Hydraulic Limits to Tree Height and Tree Growth

What keeps trees from growing beyond a certain height?

Michael G. Ryan and Barbara J. Yoder

Why do old trees stop growing in height?Trees seem to have mechanisms that slow their growth as they age and prevent them from growing beyond a certain height. For example, a young mountain ash (*Eucalyptus regnans*) east of Melbourne, Australia, may grow 2–3 m per year in height. By 90 years of age, height growth has slowed to 50 cm per year. By 150 years, height growth has virtually ceased, although the tree may live for another century or more. As they stop growing taller, trees also undergo a change in form. For many species, at the same time as the treetops become flattened, primary branches become thickened and smaller branches become more twisted and gnarled because the annual extension of all branches is also reduced (Figure 1).

Why do trees grow to different heights in different places? The mechanism that determines maximum tree height varies among sites. For example, in the front range of the Colorado Rocky Mountains, a seed from a 25 m tall ponderosa pine (*Pinus ponderosa*) may fall into a rocky crevice and never grow more than 1–2 m. On the eastern slope of the Cascade Mountains in Oregon, ponderosa pine soar to 50 m. Thirty kilometers farther east, in a drier climate, the same species struggles to attain 10 m. Similar examples can be found for all tree species. For every species—in fact, for every genotype within a species—maximum height and the rate of height growth vary remarkably from place to place (Figure 1).

A mechanism that can explain differences in maximum tree height at different locations and patterns in height growth with age has eluded ecologists and plant physiologists

Early foresters noticed that the maximum height a tree reaches is correlated with the speed at which it grew in height when young. They also noticed that total wood production was highest at locations where trees achieved the greatest maximum height. Foresters continue to use this relationship to predict growth (Figure 2), and they classify the productivity of sites based on the tree height expected for a particular species at a certain age.

What mechanism causes site-to-site differences in height growth, maximum height, and productivity, even for trees with identical genetic potential for growth? What mechanism causes the slowing of height growth with age and height for all species at all sites? We understand why trees might grow faster at one site than another (trees, like most other plants, grow most rapidly in moist, fertile sites, and slowly in dry, nutrient-poor sites). A mechanism that can explain differences in maximum tree height at different locations and patterns in height growth with age has eluded ecologists and plant physiologists. Such a mechanistic explanation would allow better modeling of tree growth and growth response to the environment (Ryan et al. 1996). It would also help us to understand whether conversion of old-growth forests to young plantations would increase rates of carbon storage (Harmon et al. 1990) and whether atmospheric inputs of nitrogen would increase carbon storage in temperate forests (Kauppi et al. 1992).

In this article, we discuss four possible mechanisms to explain the patterns of maximum tree height and age-related changes in height growth within a species. Three of these—respiration, nutrient limitation, and genetic changes in meristem tissue—have been discussed in the literature. (The respiration and nutrient limitation mechanisms were developed to explain patterns of whole tree and stand growth with age, but not tree height specifically.) The fourth, hydraulic limitation, is newer, but we believe that it is the most promising. Accordingly, we examine the hydraulic limitation hypothesis in the most detail.

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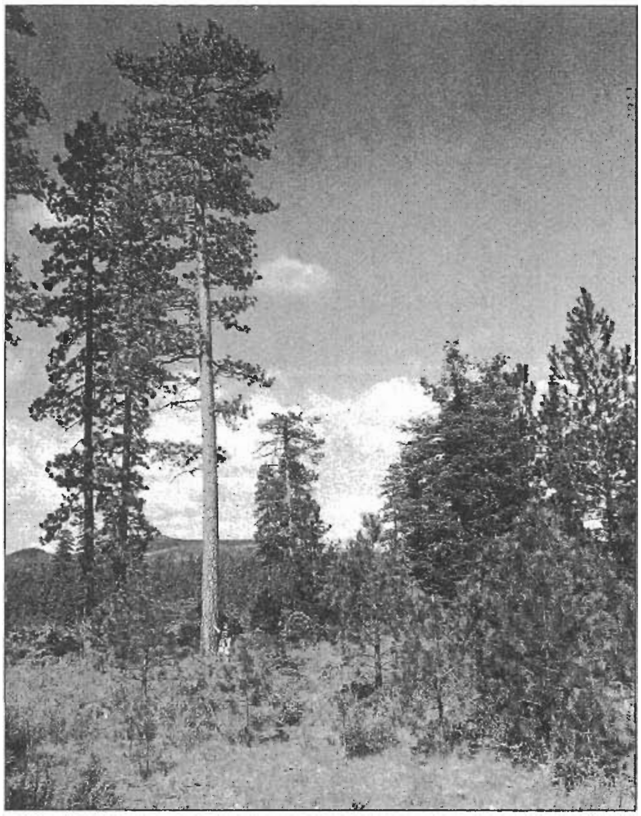

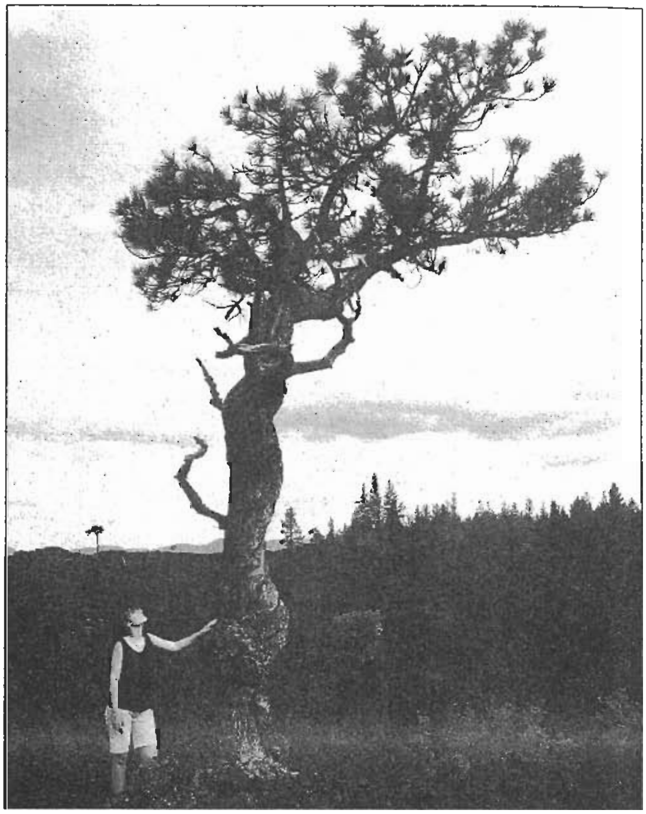

Figure 1. Ponderosa pine on the eastern slope of the Cascade Mountains in Oregon. (left) Tree near Sisters, Oregon, is approximately 250 years old and 37 m tall. (below) Tree near Bend, Oregon, on an old lava flow. Tree is approximately 250 years old and 7 m tall. Nearby trees that are not on the lava flow reach a height of 30 m. The same woman is standing next to both trees.

Proposed explanations for tree growth pattern

Several mechanisms have been proposed to explain the decline in growth with age and the differences in height growth and maximum height within a species:

- As trees grow, increased autotrophic respiration of woody tissues consumes carbon, so less is available for growth. This is the *respiration hypothesis*.
- In large trees, nutrients become sequestered in living biomass, and as whole forests age, nutrients become sequestered in woody debris and decaying wood on the forest floor. The subsequent decline in nutrient availability may reduce tree growth in two ways. First, lower nutrient availability may lead to increased allocation of photosynthetic products to root production in older stands and therefore to decreased allocation to aboveground structures. Second, the foliage of older trees with reduced nutrient supply may have lower photosynthetic capacity. This is the *nutrient limitation hypothesis*.
- Growth of the undifferentiated tissue at the growing tips (meristematic tissue) may slow as the number of cell divisions increases. This is the *maturation hypothesis*.
- Total resistance to water flow in trees varies with both the path length and the conductivity of wood in a given cross-section. Hydraulic resistance increases as trees grow taller, because water must travel a longer path and, perhaps, because slower-growing wood is less permeable to water flow. To move the same amount of water through a path with higher resistance requires a higher tension (i.e., lower water potential) in the xylem water column. However, at higher tensions, air bubbles are more likely to form in the xylem water column (cavitation). To prevent cavitation and temporary loss of the water conducting system, leaf stomata in trees with higher resistance (taller trees) close earlier in the day or earlier in a drought cycle. This closure lowers stomatal conductance and photosynthesis, reducing carbon available for wood growth. This is the *hydraulic limitation hypothesis*.

Respiration hypothesis. Yoda et al. (1965) developed the respiration hypothesis by reasoning that respiration will increase with tree size because the living portion of woody biomass (the sapwood) respires. They also observed that the ratio of woody biomass to leaf area increases as trees grow. Because photosynthesis is proportional to leaf area, higher wood-to-leaf ratios will yield greater autotrophic respiration costs relative to photosynthesis. The increased respiration costs use carbon that, in a smaller, younger tree, would contribute to wood production. Whittaker and Woodwell (1967) used the same reasoning, but with stem surface area instead of biomass.

Although textbooks (e.g., Kramer and Kozlowski 1979, Waring and Schlesinger 1985) generally favor the respiration hypothesis as an explanation for declining growth in older trees, a direct test of this hypothesis (Ryan and Waring 1992) failed to support it. Respiration rates for the living portion of the woody biomass of lodgepole pine (*Pinus contorta* var. *latifolia*) were low. In addition, much of the woody respiration was related to growth processes, and it declined as growth declined. Subsequently, Mencuccini and Grace (1996) showed that in Scots pine (*Pinus sylvestris*), increases in woody respiration with tree size could not explain the decreased growth of older trees. In general, maintenance respiration rates of woody tissues (the portion of respiration not related to tissue growth) appear to be low, using only 5% to 12% of annual carbon fixation (Ryan et al. 1995).

Other, indirect evidence also contradicts the respiration hypothesis. For example, trees at wider spacings (and therefore with higher wood-to-leaf ratios) maintained high growth after canopy closure, whereas more narrowly spaced trees experienced a decline in growth rates (Fownes and Harington 1990). The respiration hypothesis also cannot account for the variation within a species in maximum tree height for trees growing in similar climates. Finally, it does not explain why growth in diameter continues, tapering off much more gradually, long after growth in height has ceased.

Nutrient limitation hypothesis. Several observations have contributed to the nutrient limitation hypothesis. Grier et al. (1981) found that the allocation to fine roots was dramatically greater in an old Pacific silver fir (*Abies amabilis*) forest than in an adjacent, young forest of the same species. Sequestration of nutrients in biomass and detritus in the old stand lowered nutrient availability in soil, and the trees responded to the lower nutrient supply by increasing production of fine roots. Similarly, fine-root biomass was greater in a mature slash pine (*Pinus elliottii*) stand than in a young stand (Gholz et al. 1982). Although fine-root turnover was lower in the mature stand, below-ground respiration costs were higher to maintain the greater root biomass. In both studies, increased allocation below ground in the older stand used carbon that would have gone to wood production in the younger stand, thus slowing the growth of the older trees relative to the younger trees. These observations, together with the finding that nitrogen is sequestered in biomass of a larch (*Larix gmelinii*) forest (Schulze et al. 1995) and with the results of model simulations, which showed a tendency for mature forests to sequester nitrogen in woody biomass and decaying wood (Murty et al. 1996), led to the development of the nutrient limitation hypothesis (Gower et al. 1996).

Although the nutrient limitation hypothesis may sometimes account for slower growth in older trees, it is unlikely to be generally applicable. Nutrient availability in the soil of some old forests can be as much as or greater than that of younger forests (Olsson 1996, Ryan et al. 1996). Below-ground allocation in lodgepole pine is greatest soon after canopy closure and declines as rates of both tree height and diameter growth decrease.[1] The nutrient limitation hypothesis also does not explain why, in mixed-aged stands, tree height limitations occur only in older trees (e.g., Yoder et al. 1994), or why isolated old trees growing in parks with ample nutrients and water do not continue to grow in height indefinitely. Although increased below-ground allocation may sometimes slow the total growth of older trees—possibly to a greater degree than increased autotrophic respiration—the nutrient limitation hypothesis cannot serve as a general explanation for height growth patterns.

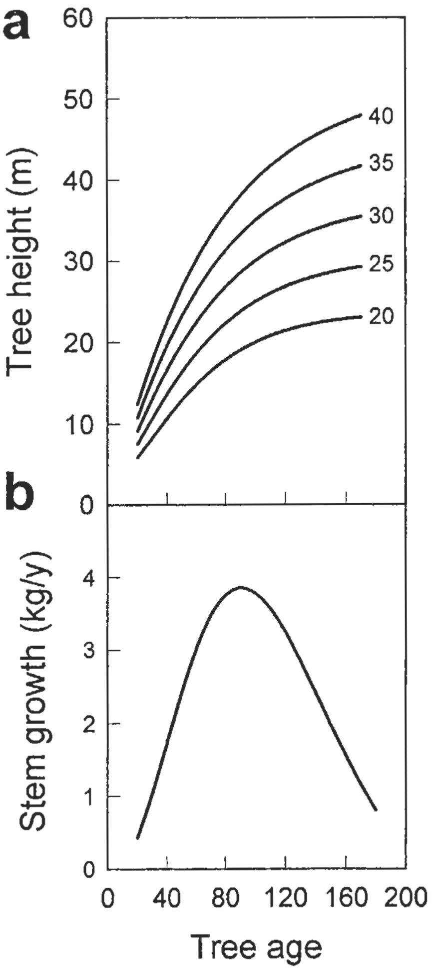

Figure 2. (a) Average tree height versus age for ponderosa pine grown on sites with different growing conditions. Numbers on right are "site index" classes (site index is the height, in meters, of a dominant tree at age 100). Curves plotted from equations given in Barrett (1978). Height growth, maximum height, and growth are clearly linked and differ dramatically within a species. (**b**) Average stem growth versus age for a ponderosa pine in site index of 30.

Maturation hypothesis. All higher organisms show maturational changes with age. In woody plants, maturational changes include differences in branching and in foliage biochemistry, physiology, and morphology (Greenwood and Hutchinson 1993). Shoots from older trees are less branchy than those from younger trees; they also have lower photosynthetic rates, are less likely to root, and show less height and diameter growth when grafted onto juvenile rootstock (Greenwood and Hutchinson 1993). When mature branches are grafted onto juvenile rootstock, mature characteristics persist; thus, maturation may involve genetic changes in the meristematic tissue of plants (Greenwood and Hutchinson 1993). The older the tree from which the grafts are derived, the lower the growth rate of these grafted branches. Genetically programmed slowing of growth is thus a potential explanation for the decrease in height growth with age (Greenwood 1989).

However, grafting experiments also provide evidence that maturation does not limit height or slow

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[1] S. Resh and F. W. Smith, manuscript in preparation. Colorado State University, Fort Collins, CO.

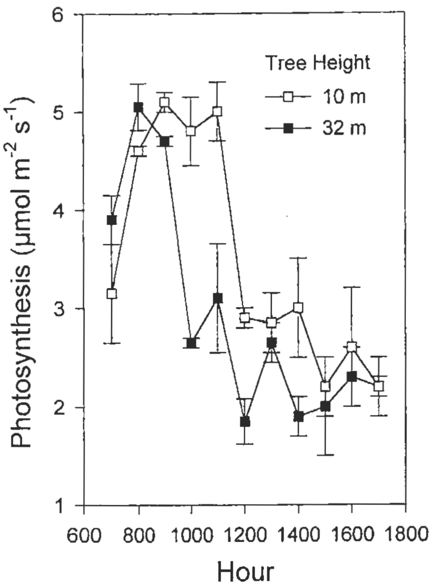

Figure 3. Diurnal course of photosynthesis for one-year-old foliage in the upper one-third of the canopy on young (10 m; open symbols) and old (32 m; closed symbols) ponderosa pine trees. Earlier closure of stomata for the old trees resulted in 25% lower total diurnal photosynthesis. Adapted from Yoder et al. 1994 with permission of the Society of American Foresters.

height growth. The transition from juvenile to mature characteristics occurs early in the life of a tree, generally well before height growth slows. For example, the greatest maturational changes occur between 1 and 4 years for Douglas fir (Ritchie and Keeley 1994) and between 1 and 20 years in larch (Greenwood 1989). Slowing of height growth occurs later in these species (at approximately 30–70 years), suggesting that maturation is not a factor in height growth patterns—trees that are slowing in growth rate are already "mature."

Another difficulty with the maturation hypothesis is the young age of the living portion of the tree: The leaves and fine roots are replaced frequently, making them much younger than the chronological age of the tree as a whole. Ray parenchyma cells (found in the water-conducting xylem) are the oldest cells in a tree, and these rarely exceed 80 years of age, even in very old trees (e.g., Connor and Lanner 1990). It is therefore unlikely that the age of an individual tree influences plant growth (Noodén 1988). Unlike animal cells, which have a mechanism that slows cell division as cells age and limits the total number of cell divisions that can occur (to a few dozen), plant cells undergo thousands of divisions, to judge by the number of vessels or tracheids in a stem, all of which derive from the same precursor cell.

Hydraulic limitation hypothesis. Yoder et al. (1994) observed differences in the diurnal patterns of photosynthesis in needles of the same age from young and old trees in two conifer species (Figure 3): old trees assimilated less carbon overall. The differences in photosynthesis did not appear to be caused by differences in photosynthetic capacity, because foliar nitrogen contents were similar, as were peak photosynthesis rates. However, stomata on the needles from old trees closed earlier in the day. Yoder et al. (1994) speculated that the earlier stomatal closure might be caused by increased hydraulic resistance resulting from increased xylem path length in taller trees with longer branches.

To understand how hydraulic resistance of stems and branches might be coupled with stomatal behavior and photosynthesis, it is necessary to consider the limitations and controls on water movement through plants. Evaporation of water from leaves provides the force to pull water from the soil, through the roots and xylem, and to the leaves. Because the water column from root to leaf is connected and under tension, this mechanism of sap ascent is called the "cohesion tension theory." Leaf water potentials in trees are generally 1 MPa (megapascal) lower than that of the water in soil, and resistance to water flow in the xylem causes most of the difference (Tyree and Ewers 1991). The high negative pressures theoretically required to move water up a large tree have been repeatedly measured with a pressure bomb and independently verified by measuring the flow of water through stems subjected to increasing water tension by centrifugation (Pockman et al. 1995).

The rate of water flow from the roots to a leaf is equal to the potential difference between the roots and the leaf divided by the total hydraulic resistance along the hydraulic pathway. This relationship is analogous to Ohm's law, which describes electrical current as voltage divided by electrical resistance. In the early morning, transpiration from leaves is low, so a small potential gradient from roots to leaves is required to supply transpirational water. As radiation and temperature increase, so does the atmospheric "pull" on leaf water. The water potential in leaves and stems falls, so that the water flux up the plant can keep pace with increased transpirational losses. But there is a limit to the water tension that leaves and stems can endure. Eventually, stomata begin to close, limiting transpirational water loss as well as the root-to-leaf water potential gradient that is required to supply the water. Because stomatal closure also limits the carbon dioxide that can enter leaves for photosynthesis, any reduction in stomatal opening caused by a hydraulic limitation in the vascular system would also decrease daily carbon assimilation by the canopy.

Hydraulic resistance varies with the permeability of the sapwood and the overall path length (height of tree and length of branches). Therefore, hydraulic resistance will increase as the tree gains height and branches lengthen. In addition, the force of gravity results in a gradient of 0.01 MPa/m, even when there is no transpiration. The slow increase of hydraulic resistance as a tree grows will increase water stress in leaves, forcing stomata to close and lowering photosynthesis compared with a shorter tree.

To some extent, trees compensate for their increased size by producing xylem elements with increased permeability (Pothier et al. 1989a), but total resistance still increases with size and age (Mattson-Djos 1981, Mencuccini and Grace 1996). The links between hydraulic resistance and stomatal opening, and between stomatal opening and photosynthesis, mean that a larger hydraulic resistance will likely reduce diurnal and seasonal carbon assimilation. If foliage on older trees produces less photosynthate, then less wood growth will result, because the other carbon costs (respiration, foliage production, root growth) are similar to or slightly greater than those in younger trees (Ryan and Waring 1992). The hydraulic limitation hypothesis predicts that new stem growth in old trees should be most severely limited where the hydraulic resistance is greatest: at the treetop and the tips of very long branches. The flattened tops and gnarled branches of old trees are, thus, an expected result of hydraulic limitations.

The hydraulic limitation hypothesis can also explain why height growth rates and maximum height of trees vary with resource availability. On a nutrient-poor site, trees tend to have low rates of photosynthesis and stomatal conductance (Schulze et al. 1994) and, therefore, slower wood growth (the production of new xylem). The xylem that does form contains a larger proportion of "late-wood" xylem, with very narrow tracheids and, thus, low permeability (Pothier et al. 1989b). Therefore, in resource-poor environments, hydraulic resistance for a given length (i.e., the tree height) will be greater than for a tree growing in a resource-rich environment. In addition, on a dry site, any given leaf water potential has less "pulling power" because the driving force for water movement is the soil-to-leaf potential difference. Similarly, in cold soils a particular leaf water potential has less pulling power than in warmer soils because water becomes more viscous at near-freezing temperatures. Therefore, increased hydraulic resistance from smaller and fewer xylem cells and reduced driving force act together to limit the stature of trees in stressful locations.

The hydraulic limitation hypothesis can also explain why different species or individuals may attain different maximum heights in the same environment. Species that can endure very low xylem tensions or that have limited hydraulic restrictions (e.g., branch nodes) in their architecture are likely to achieve greater maximum heights. Individuals that have been exposed to mechanical stresses, and therefore produce reaction or compression wood with low permeability, are likely to achieve reduced maximum heights.

Evidence for the hydraulic limitation hypothesis

For hydraulic resistance to limit tree growth, three elements are necessary. First, stomata (and, consequently, transpiration and photosynthesis) must respond to changes in hydraulic resistance. Second, hydraulic resistance must increase with tree height or tree age. Third, photosynthesis must be lower on the foliage of older trees.

Do stomata respond to changes in hydraulic resistance? Tyree and Sperry (1988) proposed that stomata may close in response to decreasing bulk leaf water potentials to prevent catastrophic loss of xylem function through cavitation. Cavitation results from tiny air bubbles that form in the xylem water column at high tensions (Zimmermann 1983). If cavitation occurs, the air bubbles interrupt the continuous column of water in the xylem, increasing total hydraulic resistance. Thus, even steeper gradients of water potential are required to maintain the same flux of water up the plant. Unless the plant limits transpirational water losses through stomatal closure, a catastrophic cycle of ever-worsening cavitation will result.

Sperry and colleagues (Sperry 1995, Sperry and Pockman 1993, Sperry et al. 1993) have shown that stomata do behave in a manner consistent with Tyree and Sperry's (1988) proposal: Experimental increases in hydraulic resistance (by cutting partially through stems) induced stomatal closure without measurably affecting leaf water potential (Figure 4). Other results suggest that the ability of the xylem to carry water may control the response of stomata to low humidity (Meinzer and Grantz 1991). Therefore, although the precise signals that induce stomatal closure are still a topic of debate, it is clear that stomatal behavior changes when hydraulic resistance changes.

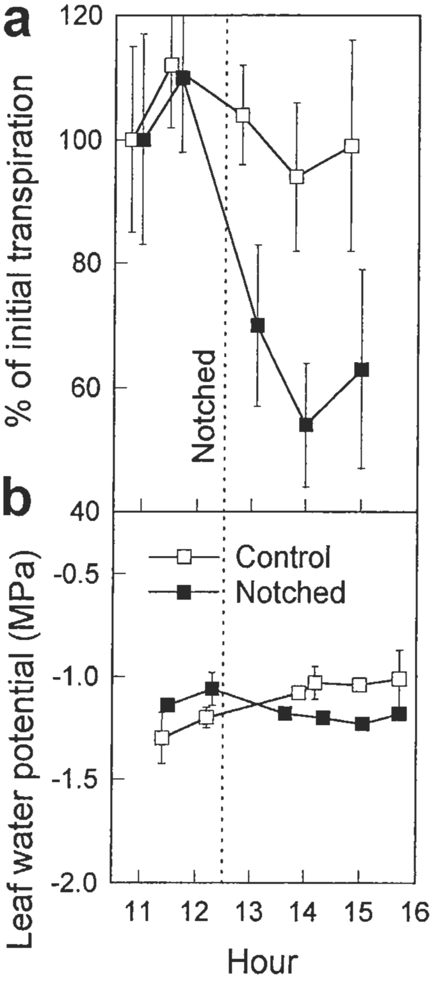

Figure 4. Response of transpiration (a) and leaf water potential (b) in *Betula occidentalis* branches before and after notching to increase resistance to water flow. Notching was done at 12.5 hours. After the hydraulic resistance increased (as a consequence of notching), stomata closed to reduce transpiration. Reprinted from Sperry et al. 1993 with permission of Oxford University Press.

Several other studies provide evidence that stomata respond to xylem resistance, independent of their well-known response to vapor pressure differences between the leaf and the air. In these studies, hydraulic resistance was either increased, by root pruning or by notching xylem (Sperry and Pockman 1993, Sperry et al. 1993, Teskey et al. 1983), or reduced (for individual leaves) by removing leaf area (Meinzer and Grantz 1990). In all cases, stomata closed when hydraulic resistance increased, and they opened when hydraulic resistance for individual leaves was reduced. Also, in all cases, leaf water potential remained stable through large changes in stomatal opening (e.g., Figure 4a, b). Additional evidence that stomata respond to changes in hydraulic resistance comes from the studies of Saliendra et al. (1995), who found that stomata that had closed in response to a high leaf-to-air vapor pressure gradient opened immediately in response to root pressurization. The response was also reversible: Releasing the root pressure resulted in stomatal closure.

Studies with stable isotopes of carbon provide further evidence of the effects of hydraulic conductance on stomatal behavior (Waring and Silvester 1994, Yoder et al. 1994). Carbon dioxide in air is mostly $^{12}CO_2$ but contains a small, constant amount of $^{13}CO_2$. When stomata are open wide, the sugar products of photosynthesis have low amounts of ^{13}C because the lighter $^{12}CO_2$ diffuses more quickly into the leaf and binds more readily with the photosynthetic enzymes (Farquhar et al. 1989). When the stomata close, in response to dry air or internal drought, more $^{13}CO_2$ is used for photosynthesis; thus, the amount of ^{13}C in sugars rises. In a recent stable isotope study of well-ventilated, open-grown ponderosa pine trees with no shading from adjacent trees,[2] the relative abundance of ^{13}C in one-year-old needles was found to increase from the base of the live crown to the treetops. This finding indicated that stomatal opening was reduced with tree height within individuals. Similar differences were found for one-year-old needles in the upper canopy of young and old ponderosa pine (Yoder et al. 1994), Douglas fir, and western hemlock.[3] The ratio of ^{13}C to ^{12}C in foliar cellulose also increases with branch length (Waring and Sylvester 1994). The increased hydraulic resistance with tree height and branch length produces an isotopic signature consistent with increased stomatal closure.

Does hydraulic resistance increase as trees age? Hydraulic resistance increases with tree height and age in several species. For example, transpiration was approximately 20% lower in a 140-year-old spruce stand (*Picea abies*) compared with a 40-year-old spruce stand.[4] These differences in transpiration between young and old spruce forests translate into lower average stomatal conductances to water vapor for the older stand.

In Scots pine, whole-tree hydraulic conductance (leaf transpiration divided by the water potential difference between leaves and soil; the inverse of hydraulic resistance) in 40-year-old trees was estimated to be approximately 20% what it was in seedlings (Mattson-Djos 1981). Similar dramatic reductions in hydraulic conductance were also found for Scots pine in a different location (Mencuccini and Grace 1996). In this study, wood growth per unit leaf area decreased linearly as hydraulic conductance (per unit leaf area) decreased. Finally, canopy hydraulic conductance in 30 m tall, 270 year old ponderosa pine trees was 50% lower than that of adjacent 10 m tall, 40 year old trees.[5]

Additional evidence for increasing hydraulic resistance with tree height comes from a study of leaf water potential gradients in a tall tree. The force of gravity on a water column will change xylem water potential approximately –0.01 MPa per meter of tree height (Zimmermann 1983). Steeper gradients in xylem water potential with height (–0.024 MPa/m) indicate the increased resistance of the xylem to water flow in tall trees.[6]

The evidence for increased hydraulic resistance in older trees is not conclusive. Zimmermann et al. (1994) did not find that water potential gradient varied with tree height, and water flow in the sapwood of older *Eucalyptus* trees was similar to that in young trees, although tree height differed by 35 m (Dunn and Connor 1993). These contrary findings do have an explanation. The pressure probe measurements of Zimmermann et al. (1994) are suspect because insertion of the probe may cause cavitation (Pockman et al. 1995). Older trees often have lower leaf area per unit sapwood area, so that the resistance per unit leaf area could have been higher for old trees in the Dunn and Connor (1993) study. Where leaf water potential gradients have been measured with a pressure bomb, and where hydraulic resistance has been expressed on a leaf area basis, hydraulic resistance was found to be greater in older trees.

Is photosynthesis reduced in old trees? In the few available studies, carbon assimilation and stomatal conductance are lower for foliage of old trees than of younger trees. For example, diurnal photosynthesis and stomatal conductance in two gymnosperms, ponderosa pine and lodgepole pine, were lower in old trees than in nearby young ones (Yoder et al. 1994); the same was true for cherry, an angiosperm (Fredericksen et al. 1996). In both studies, rates of photosynthesis in old and young trees were similar in the moist morning air, but they differed as relative humidity decreased (Figure 3). Other studies have shown that photosynthesis and stomatal conductance were uniformly lower in older conifers than in younger ones (Grulke and Miller 1994, Kull and Koppel 1987, Schoettle 1994); these findings suggest that aging and height growth lower photosynthetic capacity. Two explanations could account for the decrease in photosynthetic capacity. Older trees may experience nutrient limitations in addition to hydraulic limitations; alternatively, a chronic water deficit and lower stomatal conductance near the tops and branch tips of older trees may be accompanied by reduced allocation of nitrogen to that foliage.

Perhaps the most interesting and convincing documentation of reduced stomatal conductance and photosynthesis with age comes from measurements of whole stands rather than individual trees. As mentioned above, canopy transpiration was lower (and hydraulic resistance higher) in older spruce stands than in younger stands.[7] Another recent study compared carbon dioxide and energy fluxes between young and old jack pine (*Pinus banksiana*) forests in northern Canada (Sellers et al. 1995). Preliminary results from this study indicate that midday net carbon dioxide uptake and transpiration were consistently higher for

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[2] B. J. Yoder and J. A. Panek, 1996, submitted manuscript. Oregon State University, Corvallis, OR.

[3] See footnote 2.

[4] M. Alsheimer, B. M. Köstner, E. Falge, and J. D. Tenhunen, manuscript in preparation. University of Bayreuth, Germany.

[5] M. G. Ryan et al., manuscript in preparation.

[6] N. M. Holbrook et al., 1996, submitted manuscript. Harvard University, Cambridge, MA.

[7] See footnote 4.

the young trees, even though the old trees had more leaf area. These studies support the hypothesis that transpiration and carbon assimilation are constrained by hydraulic resistance in older stands.

A negative feedback loop?

The link between stomatal opening and hydraulic resistance suggests a feedback mechanism that may limit tree height and height growth. As a tree grows, gravitational force and hydraulic resistance increase simultaneously, resulting in limits to carbon assimilation. Because wood production apparently has a low priority for carbon allocation (Waring and Pitman 1985) and other carbon costs remain fixed, decreased assimilation will result in less new xylem. The slower growth also promotes the formation of a higher proportion of "latewood" cells in the xylem—cells that have low permeability to water. Trees may also lose water-conducting xylem to heartwood formation or to the effects of irreversible cavitation. The loss of water-carrying xylem and the decrease in xylem production ultimately combine to constrain the conducting system and maximum height of the tree.

The negative feedback described above suggests that new stem growth in old trees should be most severely limited where hydraulic resistance is greatest: at the tops of tall trees, the tips of very long branches, and the tips of twigs with very small xylem cells. The flattened tops and gnarled branches of old trees are, thus, an expected result of hydraulic limitations.

Evidence from fertilization and thinning studies suggests that this negative feedback loop can be broken if more resources are made available to the stand or to individual trees (e.g., by removing competitors for light, water, and nutrients, or by adding nutrients). For example, in 120 year old Scots pine in Sweden, fertilization increased xylem production.[8] The trees also initiated new height growth, although they were near their maximum height. Presumably, fertilization either increased photosynthetic capacity or reduced allocation to root production (Gower et al. 1996), releasing carbon for xylem production.

Conclusions

A maximum height that varies with resource availability and slower height growth in older individuals appear to be universal for trees. Old trees are different, both physiologically and morphologically, from younger trees: They have lower rates of photosynthesis, reduced height and diameter growth rates, and a distinctive architecture. Nutrition, carbon allocation (including respiration), meristematic activity, and the tree's hydraulic architecture can all potentially change with tree growth and promote slower growth in older trees. In fact, these processes may interact.

Respiration or costs of producing additional roots become more important if photosynthesis is reduced as a result of hydraulic limitation. Additionally, slow xylem growth, whatever the cause, may lead to smaller tracheids or vessels and, therefore, to increased hydraulic resistance. However, if hydraulic resistance changes with tree height and branch length, and if stomata respond to the increasing resistance by closing to avoid cavitation, then all trees will face hydraulic limitation to photosynthesis—whether as isolated individuals, in uniform stands, or in stands of mixed age classes. Regardless of other constraints, trees will have to accommodate increased hydraulic resistance and its consequences as they grow.

Assessing the physiology of large trees has been a difficult logistical problem, but new techniques and resources are now available. Construction cranes now provide access to trees more than 60 m tall in both conifer and tropical forest sites, and sap flow instrumentation can now be used to measure the whole-tree water flux and whole-tree canopy resistance. Stable isotopes of carbon allow an assessment of stomatal behavior integrated over a year or more. With these techniques, we may be close to answering some of our oldest questions about tree height.

Acknowledgments

Research was supported by USDA (NRICGP #9401021) and NSF (DEB93-06356). We gratefully acknowledge the help of the Sisters Ranger District, USDA Forest Service, for access to study sites.

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