WHITE PINES AT LOST 40 SCIENTIFIC AND NATURAL AREA BY RICHARD HAMILTON SMITH

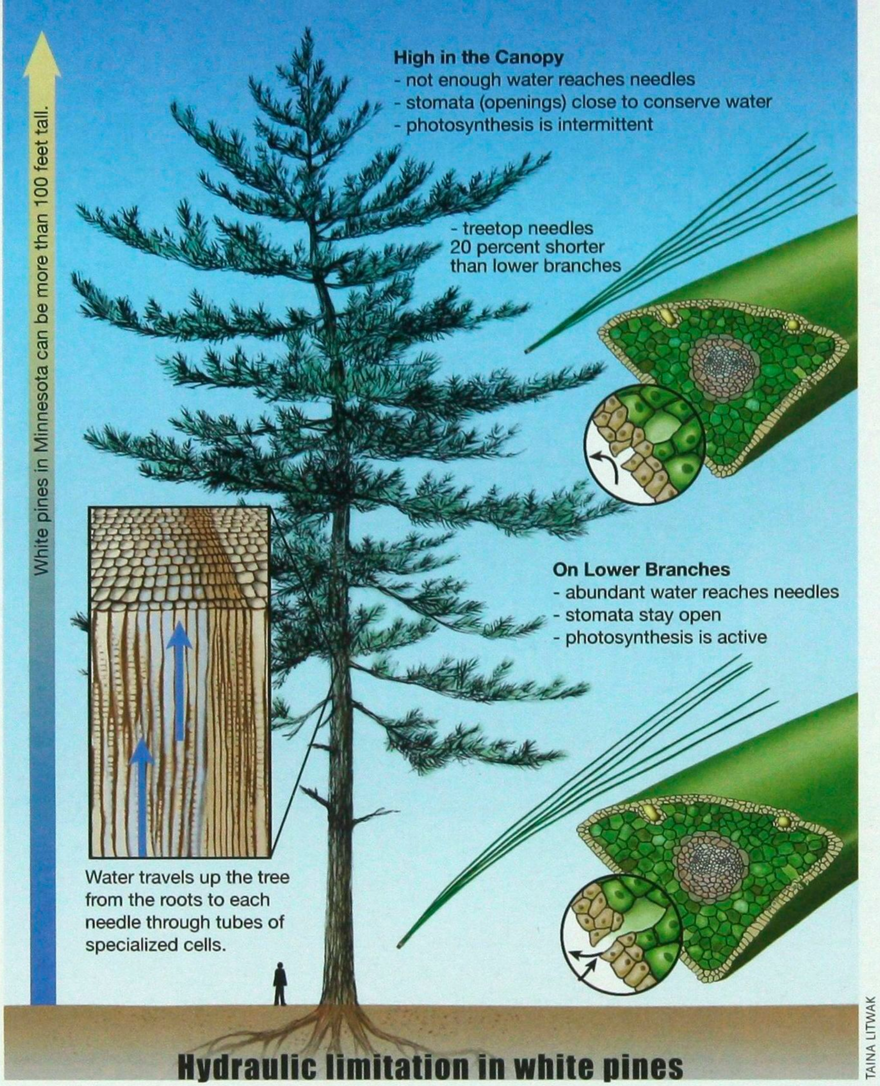
Why don't **trees** grow taller?

As long as they live, trees gain girth, adding rings year after year. But after a while, they stop growing taller. To study the limits of height, researchers go to the treetops.

By Mark Fulton

"Incoming!" shouts Bemidji State University biology graduate student Matt Coyle from 120 feet overhead. I don't duck for cover—the incoming item is a sprig of pine needles in a plastic bag. I retrieve the sample and hand it to grad student John Kamman, who loads it into a device called a pressure bomb. The pressure bomb is about the size of a shoebox, with a steel chamber, a pressure gauge, and a hose attached to a tank of compressed air. Kamman twiddles a valve and, after a minute or so, reads off a number that tells me how hard the needles were sucking to get water from the roots. By now, Coyle is sending down another sample.

It's a warm day in late June, and a lot of people are strolling in the Lost 40 Scientific and Natural Area to get a look at some of the tallest white



pines in Minnesota. When visitors ask what we are doing, I explain that I'm a Bemidji State biology professor, and my students and I are testing a hypothesis about the hydraulic limitation of tree height.

The theory of hydraulic limitation postulates that tree height is limited by the difficulty of pulling water from tree roots to treetop. The tallest trees in the world, such as the 350-foot coastal redwoods in California and the mountain ashes of southern Australia, are certainly subject to hydraulic limitation. Some trees of semiarid regions, such as ponderosa pines in the Rocky Mountains, also show clear evidence of hydraulic limitation from lack of water in the soil. What scientists don't know is how general the mechanism is. Does it only apply to world record–breaking tall trees and trees in dry regions? Or are shorter trees growing in humid climates also subject to hydraulic limitation? My students and I think white pines are a good place to look next.

White pine is a canopy emergent—it doesn't grow well in the shade of other trees, but it can survive for centuries by growing above the top of surrounding species. Many vistas in northern Minnesota have some white pines sticking up above the forest. It's the tallest tree species in the United States east of the Great Plains, reaching heights of 130 feet in Minnesota. If any tree species in the relatively humid climate of eastern North America is hydraulically limited, white pine should be.

The purpose of our study was to test the theory of hydraulic limitation for the tallest white pines in Minnesota. Evidence of severe drought stress at the tops of the trees, with decreasing stress farther down in the canopy, would constitute evidence for the theory.

Reaching for Light. Forest trees grow tall to compete with their neighbors for light. The competition is fierce, and the stakes are high. Most tree species can't reproduce without winning a place in the forest canopy. The evolution of trees is thought to be a kind of race; every time one species acquires the ability to get taller, it ups the ante for all the other species around it. In spite of this competition, trees eventually stop getting taller, even as they continue to put on girth.

Growing tall is important, but it's hard work. To grow taller, a tree needs more food and a longer lifetime to add living tissue (more than eight times its current wood volume to double its height). The taller the tree, the more water and nutrients it requires to maintain living tissue. A tall tree is exposed to more wind damage, and if upper branches break, it takes time for lower branches to grow and restore lost height. All of these factors slow down height growth as the tree gets taller, but none of them explains why height growth nearly stops in big trees. The developing consensus among forest ecologists is that hydraulic limitation stops height growth in the tallest trees.

Some of the earmarks of hydraulic limitation are easy to see. Hydraulic limitation may explain why trees are short on dry, sandy soils on hilltops where water runs off readily, and trees of the same species and age are taller where the soil is wetter. The 300-year-old pines of the Lost 40 grow on level ground, in soil that holds water fairly well. Lee Frelich, forest ecologist at the University of Minnesota, found the tallest white pines in Pennsylvania close to small springs—in effect, where the trees have a year-round drip irrigation system.

When a tree is close to its maximum height, the uppermost branches are prone to dying back. Branches farther down grow upward, and the result is that the tallest white pines get a distinctive bushy crown.

Treetop Desert. Pine needles, like all tree leaves, suffer from a dilemma: They have openings *(stomata)* to take in carbon dioxide for photosynthesis, but these openings also let out water vapor—a tree releases hundreds of pounds of water for every pound of carbon dioxide taken in. As the tree gets taller, it gets harder to slake this huge thirst. To get a drink of water from the soil, needles at the top of a tall white pine have to suck very hard, using capillary forces developed in the walls of their cells. Imagine you were standing on top of a 12-story building and sipping a milkshake through a very long, narrow straw from a cup on the ground.

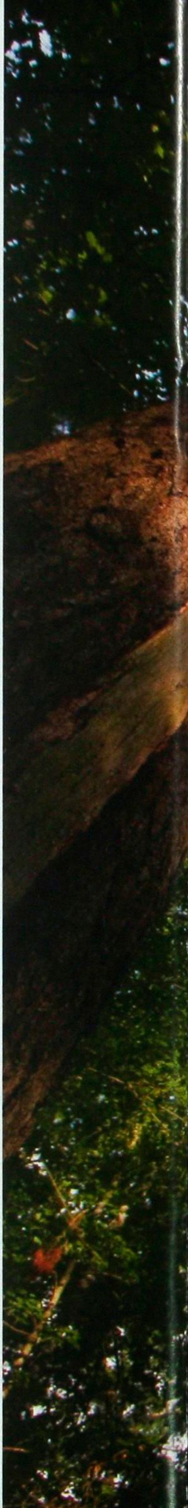
If water inside a leaf evaporates faster than it can be replaced, the cells lose water, and the leaves quickly die of dehydration. To prevent this, the openings can close—but then photosynthesis stops, and so does growth. It's a tricky balancing act, and it gets trickier as the tree gets taller.

We made three kinds of measurements to test for hydraulic limitation in the Lost 40 pines. The pressure bomb numbers told us how much suction (negative pressure) the needles were using to pull water from the soil to the canopy. We found it takes much more suction to get water to the treetop than it does to reach lower branches.

We also measured the carbon isotope content of needle samples. Needles growing under drought stress, with their leaf openings closed a lot of the time, have a slightly different mix of isotopes from well-watered needles. The needles we collected from the treetops showed a mix of isotopes consistent with prolonged drought stress.

Finally, we measured the length of needles from the bottom to the top of the canopy. Plant cells grow by taking in water and inflating like little water balloons. If needles are water stressed, their cells may not inflate as much during growth, and the needles will be smaller. Compared with needles from the bottom of the canopy, treetop needles were about 20 percent shorter.

As the pressure bomb numbers showed, water in the upper canopy needles was under more than enough suction to force the leaf openings to close. While the tree's lower branches and the plants on the ground were still doing photosynthesis, the treetop pine needles were unable to pull water from the roots—and unable to keep growing. In other words, compared with the forest floor, it was a desert up there. V



WHITE PINES AT LOST 40 SCIENTIFIC AND NATURAL AREA BY RICHARD HAMILTON SMITH