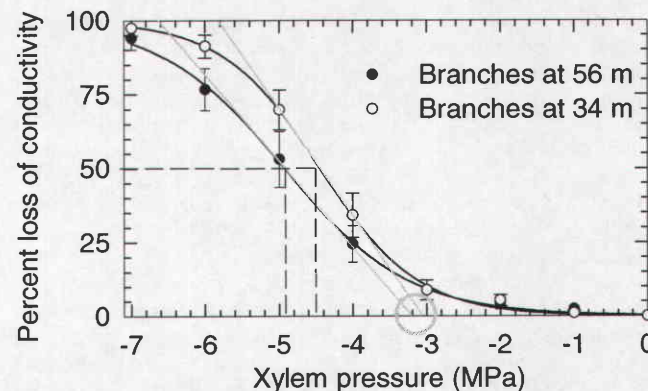


Fig. 5. Vulnerability to embolism curves for xylem of Douglas-fir branches sampled at 56- and 34-m heights. The percentage loss of hydraulic conductivity follows a sigmoidal trajectory as xylem pressure becomes increasingly negative. The gray lines represent the slope tangential to the air-seeding pressure, which is the pressure at which samples have lost 50% conductivity. The x -intercepts of the tangents (-3.2 and -3.1 MPa for branches at 56- and 34-m heights, respectively) are estimates of the threshold xylem pressure at which embolism-induced loss of conductivity begins to increase rapidly. Values are means \pm SE.