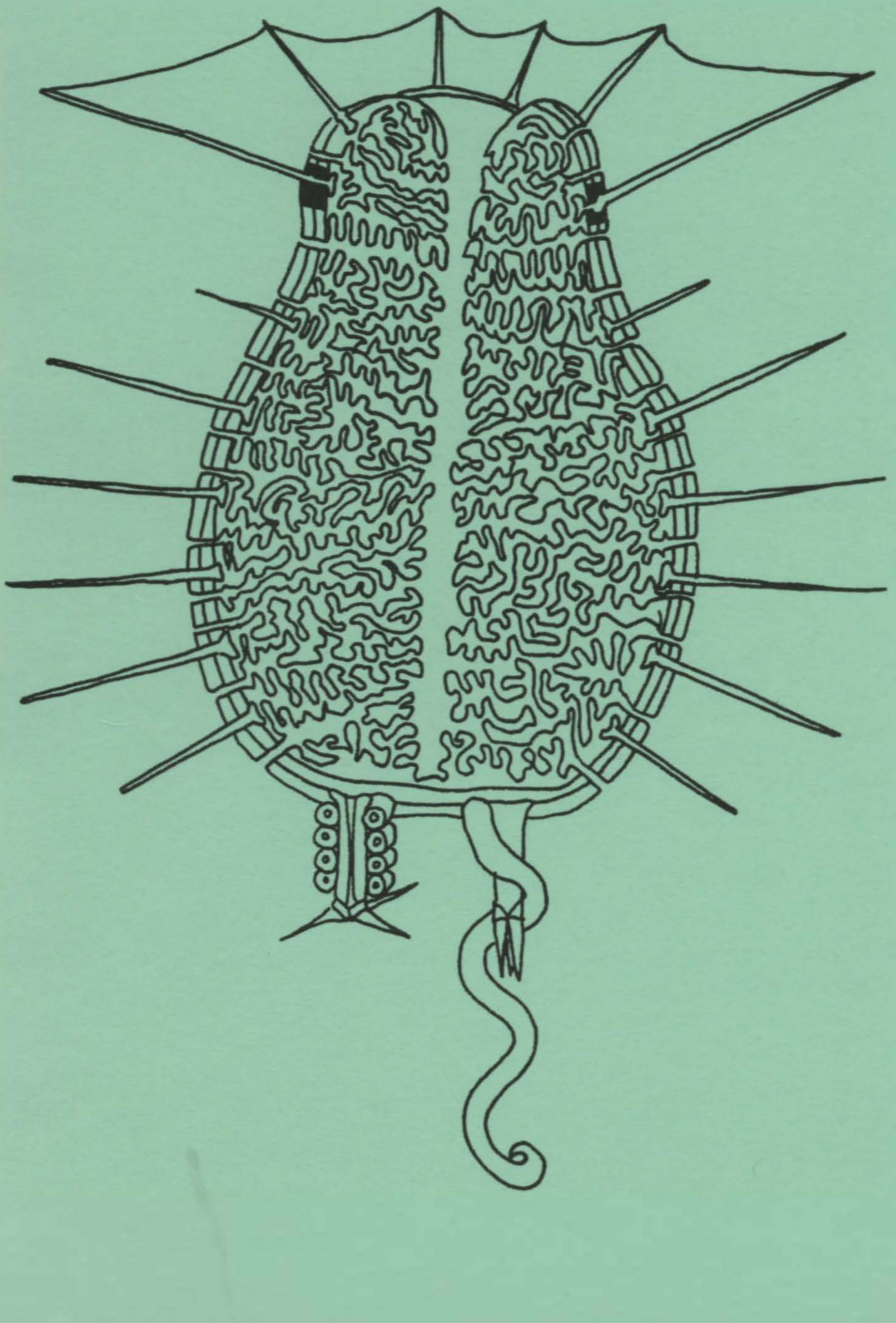
Bioscene



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Cover Illustration: Diagram of *Scirtovitrum iridothrix*, a benthic invertebrate inhabiting the shallow continental slope of Oceanus IV. The name "iridescent-haired glassy leaper" comes from the reflective coloration of the silica spines and the animal's ability to launch itself into the water column when attacked.

The species was created by Cathy Peterson, a student in the invertebrate biology class at Alma College, as part of three-species exercise throughout the term. Details on the project are available through Kay Grimnes, Department of Biology, Alma College, Alma, MI 48801.

Bioscene: Journal of College Biology Teaching

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How to Blow Air Through Sticks, or, Xylem Structure and Function

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Many botany and plant physiology courses focus on the relationship between plant structure and function. Commonly used examples include flower color and morphology, leaf size and shape, stomatal wall structure, and so on. These concepts can easily be demonstrated in the laboratory or classroom. However, although most courses include lecture or discussion about the adaptive significance of internal anatomy, relatively few labs give students practical experience with this facet of plant biology. I have developed a laboratory that focuses on the relationship between the structure and function of the tracheary elements of the xylem.

Theory

Much of the theory and data concerning water flow through the xylem was reviewed and synthesized in Zimmerman's (1983) excellent book on xylem structure. I will give only a very brief summary.

Plants may possess two types of water-conducting tracheary elements, tracheids and vessels. (The water-transporting capacity of other xylem cells is very minor and may be ignored.)

Structure strongly influences the rate at which water moves through these cells. The inner walls of tracheary elements are hydrophilic and entrain a boundary layer of water molecules. The thicker the boundary layer in proportion to the cross-sectional area of the cell lumen, the more the movement of the average water molecule is retarded, and the lower the amount of water passing through the cell. In cells of small diameter, the boundary layer is thick relative to the lumen size, the average rate of movement is slow, and the rate of water flow is low.

The relationship is mathematically described by the Poiseuille (or Hagen-Poiseuille) equation:

$$\boxed{\text{Flow rate} = \left(\frac{\pi r^4}{8\eta}\right)\left(\frac{\Delta P}{\Delta x}\right)}$$

where r is the radius of the cell lumen, η is the viscosity of water, ΔP is the pressure difference between one end of the cell and the other, Δx is cell length, and $(\Delta P/\Delta x)$ is the pressure gradient driving the flow. In the laboratory η and $(\Delta P/\Delta x)$ are experimentally controlled, so the primary factor controlling flow rate is the radius of the lumen. Because of the fourth power in the equation, the dependence of flow rate on cell size is very strong. Doubling the radius of a cell increases the flow by a factor of 16.

The Poiseuille equation, therefore, tells us that differences in the lumen size of tracheary elements can have a major influence on the rate at which they transmit water. Lumen diameter does vary quite considerably. Tracheids typically have diameters of 20 µm or less, while vessels usually range from 50 to 100 µm, with some as large as several hundred µm in diameter.

Water transport is influenced by the diameter of tracheary elements in several additional ways. Although large diameter elements conduct water more rapidly than smaller ones, larger elements have a significantly elevated risk of being blocked by air bubbles that vaporlock the element and prevent flow. Thus, in conditions where water supply is limiting, there is a tradeoff between the rate of water supply and its security.

A further factor that must be considered in interpreting wood function of angiosperm trees is the growth pattern of the xylem. Some species are ring-porous, meaning that only the current year's xylem transports water. Other species are diffuse-porous, meaning that several years' worth of xylem is active. Growth patterns and vessel diameter are correlated; ring-porous species tend to have larger vessels.

Lab Procedure

The goal of this lab was to allow students to relate the rate of gas flow through the wood to the structure of the water-carrying cells. Zimmerman

(1983) describes a number of ways to make measurements of flow rate using water or other liquids. However, gas will pass through the tracheary elements as well as water, and it is easier to measure air flow than water flow. The basic procedure in this lab is thus to pass a stream of air lengthwise through a wood sample. The flow rate of samples from various species or of different sizes of the same species is measured and related to properties of the conducting cells.

I begin by having students examine prepared slides of cross, radial and tangential sections of the woods to be used. Tangential and radial sections are especially useful in visualizing the way in which vessel elements stack up to make continuous vessels. I also have students make cross-sections of their own samples, but it is difficult to produce a useful longitudinal section by hand, so I use prepared slides in this section. Wood slides from many species are available from most biological supply houses.

Various types of wood can be used for this lab. However, the samples must be such that gas can flow lengthwise only through tracheary elements. Thus, species with hollow or very porous pith should not be used. Likewise, specimens with cracks, branches, or other alternative pathways for air flow should be rejected. Since pruners crush the tracheary elements at the cut end of the wood sample, the surface must be recut with a razor blade. I have never used herbaceous plants for this experiment, but I suspect that robust stems such as those of mature sunflowers might work.

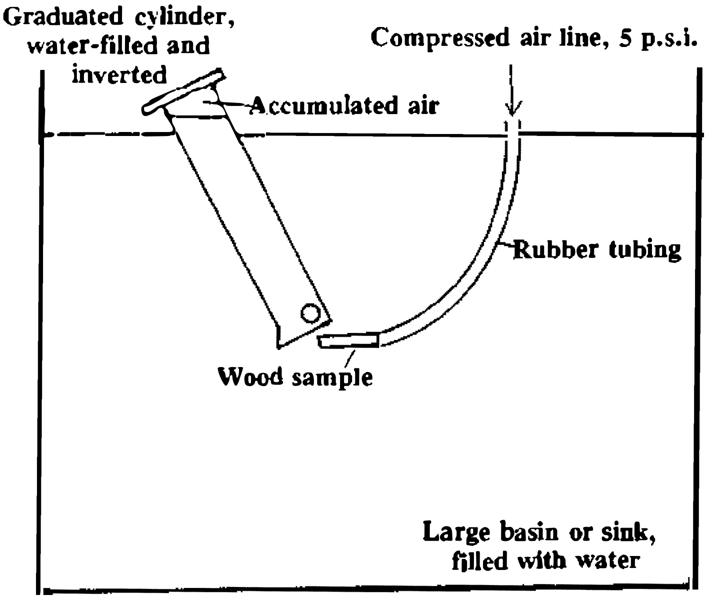

Figure 1. Apparatus for measuring air flow through a wood sample.

The technique for measuring flow rate is quite straightforward (Figure 1). An appropriate wood sample is connected to an air supply that is maintained at constant pressure. Our physiology lab has a compressed air line, to which we have added a pressure regulator. I use air at 5 p.s.i. I choose twigs that fit tightly into standard rubber tubing and wrap wire around the tubing to seal the connection.

The other end of the wood is placed under water in a basin and a graduated cylinder or other calibrated container is placed over the end of the sample to catch escaping air bubbles. (This method allows the sample to be checked for leakage through the pith or laterally through the bark, knotholes, or pith.) The collection container is filled with water by submerging in the basin. The container is then inverted while still under water. A large basin is needed; I use a sink. Air is collected for a known length of time, the volume is measured, and the flow rate (e.g., in units of ml per second) is calculated.

Since it is possible for an improperly secured sample to shoot out of the tubing, students should wear safety glasses to protect their eyes.

Size measurements of the tracheary elements are also needed. Students cut cross sections of the wood samples with razor blades. If the slices are wedge-shaped, at least some areas will be thin enough to use. The students measure the diameter of the largest tracheary elements using eyepiece micrometers or a calibrated video microscope.

Some Results

The goal of my lab was to determine the effects of tracheary element diameter and vessel length on flow rate. Thus, I use species that differ significantly in these features. The data presented here came from three angiosperm trees (white ash, *Fraxinus americana;* sugar maple, *Acer saccharum;* and white oak, *Quercus alba*), a woody vine (grape, *Vitis riparia*), and a gymnosperm tree (white cedar, *Thuja occidentalis*).

Rates of air flow through 10 cm long pieces of wood are shown in Table 1. Cedar lacks vessels, and so allows very little flow of air. Sugar maple does have vessels, but they are quite short. It can be inferred from the lack of flow that vessels do not stretch all the way through a 10 cm sample. In

Species	Flow rate, ml per second
Grape	42.0, 8.1[1]
White cedar	0.0, 0.0
White oak	4.5, 2.3
Sugar maple	0.0, 0.0
Whiteash	2.5, 6.4

[1] Commas separate measurements from different individuals.

Table 1. Air flow rate through 10 cm long twigs of woody plants.

contrast, air bubbles move through grape stems so rapidly that it is difficult to measure the rate with a small container.

Flow rate and the mean diameter of the largest vessels are strongly related (Figure 2). Species with larger vessels have higher flow rates.

Differences in vessel length can also be detected with this method. In angiosperms, most of the air flow is through vessels. Vessels range in length from less than a meter to nearly 20 m. Vessels form open tubes that start at various points in the root system and end at various points in the shoot. A stem sample will thus contain some vessels that pass all the way through it (and so will transmit pressurized air), and some that terminate within the sample (which will not let air pass through). Cutting the sample opens some of the latter. Thus, when a twig section is shortened, the air flow rate increases. For a grape twig, for instance, reducing the length from 20 cm to 5 cm nearly tripled the air flow rate. Grape, like other vines, is well known for having very long vessels. On the other hand, sugar maple has rather short vessels. For this species, no air flow was detected for samples longer than 5 cm. White cedar did not allow any air to pass until the twig was shortened to 1 cm.

It should be noted that this method can only be used for rough comparisons of speices, since the pressure gradient per unit length (ΔP/Δx) changes as sections of twig are removed.

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Questions for Students

1. Make a graph showing your relationship between mean vessel diameter and air flow rate. What is the relationship? How do these results relate to the Poiseuille equation?
2. You measured only the diameters of the largest tracheary elements. Why is this a legitimate simplification?
3. What factors might explain deviations between our observations and results expected from the Poiseuille equation? Consider fluid flow in tracheids *vs.* vessels, and in ring-porous *vs.* diffuse porous species. What further measurements or calculations could you make to correct for these factors?

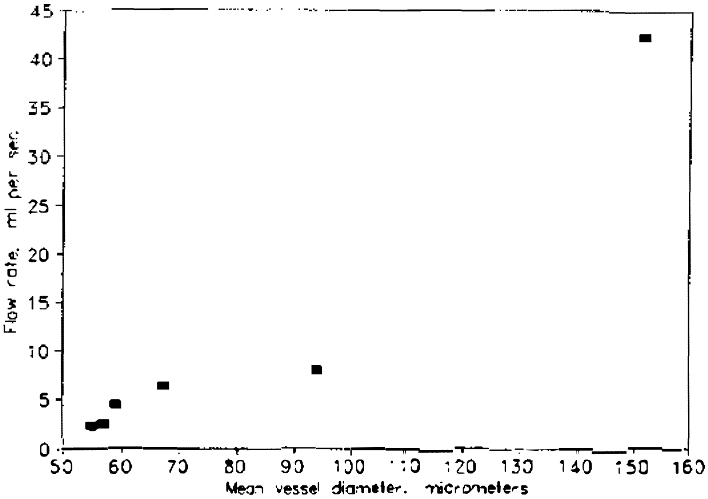

Figure 2. Relationship between the mean vessel diameter in wood samples and the rate of air flow through the samples.

4. It is frequently found that flow rates are much less than those predicted by the Poiseuille equation. What features of tracheary elements could explain this deviation? (Hint: The equation was developed for capillary tubes with completely smooth inner walls. Is this an accurate description of a tracheid or vessel element?)
5. Why did the gas flow rate increase in shorter twig samples? What can you infer from the relative lengths of vessels in different species? Why was the gymnosperm wood so different from the other species?

6. Given that large-diameter vessels can transport water most rapidly, why do some plants have small-diameter vessels or even lack them entirely?

Modifications

I have had students in introductory biology classes and in field courses do a similar exercise using lung power rather than compressed air. A length of straw can be inserted in the tubing as a disposable mouthpiece. Students are surprised by the length of stem through which they can blow air, especially if a vine is used.

Xylem anatomy and function are known to vary with environmental moisture supply. Sampling plants from habitats that differ in soil moisture might yield some interesting results.

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Editor's Note: The two reviewers liked this article very much; however, they also were concerned about more items than we would normally expect the author to have to substantially revise their manuscript. Therefore, some of their concerns are shared here because they may help others to supplement this laboratory exercise in ways that the reviewers believe would be profitable.

"Love the approach! We need more interactive, undergraduate botany labs like this! However, I'm uncertain of the conclusions. Why not leave the lab open-ended and have students hypothesize about and support the differences?

Some of the explanations are too incomplete and all of the references are from secondary sources. While Zimmerman (1983) is a fine monograph, it would be helpful if students were also pointed to some of his original research (Zimmerman 1978, Jeje and Zimmerman 1979) on hydraulic architecture and resistance to water flow. Ziegler (1982?) also has an excellent introduction to the biophysics of water movement in plants that illustrates several apparatuses for measuring positive and negative pressure gradients. Two other aspects that would be helpful to students (especially given some of the author's challenges to students) are the theoretical basis (Aifantis 1977; Rand 1983; Tyree 1988) of fluid mechanical models of plants and the evolutionary analyses of interspecies comparisons (Niklas 1984, 1985). Gartner et al. (1990) provide recent research on anatomical features that may account for the differences in conductivities of vines and trees as emphasized in the discussion by the author. Please give students the resources and freedom to explore such an interesting approach that you have developed."

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