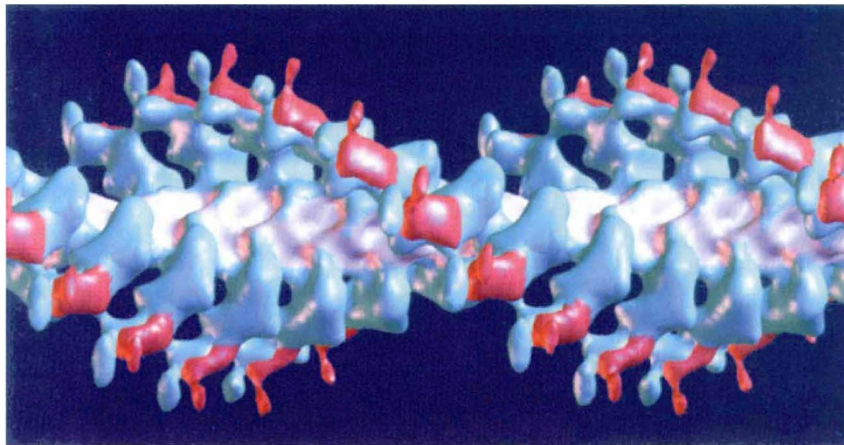


Hops, steps and jumps



EVER since 1771, when Luigi Galvani hung out frogs' legs in a thunderstorm, the determination of how muscle contraction takes place has been at the forefront of biophysical research. In two papers on pages 748 and 751 of this issue, Milligan, Sweeney and colleagues take one of the major steps in this quest. The power house of contraction is the protein myosin (red and blue in the figure) which acts against the filamentous protein actin (white in figure). Through sophisticated processing of electron microscopy images, the conformation of myosin with (red) and without (blue) bound ADP (a change thought to be a major part of myosin's powerstroke) is revealed. The head domain remains essentially immobile against the actin while an extended 'arm' pivots through upwards of 20° producing a potential movement of at least 35 Å. (The figure shows an actin filament decorated with smooth muscle myosin; graphics by A. J. Olson, D. Goodsell and G. Morris of Scripps Research Institute.) Christopher Surridge

Unlike the cohesion mechanism, the root pressure mechanism requires metabolic energy to drive the uptake of solute and it does play a role in plants in the absence of transpiration. The highest root pressures measured are around 5 to 6 bar⁷. Because the osmotic pump mechanism cannot compete with the loss of water caused by transpiration, there is no positive pressure in the root xylem during transpiration. This would require large amounts of nutrient salts to be taken up at high energy cost and would cause problems in getting rid of the solutes in the shoot as the water evaporates.

Pressure probes⁸ can be used to puncture individual xylem conduits of transpiring plants and to measure xylem pressures directly⁹⁻¹¹, and the results suggest that pressures are much higher (less negative) than those obtained by conventional (indirect) techniques. Tensions were found to be hardly larger than 5 bar, with only subatmospheric (still positive) pressures in many cases. It was concluded that although there may be some contribution of tension to the overall flow, this is not the main mechanism. These conclusions have brought the validity of the cohesion theory into question.

Holbrook *et al.*² and Pockman *et al.*³ have now added to the debate. Both groups used a similar technique which circumvents the problems inherent in the more direct methods. Stem segments of trees were spun in a centrifuge to create

tensile forces and equivalent negative pressures acting on the xylem sap — a 40-year-old technique¹² adapted here for plants. Holbrook and co-workers detected changes in the water potential of the twig which were associated with the change in tension. Tensions of up to 15 bar could be created in the xylem by centrifugation and measured as an equivalent decrease in water potential.

Pockman *et al.* measured the increase in axial hydraulic resistance caused by cavitation as a function of tension (spinning rate). They were able to detect the critical tension that could be maintained in the xylem conduits. The results indicated that the vessels of the trees used remained water-filled at tensions of up to 35 bar, depending on the tree species — tensions that were never reached using the pressure probe. The authors then went a step further. They related the critical tension that caused cavitation to the external gas pressure that produced air seeding in stem sections, and found that these pressures were quite high and similar to those that caused cavitation during spinning. Although the approach is indirect, these cross-check experiments provide strong evidence for the maintenance of fairly negative pressures in xylem vessels of transpiring plants and support the cohesion-tension mechanism.

It might be argued that the range of tensions measured by Pockman *et al.* and by Holbrook *et al.* are too high, and that

liquid water is unlikely to sustain such tension without cavitation (although this can be avoided if gas nucleation is suppressed). Experimental values for the tensile strength of water range between 50 and 2,000 bar¹²⁻¹⁶. They are much lower than theoretical estimates in the absence of seeding, which has been put down to catalytic effects of the walls or of impurities present during the formation of gas nuclei¹⁷⁻¹⁹. Nevertheless, experimental values of the tensile strength of water, as measured in physics and physical chemistry, are sufficient to support the new results^{2,3}.

These results also serve as a warning that direct measurements of negative pressure with probes have to be taken with caution because of cavitation problems. We do not yet know whether current pressure probe techniques are able to measure tensions of the magnitude predicted by the indirect measurements, which may be as large as say 20 to 30 bar, without cavitation. So far, artificial systems have not been tested to demonstrate this crucial point, which means that conclusions drawn from pressure probe experiments about the existence of high tensions are suspect. We need further improvements in this technique.

Although the results of Pockman *et al.* and Holbrook *et al.* still provide only indirect verification of the cohesion theory, they indicate that it has a sound physical basis and that botanists have not been deluding themselves all these years after all. □

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1. Kramer, P. J. & Boyer, J. S. *Water Relations of Plants and Soils* (Academic, San Diego, 1995).
2. Holbrook, N. M., Burns, M. J. & Field, C. B. *Science* **270**, 1193-1194 (1995).
3. Pockman, W. T., Sperry, J. S. & O'Leary, J. W. *Nature* **378**, 715-716 (1995).
4. Scholander, P. F., Hammel, H. T., Bradstreet, E. D. & Hemmingsen, E. A. *Proc. natn. Acad. Sci. U.S.A.* **52**, 119-125 (1964).
5. Pfeffer, W. *Pflanzenphysiologie, Erster Band* (Engelmann, Leipzig, 1897).
6. Plumb, R. C. & Bridgman, W. B. *Science* **176**, 1129-1131 (1972).
7. Steudle, E. *Pl. Soil* **167**, 79-90 (1994).
8. Steudle, E. in *Water Deficits: Plant Responses from Cell to Community* (eds Smith, J. A. C. & Griffiths, H.) 5-36 (Bios Scientific, Oxford, 1993).
9. Zimmermann, U., Haase, A., Langbein, D. & Meinzer, F. *Phil. Trans. R. Soc.* **B341**, 19-31 (1993).
10. Zimmermann, U. *et al.* in *Water Deficits: Plant Responses from Cell to Community* (eds Smith, J. A. C. & Griffiths, H.) 87-108 (Bios Scientific, Oxford, 1993).
11. Zimmermann, U. *et al.* *Pl. Cell Environ.* **17**, 1169-1181 (1994).
12. Briggs, L. J. *J. appl. Phys.* **26**, 1001-1003 (1955).
13. Berthelot, M. *Ann. Chim. Phys.* **30**, 232-237 (1850).
14. Tempeley, H. N. V. *Proc. phys. Soc.* **59**, 199-208 (1946).
15. Green, J. L., Durben, D. J., Wolf, G. H. & Angell, C. A. *Science* **249**, 649-652 (1990).
16. Ursprung, A. *Ber. Deutsch. Bot. Ges.* **33**, 153-162 (1915).
17. Kenrick, F. B., Wismer, K. L. & Wyatt, K. S. *J. phys. Chem.* **28**, 1308-1315 (1924).
18. Greenidge, K. N. H. *Am. J. Bot.* **41**, 807-811 (1954).
19. Fisher, J. C. *Appl. Phys.* **19**, 1062-1067 (1948).