How water travels up trees

Why do giant redwoods grow so tall and then stop? It all has to do with how high water can travel up their branches.

Photo courtesy of Allie_Caulfield/Wikimedia Commons

Coast redwood,
Sequoia sempervirens

By Clare van der Willigen

The redwoods of northern California, *Sequoia sempervirens*, are the tallest trees in the world and can grow to heights of more than 110 m. However, what finally limits their height is still debated.

The most popular theory is the 'hydraulic limitation hypothesis' (Ryan & Yoder, 1997), which suggests that as trees grow taller, it becomes more difficult to supply water to their leaves. This hydraulic limitation results in reduced transpiration and less photosynthesis, causing reduced growth.

In tall trees, water supply can be limited by two factors: distance and gravity. Tall trees have a longer pathway of transport tissue – known as xylem – which increases the difficulty of water to travel, something we call hydraulic resistance. In addition, not only is the xylem pathway long, but the trees are tall and the water has to overcome gravity. Increased force is necessary to pull the water up to the highest leaves. This situation differs

☑ **Biology**
☑ **Mathematics**
☑ **Ages 15–18**

The article describes two experiments that can easily be conducted in science classrooms or laboratories to study water movement in plants.

Although the procedures are easy to carry out, the concepts and knowledge that are explored aren't so simple, but are appropriate for upper secondary-school students (aged 15-18). In my experience, there are not very many procedures that consider water movement for this age group, so many science teachers will welcome this article.

There are also relevant opportunities for interdisciplinary teaching involving mathematics in particular. It would be quite interesting to use this experiment as a starting point to introduce students to the development of a database and subsequent statistical analysis (not too complex). For example, students could estimate maximum xylem vessel lengths and measure xylem hydraulic conductivity of different plants and at different times (e.g. winter vs. summer). This database could be extended from year to year with other students. Such a strategy could help students to understand science as a collaborative activity – not only between different disciplines but also between different 'generations' of scientists.

Betina Lopes, Portugal

from a long hosepipe lying along the ground: it would have high resistance due to its length, but not the additional difficulty of being upright.

Fast-growing trees often have shorter life spans. To achieve their rapid growth, pioneer trees have wider xylem vessels, increasing their hydraulic efficiency but also increasing the risk of embolisms (air locks). Air locks in xylem vessels prevent water from being able to travel through them.

In contrast, very tall trees are often very long-lived. It is thought that this is partly because they are more likely to adopt a safe hydraulic design, with multiple narrow xylem vessels instead of a few wider ones. This increased safety is counteracted by a decreased efficiency of water transport, which consequently limits growth rates. Tree height, therefore, may also be limited by the safety versus efficiency trade-off in xylem function (Burgess et al, 2006).

The following two activities explore the trade-off that plants make between being efficient with water transport and having a safe design. Both activities can be adapted for students aged 15–18 with a wide range of abilities, but you should assess whether the students can perform all of the experiments or whether it is safer for the teacher to do the cutting. Each activity will take about 50 minutes.
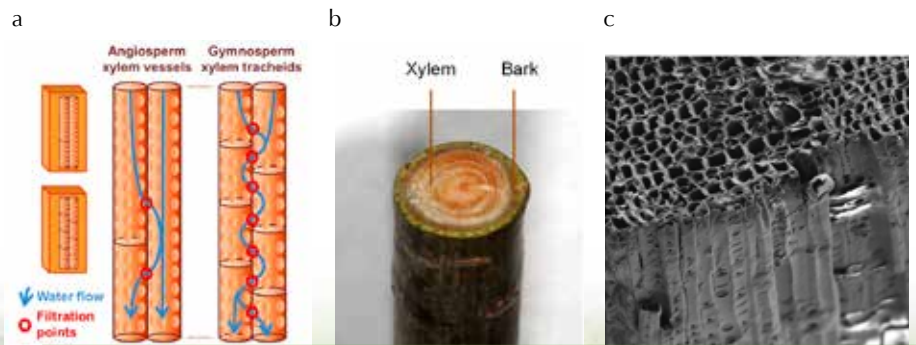
a) Structure of xylem vessels in flowering plants and tracheids in conifers b) Photograph of ~1 cm diameter pine (pinus strobus) branch c) Scanning electron microscope (SEM) image of cut section

Species	Mean xylem length (m)
Acer saccharum (Sugar maple)	0.0312
Cinnamomum camphora (Camphor tree)	0.1184
Rhododendron maximum (Great Rhododendrum)	0.0246
Vitis vinifera (Common Grape Vine)	0.1503

Table 1: Some example xylem lengths of branches less than 15 cm in diameter, taken from Jacobsen et al. (2012)

Estimating maximum xylem vessel lengths

Comparing the lengths of the xylem vessel will allow students to predict their relative resistance to water flow.

Materials

- Selection of recently cut branches from a tree or shrub, including any leaves or side branches, up to 2 m in initial length. If the experiment is to be performed within a few hours of harvesting, keep the plant material in a plastic bag to avoid excessive water loss.
- Rubber/silicon tubing
- Cable ties or jubilee clips
- Sharp pruning shears or scissors
- 60 cm^3 syringes
- Large basin of tap water
- Hand lens
- Ruler

Procedure

1. Cut a length of branch over 1 m, making sure the cut is clean and the end of the branch is not crushed. The branch will be much longer than the xylem vessels inside.

2. Attach a 60 cm^3 syringe, filled with air, to the proximal (wider) end of the branch using silicon tubing and cable ties as required.

3. Pressurise the air in the syringe and branch by compressing the volume of air in the syringe by about half (e.g. from 60 cm^3 of air to 30 cm^3). This pressure must be maintained through steps 4–6.

4. Hold the distal end of the branch under water.

5. Use a hand lens to see if a steady stream of bubbles can be detected from the distal end of the branch.

6. Progressively cut the distal end of the branch back by about 1 to 5 cm at a time, making sure each time that the end of the branch is not crushed and has a clean cut.

7. When a stream of bubbles is observed, the length of the branch gives an approximate maximum length of the xylem vessels.

Safety Note

Students should be warned about the safety precautions necessary when using sharp objects. See also the general safety note.

Follow-up activity

Students could compare maximum xylem vessel lengths in a variety of different plants or different parts (roots, main and side branches) of the same plant. It is common for fast-growing plants to have longer xylem vessels and therefore fewer breaks between xylems. Can the students suggest why this might be?

About what happens

A branch contains several xylem vessels linked together. Between the xylem vessels are perforated wall plates. The fewer of these divisions there are, the lower the resistance, and the faster water can travel.

A detailed study of vessel length in *Chrysanthemum* stems (Nijsse et al, 2001) and in a wide range of shrubs and trees (Jacobsen et al, 2012) can be used for cross-reference.

Pressurise the air in the syringe

Stream of bubbles

ACTIVITY

Measuring xylem hydraulic conductivity

Measurements of xylem hydraulic properties show how well plants can supply water to their leaves. It is possible to measure the hydraulic conductance of stems, branches and roots in the classroom with some simple, inexpensive equipment. To measure hydraulic conductivity, the branch length should be longer than the mean length of the xylem vessels (see previous activity).

Materials

- Selection of recently cut branches from a tree or shrub investigated in the previous experiment. Ensure that the pieces are longer than the longest xylem vessels measured. If the experiment is to be performed within a few hours of harvesting, keep the plant material in a plastic bag to avoid excessive water loss.
- Rubber/silicon tubing
- Cable ties or jubilee clips
- Sharp secateurs, scissors or a large scalpel
- Chopping board
- Large basin of water
- Metre rule
- Reservoir of degassed, distilled water in a container with a tap at the bottom. Degas the water by boiling it or using a vacuum pump for approximately 1 h until all the gas has been expelled from the water. Air bubbles in water that is not degassed may block the xylem vessels.
- Hydrochloric acid
- 1 cm^3 pipette (a pipette with a 90° bend is most effective. A standard glass pipette can be bent in a very hot flame)
- 50 cm^3 plastic beaker
- Retort stand and clamp
- Balance (precision of at least 0.01 g)
- Stop watch or stop clock

Procedure

1. **Set up the apparatus as illustrated in the diagram:**

a   Add hydrochloric acid to the degassed, distilled water to give a final concentration of 0.01 M. For example, add 0.5 cm^3 of 0.1 M HCl to 5 dm^3 degassed, distilled water. Hydrochloric acid prevents the long-term decline in conductance by reducing microbial growth in the xylem. **Safety tip:** Remember to always add acid to water, not water to acid.

b   Fill the reservoir with the acidified water. Insert a piece of tubing, sealed at one end with a bung, into the top of the reservoir. The open tubing ensures a constant pressure head because even if the water level drops, the effective height of the reservoir will remain the same.

c   To the tap of the reservoir, add some tubing, fill with water from the reservoir, seal the open end and place into the large basin of water.

d   Close the tap.

e   Submerge the proximal end of the branch in the large basin of water. This is the end of the branch that was nearest to the main stem of the plant.
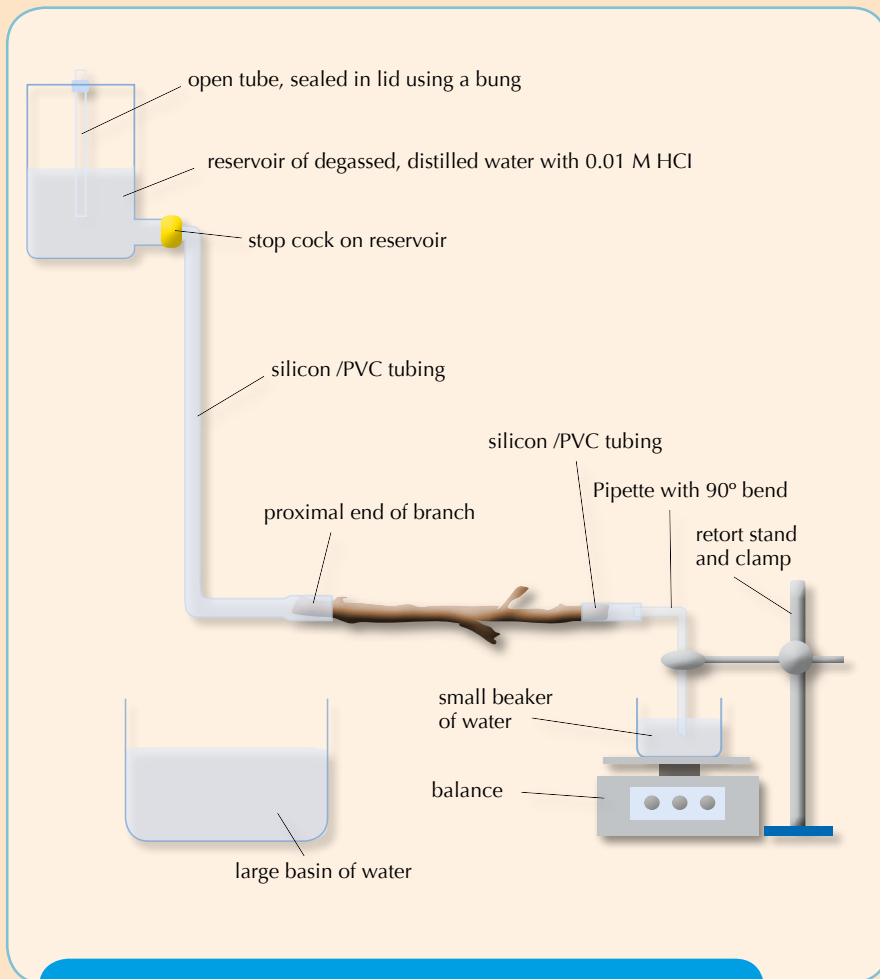

Branch connected to tubing

Cut end under water

ACTIVITY

open tube, sealed in lid using a bung

reservoir of degassed, distilled water with 0.01 M HCl

stop cock on reservoir

silicon /PVC tubing

silicon /PVC tubing

proximal end of branch

Pipette with 90° bend

retort stand and clamp

small beaker of water

balance

large basin of water

Diagram of the apparatus setup to measure hydraulic conductivity

Whole setup

Image courtesy of Nicola Graf

Connect tubing to end under water

Cut proximal end under water

f   Cut approximately 3 cm off the proximal end of the branch under water to ensure that no air pockets remain in the xylem. Shave off the end of the cut using a sharp blade.

g   Connect the newly cut end of the branch to the water-filled tubing attached to the reservoir under water. If the bark is very rough, it can be stripped back prior to connection. A watertight seal should be achieved using cable ties or jubilee clips if necessary, however do not over-tighten and compress the xylem vessels.

h   Submerge the other end of the branch in the tub of water.

i   Cut approximately 3 cm off the end of the branch under water to ensure that no air pockets remain in the xylem. Shave off the end of the cut using a sharp blade.

j   Measure and record the length of the branch. Ensure it is longer than the maximum xylem vessel length (see above).

k   Connect the bent pipette to more rubber tubing and submerge into the basin of water.

Measure water collection on balance

Measure reservoir height

l Connect the newly cut end of the branch to the water-filled tubing attached to the pipette as above.

m Fill the 50 cm³ beaker with water and place on the pan balance.

n Take the branch end and pipette out of the basin of water with the end of the pipette sealed.

o Place the end of the pipette in the 50 cm³ beaker on the balance.

p Use the retort stand and clamp to hold the pipette in place. The tip of the pipette should not lean on the bottom of the beaker, but should be below the water level. This ensures that as the water drips through the branch, there is a smooth increase in the mass of water in the beaker.

2 Open the tap from the reservoir.

3 Measure the mass of water every 30 s for 3 min.

4 Measure the effective height of the reservoir using the metre rule. This is the height from the bottom of the open tubing in the reservoir to the proximal end of the branch.

Safety Note

Students should be warned about the safety precautions necessary when using sharp objects and acids. See also the general safety note.

Analysis

Hydraulic conductivity is measured as the mass of water flowing through the system per unit time per unit pressure gradient (Tyree & Ewers, 1991). The hydraulic

Table 2. Raw data table to calculate the hydraulic conductivity of a side branch from a Laurel tree (Laurus nobilis)

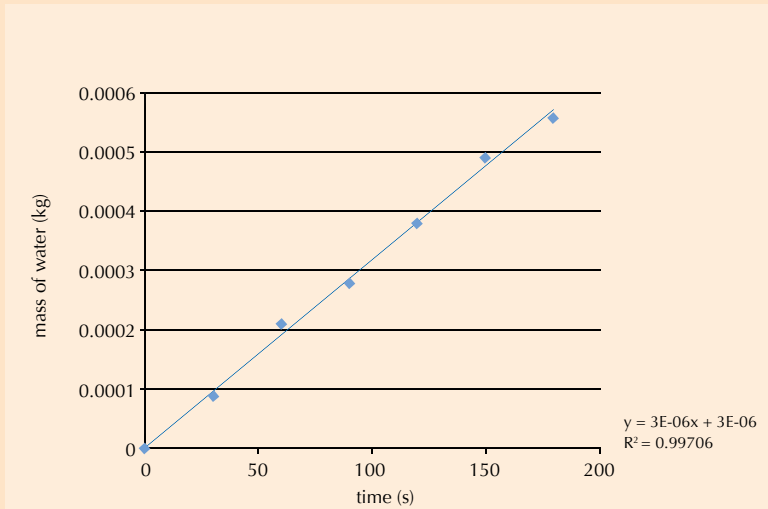| Time (s)	Mass of water (g)	Mass of water (kg)	Branch length (m)	Effective reservoir height (m)
0	0.00	0.00000		
30	0.09	0.00009		
60	0.21	0.00021		
90	0.28	0.00028	0.32	1.5
120	0.38	0.00038		
150	0.49	0.00049		
180	0.55	0.00055		

Figure 1: Worked example of plot to calculate flow rate. Data from table 2.

Table 3: Processed data from worked example of a side branch from a Laurel tree (*Laurus nobilis*)

Flow rate (kg/s) see figure 1	Branch length (m)	Hydrostatic pressure head (MPa) w	Hydraulic conductivity k_h (kg m/MPa s)
3 x10^{-6}	0.32	0.0147	6.53 x 10^{-5}

conductivity of the branch, k_h, is calculated using the following formula:

$$k_h = \frac{\text{flow rate x branch length}}{\text{hydrostatic pressure head}}$$

where the flow rate is measured in kilograms per second (kg/s); branch length in metres (m); and the pressure head in megaPascals (MPa).

To calculate the flow rate, plot the mass of water (in kg) measured in step 3 against time (in s). The flow rate will be the gradient of the line of best fit (in kg/s). See table 2 and figure 1 for a worked example.

The hydrostatic pressure head is found by multiplying the effective height of the reservoir, measured in step 4, with the density of liquid and the acceleration due to gravity. The density of the acidified water can be assumed to be 1000 kg/m³ (at room temperature) and a value of 9.81 m/s² can be used for acceleration due to gravity. Thus, with an effective height of the reservoir of 1 m, the hydrostatic pressure head would be 1000 x 9.81 x 1 = 9810 Pa or 0.00981 MPa.

Remember, maximum hydraulic conductivity is only achieved if none of the xylem vessels are embolised (filled with air). To try to prevent this, branches can be flushed with water at a pressure of approximately 200 kPa for 20 min before measuring conductivity. Alternatively, ensure that branches are selected from well-watered trees and that the leaves are covered in a large plastic bag prior to measurement

Follow-up experiments

Investigations on different levels of water stress on the same, or similar, branches would give an indication of plants that are more vulnerable to cavitation, or air bubbles. Hydraulic conductivity can change depending on environmental conditions, and the same species of plant that have adapted to different environments could be tested in the laboratory or in the field. Compare branch cross-sections of different diameter or those supporting different leaf areas.

Students could observe the effect on hydraulic conductivity of changing the branch length and relate this to the height of the plant. They could also investigate the effect on the flow rate of changing the height of the reservoir. The reservoir height (pushing force) could be considered as equal, but opposite, to the pulling force created by the low water potential in xylem vessels.

References

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Jacobsen A.L., Pratt R.B., Tobin M.F., Hacke U.G., Ewers F.W. (2012) A global analysis of xylem vessel lengths in woody plants. *American Journal of Botany* **99**: 1583-1591 doi: 10.3732/ajb.1200140

Nijsse J., van der Heijden G.W.A.M., van Ieperen W., Keijzer C.J., van Meeteren U. (2001) Xylem hydraulic conductivity to conduit dimensions along chrysanthemum stems. *Journal of Experimental Botany* **52**: 319-327 doi: 10.1093/jexbot/52.355.319

Ryan M.G., and Yoder B.J. (1997) Hydraulic limits to tree height and tree growth. *BioScience* **47(4)**: 235-242 doi:10.2307/1313077

Tyree M.T., Ewers F.W. (1991) The hydraulic architecture of trees and other woody plants. *New Phytologist* **19:** 345-360

Did you know?

Xylems are essentially porous filters, and scientists think that they could be used to filter water and make it safe to drink. Earlier this year, a group at the Massachusetts Institute of Technology in the USA showed that a 3 cm³ piece of pine branch could act as a filter and remove 99.9 % of bacteria from water, at a rate of several litres a day. The technique isn't perfect yet: viruses and chemical contamination can't be stopped by twigs, but the work by Boutilier et al (2014) suggests a cheap way to purify water in developing countries.
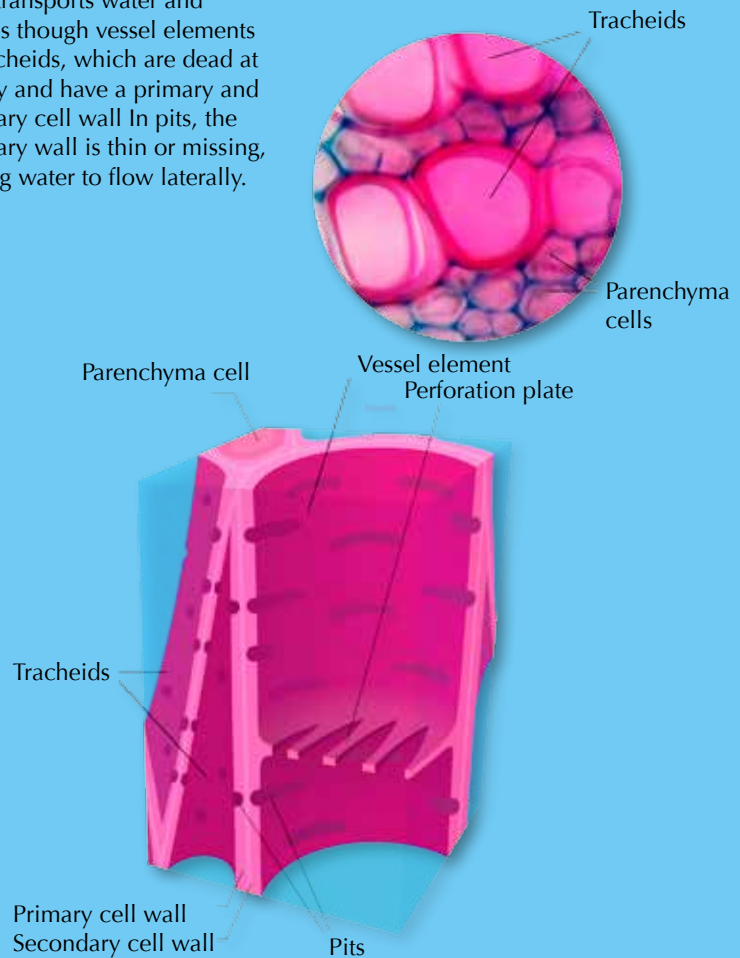

cut branch

peel off bark

fasten into tube

xlem filter

Image courtesy of Boutilier et al.

BACKGROUND

Image courtesy of Kelvinsong/Wikimediacommons

Xylem

Xylem transports water and minerals though vessel elements and tracheids, which are dead at maturity and have a primary and secondary cell wall In pits, the secondary wall is thin or missing, allowing water to flow laterally.

Tracheids

Parenchyma cells

Parenchyma cell

Vessel element
Perforation plate

Tracheids

Primary cell wall
Secondary cell wall

Pits

Resources

For a scientific analysis of maximum possible tree height, see:

Koch G.W., Sillett S.C., Jennings G.M., Davis S.D. (2004) The limits to tree height. *Nature* **428:** 851–854. doi: 10.1038/nature02417; available free from http://bit.ly/1lsNILK

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Clare van der Willigen has an MSc and a PhD in plant physiology from the University of Cape Town, South Africa. Following postdoctoral research on water stress in plants and aquaporins, she pursued her passion for teaching. She has worked in South Africa, France, The Netherlands and the United Kingdom, and is currently a senior examiner and teacher of many years' experience.

To learn how to use this code, see page 57.