

# 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  $\approx 107$  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  $\approx 1$ –4 mm long and 10–55  $\mu\text{m}$  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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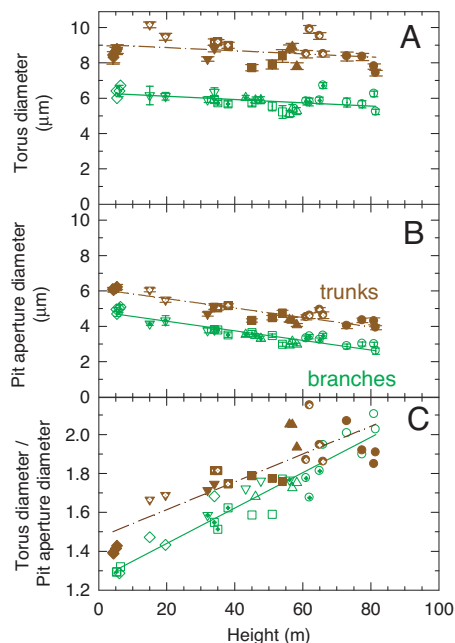
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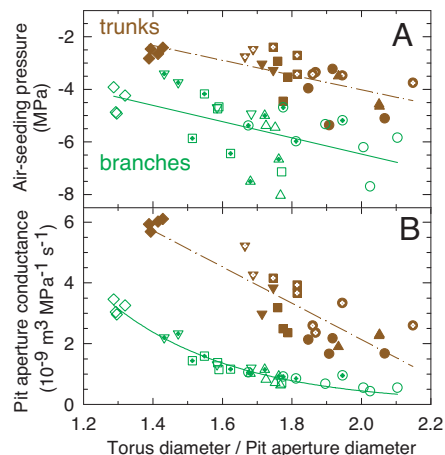
**Fig. 1.** Pit anatomical characteristics of tracheids as a function of height in branches and trunks. (A) Torus diameter with height in branches ( $r^2 = 0.25$ ,  $P = 0.01$ ) and trunks ( $r^2 = 0.11$ ,  $P = 0.10$ ). Values are means  $\pm$  SE. (B) Pit aperture diameter with height in branches ( $r^2 = 0.87$ ,  $P < 0.001$ ) 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 ( $\Delta P$ ) 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  $\Delta P$  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  $\Delta P$  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  $\approx 25\%$  the conductance of the membrane. As pit aperture conductance approaches zero, it sets an ultimate limit on xylem



−3.1 MPa, respectively (Fig. 5), and consistent with the embolism threshold observed for Douglas-fir seedlings in an earlier study (27). Thus, the height-related trend in the air-seeding pressure of branches was markedly steeper than that of the embolism threshold. The tracheids that begin to embolize at this threshold are likely to be among the largest and first formed in the earlywood, so stem sections having earlywood tracheids of similar size would likely have similar embolism thresholds. However, if properties such as pit membrane flexibility, cell wall fraction represented by pits, or pit chamber depth of the subsequently produced tracheids vary among samples, then their vulnerability curves could have different shapes (9) but similar embolism thresholds.

We used field observations of daily minimum twig water potential during the dry season to assess the extent to which modeled and measured trends in xylem safety and efficiency may impose constraints on water transport in intact trees. Douglas-fir is a largely isohydric species in that although twig water potential decreases linearly with increasing height (Fig. S3), daily minimum twig water potential at a given height tends to remain constant throughout the dry season, giving rise to a strongly conserved relationship between water potential and height across different years and sites (2, 30, 31) and resulting in shorter trees in drier sites. The height-related trend in the air-seeding pressure was approximately three times steeper than the vertical trend in daily minimum twig water potential (compare Fig. 3A with Fig. S3). Although the ultimate hydraulic safety margin in branches, measured as the difference between daily minimum twig water potential and the air-seeding pressure, increases with height, the relevant physiological safety margin appears to diminish with height as twig water potential approaches the embolism threshold of approximately −3.2 MPa at 110 m (96 to 134 m, 95% confidence interval) (Fig. S3), which is consistent with both the range of maximum height we estimated from vertical trends in pit aperture conductance (Fig. 3B) and historic records (16, 17).

These data suggest that Douglas-fir regulates its water loss (via stomatal closure) such that it avoids reaching the low xylem pressures at which embolism formation would become rampant. This highly conservative behavior of stomata suggests that tension-induced embolism may not be readily reversible in the xylem of Douglas-fir branches and that cumulative increases in the number of embolized tracheids must be avoided if branch xylem is to remain conductive for many years (1). Studies carried out with tropical and temperate angiosperm trees show similarly conservative stomatal regulation of branch xylem pressure at critical values corresponding to thresholds where embolism begins to increase abruptly with declining pressure (33–35). It is intriguing that the maximum height of 122–130 m predicted for coast redwood is consistent with the observed and predicted maximum heights of Douglas-fir and that coast redwood also exhibits highly conservative regulation of xylem tension near its embolism threshold of −1.9 to −2.0 MPa (1).

Runaway embolism becomes increasingly likely once xylem pressure reaches the steep portion of the hydraulic vulnerability curve because tissue hydraulic capacitance is no longer sufficient to adequately buffer fluctuations in tension induced by rapid changes in transpiration (34). Under these conditions, half-times for changes in xylem tension are likely to be substantially shorter than half-times for changes in stomatal aperture that would constrain transpiration-induced changes in xylem tension. It is unlikely that tension exceeds species-specific embolism thresholds, except during periods of extreme drought that ultimately lead to branch dieback and shedding. Thus, despite its utility as a general index of hydraulic vulnerability, the air-seeding pressure may have no special physiological relevance in the context of stomatal regulation of xylem tension under most conditions.

Our study shows that the morphology of tracheid bordered pits affects not only their resistance to embolism via air-seeding, but also their hydraulic conductance, implying that variation in pit structure reflects an adaptive balance between hydraulic efficiency and hydraulic safety at different locations within a Douglas-fir tree (9, 36, 37). To accommodate inevitable height-related increases in xylem tension, a decrease in pit aperture diameter with no concomitant change in the size of the torus lessens the risk of embolism. This decrease in pit aperture conductance, however, severely limits tracheid water conductance. Thus, as Douglas-fir trees grow taller, they appear to approach a height at which the tradeoff of xylem safety against efficiency ultimately becomes untenable. Despite differences in tree age and climate among sites for the trees studied here, height has a strong influence on pit structural features. It might be expected that in drier sites, greater soil and root water deficits would result in lower minimum xylem pressures, but our data suggest that stomatal regulation of xylem tension in Douglas-fir is so conservative that height exerts the dominant influence on xylem pressure and ultimately on tracheid structure.

The negative hydraulic impact of height-related reductions in the dimensions of tracheids and their structural components may be an inevitable consequence of gravity acting on tall water columns. Shoot expansion and cell size at the tops of Douglas-fir, coast redwood, and other tall conifers (1, 2, 38, 39) appear to be limited largely by vertical gradients of declining turgor during critical periods of expansive growth when osmotic adjustment is insufficient to compensate for the vertical hydrostatic gradient (1, 2, 40). Height growth in Douglas-fir and other tall conifers is thus likely to be constrained by a syndrome involving (i) gravity-induced effects on dynamic tissue level processes (such as osmotic adjustment, growth, photosynthesis) and (ii) their lasting consequences on plant structure and allometry rather than a single physical or physiological limitation. The hydraulic effects of gravity would act in addition to the localized hydraulic constraints that steepen the tension gradient at the terminal portions of the water transport pathway.

Mechanisms governing ultimate tree height must be considered in an evolutionary context, and so it is unlikely that the tradeoffs discussed here are identical to those of all other species. A number of coniferous species adapted to arid and semiarid zones can maintain adequate water transport at substantially greater xylem tensions than those normally experienced by the mesic-environment species Douglas-fir and coast redwood. Arid-adapted conifers are likely to be constrained by tradeoffs of xylem safety against efficiency similar to those in Douglas-fir, but with trajectories substantially offset from those reported here. Selective pressures operating in contrasting environments are expected to result both in adaptations to the appropriate limiting resources and in evolutionary canalization, yielding species with very different combinations of bordered pit features. Natural selection has not favored a wood structure in Douglas-fir that facilitates water transport at even greater tensions. Apparently, such structures would have a negative impact on its competitive ability, given the comparatively resource-rich environment in which Douglas-fir has evolved. In this context, lower stature arid zone conifers would be at a competitive disadvantage in more mesic environments because of the hydraulic and physiological constraints associated with maintenance of xylem transport at high tensions. Further studies of the functional consequences of suites of xylem structural features in species representing different growth forms and environments may give further insights into the proximal controls of woody plant form.

## Materials and Methods

**Plant Materials.** Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees ranging from 6 to 85.5 m in height were sampled from three sites located in

southwestern Washington and two sites located in Oregon (Table S1). Canopy access was provided by fixed climbing ropes, except at the Wind River Canopy Crane Research Facility, which contains a 75-m-tall construction tower crane. Within each tree, we took a trunk core (12-mm increment borer) and a branch sample in the lower third of the crown and at the top of the crown, for a total of three samples from each tree.

**Light Microscope Observations of Bordered Pit Structures and Calculation of Pit Conductance and Air-Seeding Pressures.** Both pit conductance and air-seeding pressures were estimated for this component of the study from morphological measurements. We made transverse and radial sections in the outer sapwood (3 cm wide, representing at least five growth rings) of each trunk core and branch sample. Radial sections were stained in a solution of toluidine blue to enhance the torus. Each section was analyzed with an image analysis system consisting of a compound microscope and video camera. We used the radial sections to measure the pit border diameter ( $D_b$ ), the pit aperture diameter ( $D_a$ ), and the torus diameter ( $D_t$ ) (Fig. S1). We measured pit diameters only from the second to the fourth ring of the earlywood, because a previous analysis showed that this sapwood section contributes >50% to the total water flow (9). Therefore, when all of these tracheids fully embolize through air-seeding, the sample will lose 50% of its hydraulic conductance. On transverse sections, we measured the cell wall thickness (average between tangential and radial cell walls), the thickness of the whole pit (measured from aperture to aperture), and the pit chamber thickness (measured between the inside edges of the pit borders) on 40–70 bordered pits per sample.

Hydraulic conductance of conifer wood is a function of both the tracheid lumen conductance and bordered pit conductance. We used only pit aperture conductance as a surrogate for tracheid hydraulic efficiency, because the main determinant of overall xylem conductivity in conifers is in bordered pit conductance (14, 20–22), which is mainly controlled by pit aperture conductance rather than by pit membrane conductance (9, 12, 20). The conductance of the pit aperture was calculated as the inverse of the hydraulic resistance ( $R_a$ ) of a circular opening of finite length (pit aperture depth), which combines the equation to calculate the resistance of a circular hole of diameter  $D_a$  with the Hagen–Poiseuille equation (41), in which  $R_a = 24\eta/(D_a^3) + 128d_a\eta/(\pi D_a^4)$ . In this equation,  $\eta$  is the dynamic viscosity of water (0.001 Pa·s at 20°C), and  $d_a$  is the pit aperture depth, taken as half the difference between the thickness of the whole pit and the thickness of the pit chamber. On average, the pit aperture depth at each sampling location was equal to 70% (SE = 6%,  $n = 16$ ) and 81% (SE = 9%,  $n = 16$ ) of the cell wall thickness in trunk and branches, respectively.

The air-seeding pressure was used as a surrogate for pit hydraulic safety (the more negative the air-seeding pressure, the safer the xylem) and was defined as the pressure difference required to move the membrane of an aspirated pit enough so that its torus no longer entirely covers the aperture (Fig. S1A), exposing the edge of the torus where the margo strands are attached. At pressures beyond this value, air-seeding can occur through the margo pores exposed at the pit aperture. We used the analyses in refs. 12 and 41, which allow membrane deflection beyond aspiration, with the assumption that the torus is inelastic and confines all stretching to the margo. In the equation to calculate the air-seeding pressures, the number of strands supporting the torus (55 and 65 strands in branches and trunk, respectively) and the thickness of the strands (141 nm and 155 nm in branches and trunks, respectively) were taken from ref. 9, and we used the measured depth of the pit chamber as a surrogate for twice the maximum torus displacement (9). On average, the maximum torus displacement was equal to 25% of the cell wall thickness in the trunk and 20% in the branches.

**Water Potentials and Measured Air-Seeding Pressures.** Minimum water potential was measured between 1300 and 1500 hours with a pressure chamber (PMS Instrument Company) on twigs excised from the top and lower third of the canopy on the same days that the cores and branches were collected. During clear weather, daily minimum twig water potential is typically observed between 1200 and 1500 hours (42). Water potential data reported here are means of three to five samples per sampling height. For the site in the Wind River Experimental Forest (35-m-tall trees), we used published values of minimum water potentials measured on trees of similar size at a nearby site (31).

Loss of conductivity is caused by the aggregate conductivity through a population of conduits, some of which transport and others of which do not. The tension required to cause 50% loss of hydraulic conductivity is the point at which the conduits with diameters that represent the mean hydraulic diameter embolize (43, 44), and so there is no transport through those conduits or through the conduits with diameters larger than the mean hydraulic diameter. Our study in ref. 9 showed that, in Douglas-fir, most of the tracheids in this diameter range were in the inner third of the earlywood, which corresponded to the tracheids on which we measured pit anatomy and calculated pit conductance and air-seeding pressure. For comparison with the air seeding pressures calculated from the structure of bordered pits, we determined empirically the pressure difference required to cause a 50% loss of hydraulic conductivity. Using the air-injection method (45), we constructed xylem vulnerability curves, which describe the relationship between the percentage of loss of hydraulic conductivity (caused by embolism through air-seeding) and xylem pressure. We measured the vulnerability to embolism on branches from the top (56 m) and from the base of the live crown (34 m) of the 62-m-tall trees at the Wind River Canopy Crane site and from the 6-m-tall trees at Roseburg. Vulnerability to embolism was measured on different branches, but on the same trees and at same height as the ones used for anatomy. Vulnerability data reported here are means of curves obtained from four to five samples per sampling height. We also used published values of trunk and branch vulnerability to embolism and aperture conductance (9, 46).

**Regression Analysis.** Least-squares methods were used to fit relationships between the variables. All stated equations had significant regression coefficient at  $P < 0.05$ . We first used linear regressions and examined the residual plots to detect any trends. If the residuals showed trends, we then used other forms of regression equations until we found the model that provided the most uniform distribution of residuals. The only relationships for which linear models were not appropriate were the following. For branches, an exponential relationship of the form  $ae^{bx}$  was used for pit aperture conductance vs. torus diameter/pit aperture diameter (Fig. 2B) and for pit aperture conductance vs. air-seeding pressure (Fig. 4). For pit aperture conductance vs. height (Fig. 3B), we used a logarithmic function of the form  $a + b \ln(x)$ .

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