

Sap Pressure in Vascular Plants

Negative hydrostatic pressure can be measured in plants.

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The cohesion theory (1), proposed independently by Dixon and Joly (1894) and Askenasy (1895), has been recognized since the turn of the century as the only consistent theory explaining how sap can be lifted ten times higher by a tree than by a vacuum pump. It assumes that evaporation from the leaves pulls cohesive water through the tree and that cavitation is prevented by the dimensions of the capillaries of the conductive system. A pressure of at least -20 atmospheres would have to exist at the top of a 100-meter redwood to take care of the hydrostatic gradient of 10 atmospheres and a similar drop caused by flow friction. Ever since its incipience this venerable theory has been beset with seemingly conflicting observations, and the stumbling block has always remained the same, namely, lack of means for measuring negative sap pressure.

Much effort has been expended, of course, to determine this fundamental parameter. Renner (2) observed that water can be drawn through an artificially constricted stem faster by leaves than by vacuum pump, and ideally, if one assumes proportionality between flow rate and pressure difference, the sap pressure can be calculated. Negative pressures were frequently indicated by this approach, but since we have applied the same technique and modifications thereof to material where the pressures are now known, namely, mangroves, we may state that the values obtained are generally far off the mark. Arcichovskij and his collaborators (3) measured the concentra-

tion of a sucrose solution that would neither gain nor lose water when in contact with intact cambium or xylem, or both. If the barrier is semipermeable, the sap pressure should equal the osmotic potential of the solution. A birch tree, accordingly, had sap pressure of -37 atmospheres and a desert shrub had -143 atmospheres, with apparent diurnal variations. Rather unlikely gradients were also found, such as 5 atmospheres per meter in the birch and 44 atmospheres per meter in the shrub. In other plants, pressure gradients, because of sap flow, are more like 0.1 to 0.2 atmosphere per meter (4). The reason for the discrepancy may have been a shifting base line, but final appraisal of this interesting approach must await further work.

The first truly quantitative study of water under negative pressure was performed by Lyman Briggs (5) in 1950. By spinning a Z-bent capillary across the center of a centrifuge he could put known G forces on the water, and it turned out that the column did not break until it reached -260 atmospheres when at room temperature. This of course does not prove that negative pressure could exist in a tree, for how could broken columns ever be repaired? Why, for instance, would not cosmic radiation cause cavitation in tensile columns, as in the celebrated bubble chamber of Glaser (6)? Furthermore, what happens to tall trees during subzero temperature in the winter? If they freeze the freezing must cavitate the water, for gases have no solubility in ice. Some of these points have been looked into, and it was found that potent ionizing irradiation of a solution from within or from an outside cobalt-60 source would not cavitate water stretched to -20 atmospheres in a spinning Briggs capillary. But when the center of the spinning capillary was

frozen with CO_2 the water cavitated immediately; it was also established that both conifers and hardwood trees readily freeze in the winter, seeding the xylem throughout with visible gas bubbles (7). How are the columns repaired? Only a few trees show positive stem pressures in the springtime.

We meet the problem of tensile water even more forcefully in halophytes, plants living in salty media. Particularly striking are the mangroves and other plants that have roots inundated by sea water. In their classical study of East African mangroves, Walter and Steiner (8) determined the freezing-point depression of juices from crushed roots and leaves and found that it usually exceeded that of sea water. There was no evidence of progressive salt accumulation in the leaves, however, and hence they reasoned that the transpiration stream must be essentially free of salt. Somehow, therefore, the roots must be able to hold back the salts and take in only fresh water, and, assuming this process to be a simple osmotic separation through a semipermeable membrane, they predicted that the hydrostatic pressure in the xylem sap must be at least -24 atmospheres, which would in fact balance the osmotic potential in the sea water and allow for turgor in the cells. They pointed out that this tension naturally would have to exist continuously day and night.

From these considerations it appeared that really high tensions might be found in halophytes rather than in tall trees, and it seemed that a lab bench next to a lowly mangrove bush presented a more favorable approach than simian acrobatics in the fog-shrouded top of even the highest redwood tree, so we decided to have a try at the mangroves first.

On a Scripps expedition to Cape York in northern Australia in 1960 we found, true to prediction, that the xylem sap in all of a variety of mangroves consisted of essentially fresh water. In most species the salt concentration averaged only 1/100 of that of the sea water, but in a few it may rise to 1/10, and in such plants the salts are excreted by special glands on the leaves (9). On a Scripps expedition to Baja California in February and March 1964 the mangroves still held their fascination, and this time instrumentation was contrived aboard ship which at long last provided direct and accurate measurement of the negative pressures (10). Again the prediction held.

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Let us incorporate in a symbolic diagram the relations proposed for mangroves by Walter and Steiner (8) (Fig. 1). A rigid stem is provided with capillary channels so that water under tension will not cavitate. A capillary extension at the top has fine perforations upon which a leaf cell rests. The cell wall is micellar and permits mass flow of water and solutes. It is separated from the cytoplasm by a semipermeable membrane, which permits diffusion of water only. Like a xylem vessel, the capillary has micropore cross walls which permit mass flow of water but not an air-water interface.

the sea water. The hydrostatic pressure of the pure water in the stem and capillaries will therefore be -30 atmospheres.

If there is evaporation from the cell the balance is upset and the activity drop is transmitted through the system to the sea water. The resultant transpiration stream is purely diffusive through leaf and root membranes and depends upon bulk flow through the xylem. Fresh water is pulled from the sea water through a nearly balanced system. Conversely, if it rains on the leaf cell the activity gradients should be reversed, and pure water should diffuse into the sea.

How can we measure the negative pressure within our model system? This is simple indeed. When the capillary is severed (Fig. 1*A*) the water recedes from the cut until it hangs up on the cross wall (Fig. 1*B*). The reason for the recession is, of course, that the pressure was 30 atmospheres higher on the outside than on the inside. If the same difference were to be reestablished the meniscus would move back exactly to the cut. We therefore place the severed system in a pressure bomb, leaving the capillary protruding. Gas pressure is applied, and when the meniscus is back at the cut we have the answer (Fig. 1*C*).

Fig. 2. Pressure bomb for measurement of sap pressure in the xylem of a twig. Left, direct observation; right, stepwise sap extrusion and pressure measurement to obtain a pressure-volume curve.

ing with an elastic system, an osmotic equilibrium, or both. Indeed, if we squeeze out water until the cell becomes limp, the balancing pressure simply measures the osmotic potential in our cell. In general, the technique, to be valid, requires a direct pressure transmission from the outside of the system to the liquid within, and in this respect a leaf is ideal, for its parenchyma cells are exposed to air, and they drain through cell walls and xylem vessels.

The technique of measurement on a leafy twig is straightforward. The bark and phloem are peeled back at the cut end, which is trimmed off with a razor blade. The twig is fitted through the lid of a pressure bomb (Fig. 2). The cut end is sealed air-tight through a rubber compression gland with the free end protruding, for observation through a lens or binocular. As pressure is increased the sap suddenly moves to the surface, where it bubbles vigorously as it spills over. The pressure at which the liquid just wets the surface is noted. This pressure, with a negative sign, ideally equals that which existed in the twig before it was severed from the tree.

Certain precautions must be observed. Evaporation loss from the twig must always be kept to a minimum. It is essential that all the liquid that receded from the original cut be brought out again before the pressure is measured. When the vessel elements are long a significant amount of sap withdraws from the cut, producing a steep rise in the turgor in the leaves. If a piece is then trimmed off to make the twig fit the chamber, the elevated pres-

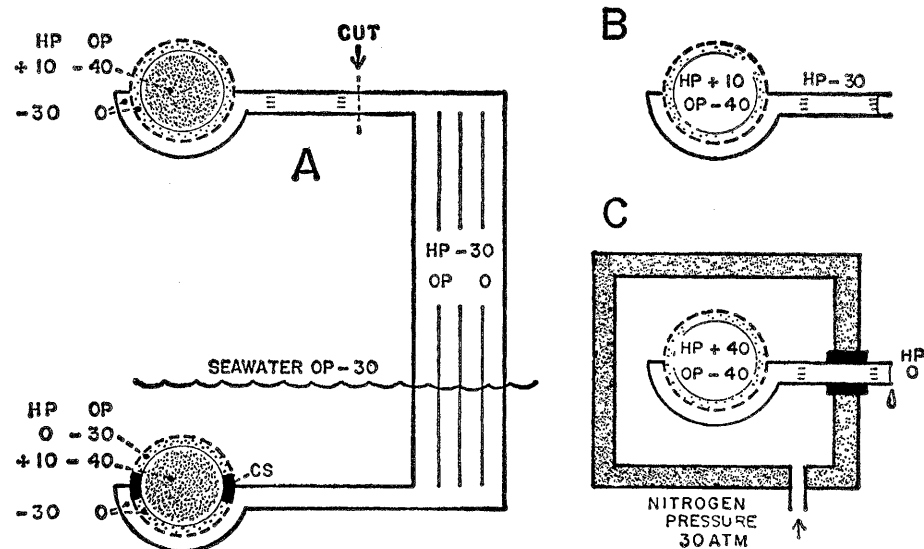


Fig. 1. Schematic concept of water relations in mangroves, incorporating the ideas of Walter and Steiner (8). (A) Complete model with vascular stem and semi-permeable leaf and root cells. CS, Casparian strip. (B) Leaf capillary severed, with meniscus receded and hung up on a cross wall. (C) Leaf capillary in pressure bomb, with meniscus freed by the balancing pressure. HP, change in hydrostatic pressure from 1 atmosphere ambient. OP, change in activity of water by solutes. All numbers are atmospheres. Turgor is difference between intracellular hydrostatic pressure and extracellular pressure (10 atm in A, B, and C).

sure persists and gives a wrong reading for the tree. It is therefore necessary to cut the proper length from the tree and carefully limit the trimming. In conifers the very short tracheids make repeated cutting no great concern, nor do the mixed vascular bundles of the monocotyledons offer any special problem as long as the individual xylem vessels are clearly seen. Many plants, however, have a stem so weak that the vessels are obliterated by the pressure seal.

When carefully executed, this technique will give the sap pressure that existed in the twig at the time of cutting. Reproducibility of repeated readings is very good, usually within 1 percent.

Sap Pressure in Relation to Habitat

In Fig. 3 a series of sap pressures is presented which were taken for the most part in the daytime. A great variety of vascular plants always showed negative pressures, ranging from some -5 to -80 atmospheres. The considerable variability depends upon such obvious factors as soil satu-

ration and air humidity, and in all cases tested there is a marked diurnal variation, commonly of 10 to 20 atmospheres. Many desert plants have very high negative pressures, with the California juniper and the creosote bush so far holding the records.

Plants under the damp forest canopy had little suction, but it is remarkable that those that grew in fresh-water lakes nevertheless had 5 to 10 atmospheres of negative pressure.

It is of particular interest that halophytes (the mangroves, *Salicornia*, *Batis*, and others) have strong negative pressures ranging from some -35 to -60 atmospheres, as against osmotic potential of about -25 atmospheres in the sea water. This gives them an ample margin for obtaining fresh water from the ocean by transpiration and diffusion at the roots, and such indeed seems to be the mechanism. Thus, the activity of the water in the sea is always higher than that of water in root cells, xylem sap, or leaf cells. It is immaterial in this context whether the transpiration stream passes through the cytoplasm of the leaf cells or whether it goes around the cytoplasm within

the micellar cell walls. In either case the evaporative surface is a semipermeable membrane in the sense that it passes only water molecules.

The sap pressure in leafy twigs of some typical "tank" trees was measured near the Vermillion Sea Field Station of the Natural History Museum of San Diego in Baja California (each number represents a different plant):

Boojum tree (*Idria columnaris*), -6.1 , -6.8 , -8.8 atm.

Elephant tree (*Bursera Hindsiana*), -9.2 , -10.5 atm.

Elephant tree (*Bursera microphylla*), -6.8 atm.

Elephant tree (*Pachycormus discolor*), -16.7 atm.

Cactus (*Opuntia tejaho*), -13.6 atm.

The suction in all these extreme desert plants was moderate. It had rained 1 month earlier and undoubtedly, like cacti, these plants avoid excessive tension by storing water. Presumably the leaves are shed early, before the tension has risen much.

The hydrostatic pressures in some mistletoes as related to those in their host plants are presented in Fig. 4.

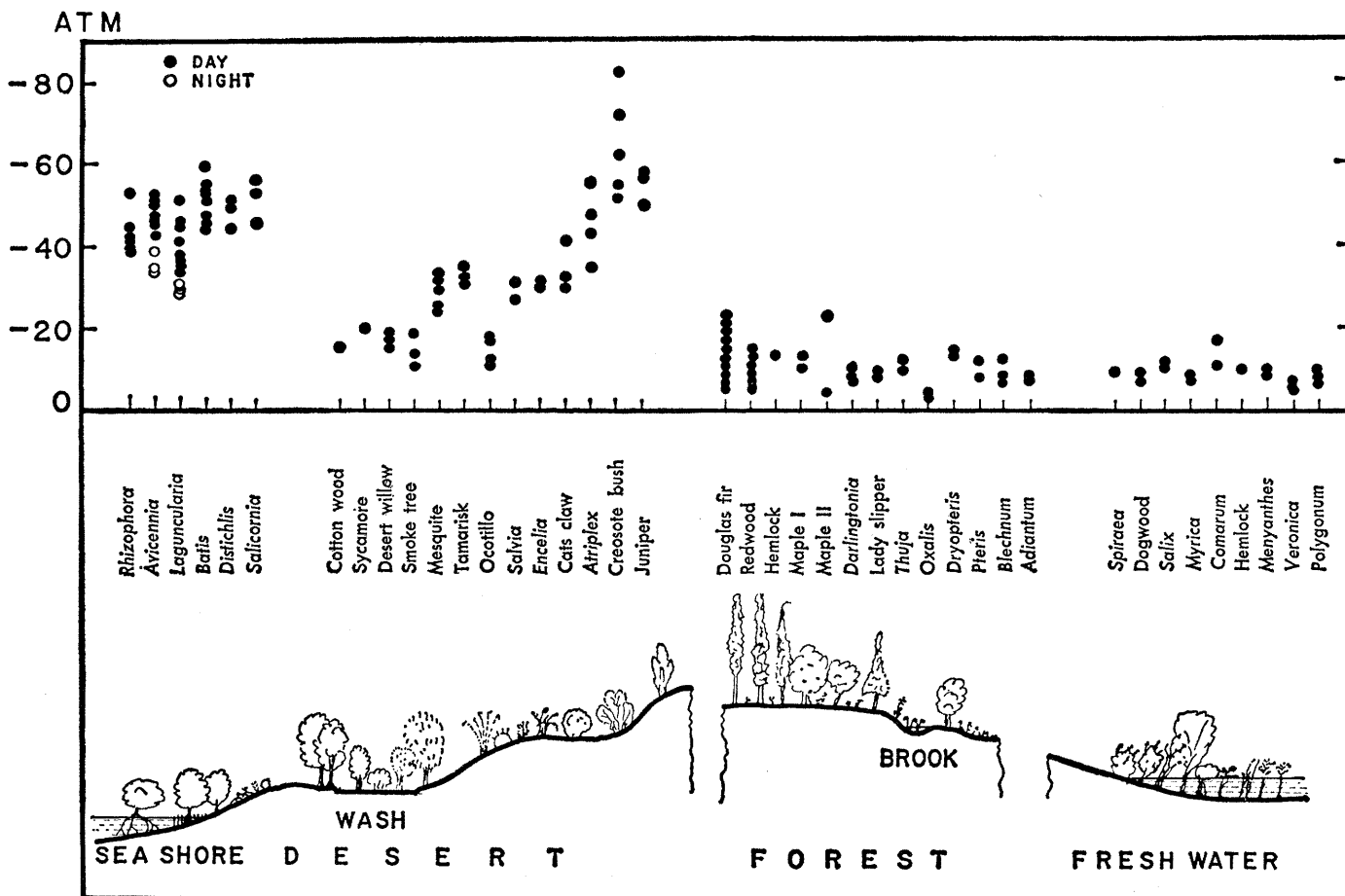


Fig. 3. Sap pressure in a variety of flowering plants, conifers, and ferns. Most measurements were taken during the daytime in strong sunlight. Night values in all cases are apt to be several atmospheres less negative.

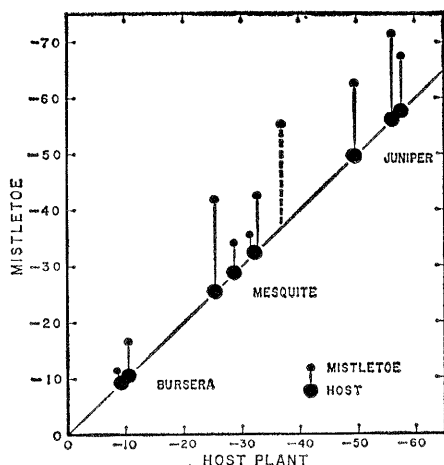


Fig. 4. Sap pressure (atmospheres) in mistletoes and their host plants, *Phoradendron californicum* on mesquite, *Phoradendron bolleanum* on the California juniper, and *Phrygilanthus sonora* on *Bursera Hindsiana*.

Without exception the parasite was able to outsuck its host, often by 10 to 20 atmospheres, and the expressed sap in both is close to fresh water; that is, it had a freezing point near -0.01°C . What maintains this pressure difference? Does it disappear at zero transpiration?

Sap Pressure in Relation to Height

A simple capillary transport system would exhibit an exact hydrostatic gravity gradient when there is no flow. In the springtime, before the buds are bursting, the grapevine, birch, and a few other trees have positive sap pressures which may reach several atmospheres. In that situation pressures can be easily and accurately measured, and

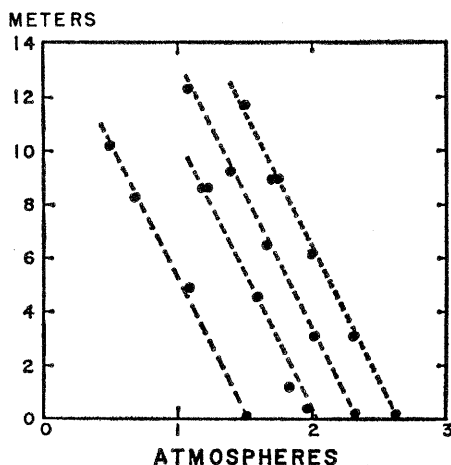


Fig. 5. Hydrostatic gradients in grapevines (*Vitis labrusca*) in the springtime, before the leaves are out (11). Dotted lines represent the gravity gradient.

they present an exact gravity gradient of 0.1 atmosphere per meter (11) (Fig. 5).

With our new pressure-bomb technique it was tempting to look for a hydrostatic gradient in trees under their normal negative pressure conditions. Obviously the taller the tree the better our chances of success, and through the cooperation of the Weyerhaeuser and Arcata companies we were able to measure tall Douglas fir and redwood trees in southern Washington and northern California, respectively.

How then to obtain samples from the top of these trees? A helicopter was one possibility, but it was unduly risky for trees and men. A high-climbing rigger cuts the branches off as he goes up, thus we were left with the prospect of shooting the twigs down. We needed the tallest possible tree with, at the same time, a low branch, and the tree had to be free standing so the twigs would not be caught in other trees. Since it could be anticipated that the pressure would change rapidly with changing humidity, repeats would be necessary in order to determine the drift of the base line. Ideally, one shot should bring down both twigs at once, and preferably at night, but our marksman, Paul Fleischer, felt that one little twig 100 meters up and swaying in the breeze provided challenge enough for him, even in the daylight. He chose to pick the twigs off one after the other, while repeated sampling and accurate timekeeping kept track of any base line drift.

As the twig came sailing down it was usually captured in the air, placed in a vapor-tight bag, and sprinted to the instrument table at the base of the tree. From the time of shooting it took between 3 and 5 minutes to get the twig safely into the bomb, and for about half of this period exposure was unavoidable. Serial checks on twigs from the same branch showed that the tension increased by about 1 atmosphere per 5 minutes of exposure in the early morning and twice as fast during midday. High and low samples behaved alike, so errors in the pressure difference are likely to be less than 1 atmosphere. The heights were measured by expert foresters.

The results of the shooting are shown in Figs. 6 and 7. The elevations of high and low branches are drawn as lines, and, taking the top pressure arbitrarily as standard, we have plotted the low twig down from this in terms of hydrostatic drop. It will be seen that

there is an apparent agreement between the pressure drop and the vertical distance. Similar results were obtained on redwood trees where intermediate twigs also were shot down.

One would have expected, especially during the midday transpiration, that the pressure drop would be greater than the height difference. Even though seemingly too small, our gradients at least came out right side up (12).

Let us scrutinize the relation of sap pressure to osmotic potential by returning to our model (Fig. 1C). If external gas pressure is applied in excess of the balancing pressure, pure water runs out, and at zero turgor the molal concentration in the cell should therefore be proportional to the sap pressure, according to the following equation:

$$S/(I - V) = KP$$

or, restated,

$$I - V = K_1 P^{-1},$$

where S stands for the solutes, I the cell volume, V the water run out, and P the equilibrium pressure. If, therefore, we plot the inverse of the pressure ($1/P$) against liquid removed (V) we get a straight line whenever the concentration is proportional to the pressure, and the intercept with the abscissa gives the volume of water that is being concentrated—that is, the intracellular water (I). We disregard the elastic deformation of the capillary.

When we put a twig in the pressure chamber in such a way that the extruded liquid can be collected (Fig. 2), we find that the liquid is always accompanied by more or less gas coming from inactive xylem vessels or pith. If the gas yield is low, as in most conifers, a train of drops will flow slowly through the discharge tube, and both volume and equilibration pressure can be accurately determined. In some hardwoods, however, the gas flow may be too large for useful measurements. It is essential that leaf stalks be neither kinked nor broken, for the pressure may easily collapse damaged channels, excluding leaf tissue from the measurement. This need not invalidate the curve, but the total water will be wrong.

It will be seen from Figs. 8 and 9 that, except for one or two points in the beginning, the curves remain linear until about half the intracellular water has been yielded, which means that the pressure drops linearly with the molal concentration. It is crucial that the fluid

yielded is practically fresh water with a freezing point depression of at most 1/100 or a few hundredths of 1 degree Celsius. This holds for every one of 26 species of flowering plants and conifers tested, including extreme halophytes and desert plants. The first portion that comes out is contaminated with normal xylem sap which is usually a little higher, and toward the end there is generally also a rise, but neither of these elevations is significant compared with the high concentration of the cell sap. *Avicennia* and a few other salt-

secreting species normally carry 0.2 to 0.3 percent salt in the xylem sap, but even so the leaves of *Avicennia* yield practically fresh water when under pressure in the bomb.

The initial points of the curves normally show a steep fall which is caused by loss of turgor in the parenchyma cells. Thus if the petiole is cut off under water and joined without air contact to a graduated capillary with gas-free water, the drinking and transpiration rates can be determined simultaneously by putting the assembly on a

balance. It will be seen from Fig. 10 that the drinking, upon release of the negative pressure, shoots up tenfold or more. When steady state has been attained the leaf may have added only 10 percent to its intracellular water, and still the xylem pressure has risen from -40 atmospheres to ambient pressure. Taking into account a 10-percent dilution, this corresponds to a rise in turgor pressure of 36 atmospheres. The turgor pressure, therefore, nearly equals the pressure drop down to the linear part of the curve.

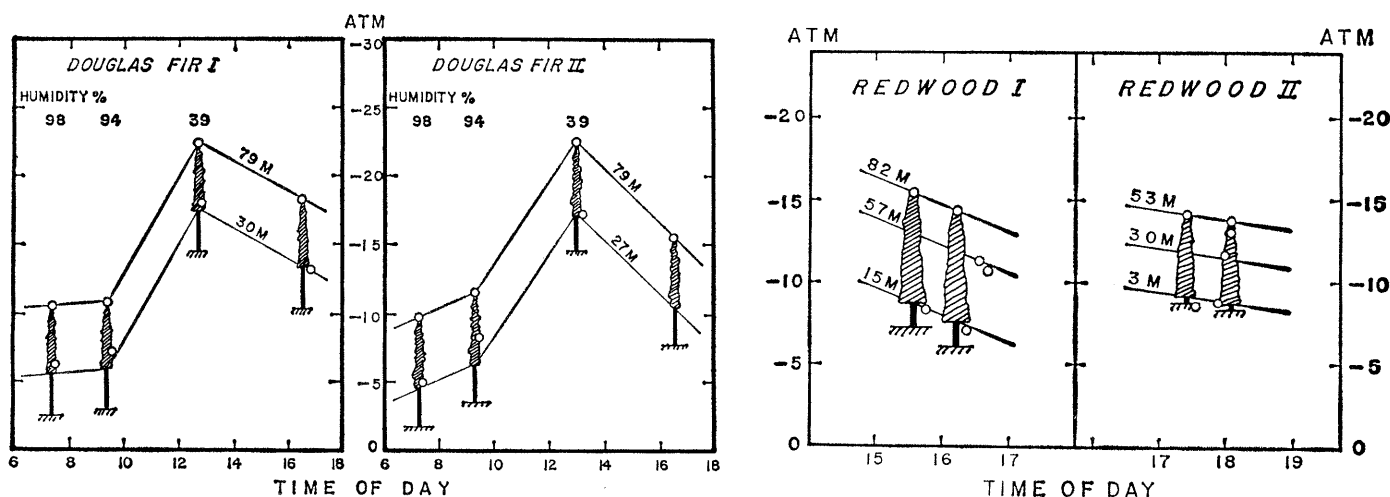


Fig. 6 (left). Hydrostatic gradients in two Douglas firs. Samples obtained by shooting down twigs. The true elevations are indicated by lines and the circles denote the pressures at a given clock time, taking the top measurement arbitrarily as a standard. Fig. 7 (right). Hydrostatic gradients in two redwood trees, denoted as in Figs. 5 and 6.

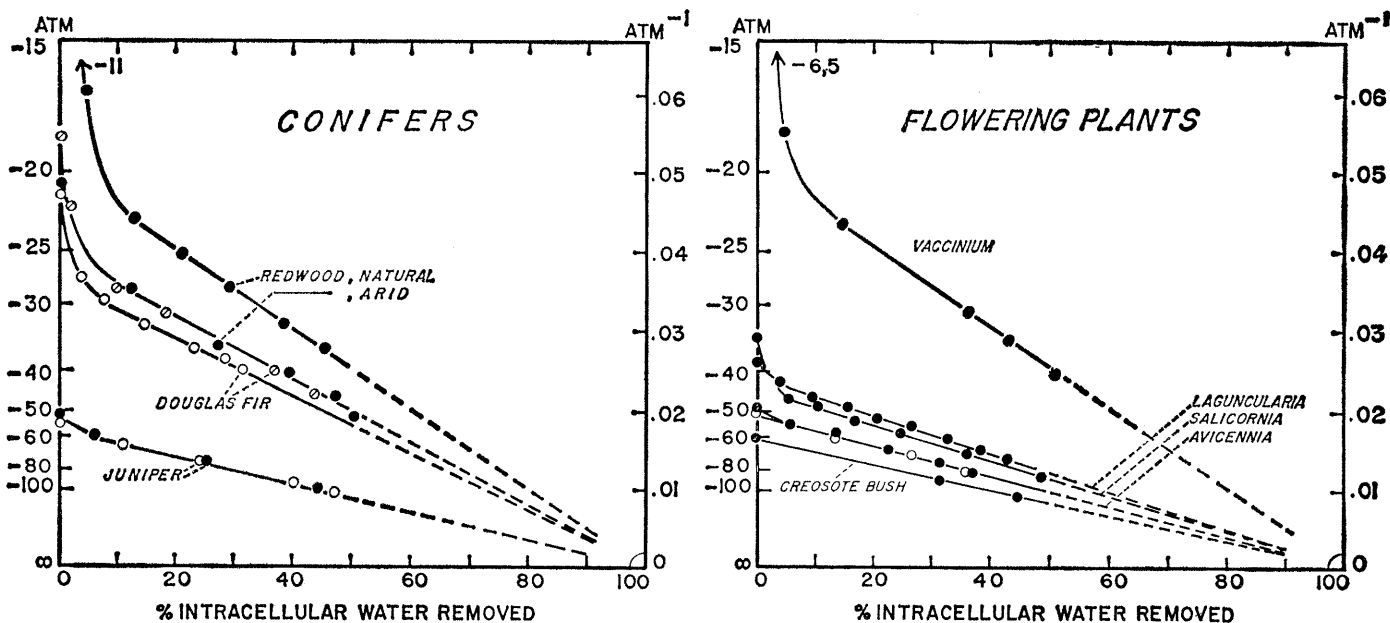


Fig. 8 (left). Pressure bomb experiments measuring the gradual increase in balancing (sap) pressure as water is extruded. The initial steep drop to the straight part of the curves measures in atmospheres 90 percent or more of the turgor. The linear part (zero turgor) demonstrates proportionality between intracellular concentration and balancing pressure. The hypothetical intercept within the abscissa gives the intracellular water volume, here called 100. Total water in the leaf is then: Redwood, 109, 112; Douglas fir, 135; California juniper, 150. Fig. 9 (right). Pressure-volume curves in various hardwoods. Intracellular water volume, 100. Leaf water volumes: *Vaccinium atrococtum*, 114; *Laguncularia*, 115; *Salicornia*, 110; *Avicennia*, 115; *Larrea*, 132.

Sap Pressure in Relation to Osmotic Potential

If we wish to compare the osmotic potential of parenchyma cells with the balancing pressure it is expedient to be on the linear part of the pressure-volume curve.

1) The pressure-volume curve is taken, and the water left in the leaves is immediately measured by drying and weighing, stems and midribs being left out. The curve is plotted, showing the intracellular intercept and the total water (10).

2) A neighboring twig is pressed in the bomb or simply left drying until enough water has been yielded to give zero turgor, let us say, at -40 atmospheres. The leaves, stripped of stems and midribs, are stuffed into a Tygon tube, which is closed and frozen on CO_2 ice. When thawed, the tube is crushed in a powerful vise as the sap is collected. The freezing point is determined in the clear filtrate (13). To derive from this the intracellular freezing point, a correction for dilution with extracellular water must be made by multiplying with the ratio of total to intracellular water, both defined at the same pressure, which is 40 atmospheres in this case.

In Fig. 11 such determinations at zero turgor pressure have been made

on a variety of halophytes and trees, and the freezing-point depressions are correlated with the equilibrium pressures corrected to 25°C , where -1.86°C corresponds to an osmotic potential of -24.5 atmospheres. All the data fall remarkably close to the theoretical line, showing that the leaves behave indeed very nearly like osmometers, in complete conformity with the observation that nothing but water is extruded.

Figures 8 and 9 also show that the slope of the curves reflects the habitat of the various plants. The normal redwood growing in a foggy coastal area is relatively well hydrated in comparison with one individual artificially eking out its life in arid La Jolla. The latter has more solutes in its leaves to support the high transpirational pull necessitated by the arid soil. Indeed, whenever a plant wilts, "suction," and hence its power to get water, goes up automatically. In line with this, the highest suction (80 atmospheres) that we have so far encountered was found in a creosote bush after many months of drought. Very low pressure also exists in the California juniper, which bears a mistletoe with an even lower pressure. The curves also reveal the degree of turgor in the leaves and in general reflect the state of hydration in the plant.

Experiments with Pressure on the Roots of Mangroves

In a balanced system like that in Fig. 1, a change in the diffusion pressure of water at either top or bottom would activate a fresh water transport through the xylem. If the substrate were diluted by rain, or if the hydrostatic pressure were raised, one would expect water to diffuse into the xylem. This was tested by placing a potted mangrove plant in a large pressure bomb with the bared xylem stump protruding through the pressure seal (Fig. 2, right). Several plants had been potted 1 to 2 weeks before the experiments and watered with sea water. They all had turgor and looked reasonably well.

All but one of these leaked sea water when pressure was applied. This one, a *Laguncularia* with nine leaves, must have healed the root damage completely. When decapitated and placed in the bomb it showed a normal balancing pressure (51 atm), and when the pressure was raised to 68 atmospheres it yielded 2 cm^3 of water in 6 hours, with the rate dropping to half. The first 0.2 cm^3 had 0.3 percent chloride, and the next three samples all had only 0.14 percent, which is normal stem sap for this species. The total water in root and stem was 4.3 cm^3 , about 2 cm^3 of

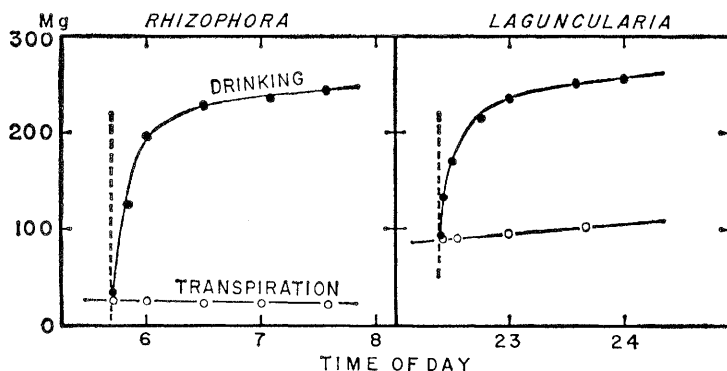
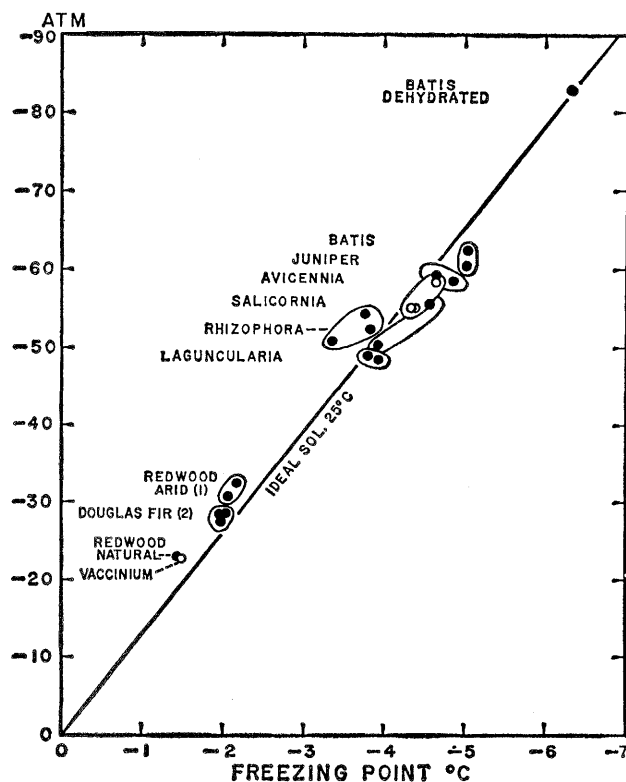


Fig. 10 (above). Accelerated drinking when negative pressure is relieved in the leaves of two mangroves. The vertical distance between the curves is the accumulation of water. *Rhizophora* increased its water content by 9 percent, and *Laguncularia* by 11 percent, while the sap pressure rose from near -40 atmospheres to ambient. Fig. 11 (right). Freezing point of juices from crushed leaves in relation to sap pressure measured at zero turgor. Freezing points corrected for dilution by extracellular water. (Factors: *Batis*, 1.27, 1.20; *Juniperus*, 1.55; *Avicennia*, 1.17; *Salicornia*, 1.14; *Rhizophora*, 1.20 (guessed at); *Laguncularia*, 1.18; *Redwood*, 1.10, 1.15; *Douglas fir*, 1.36; *Vaccinium*, 1.16.) "Ideal solution" line drawn to fit 25°C .



which could have been intracellular and would yield no more than 1 cm³ of water. This would double the intracellular concentration and hence would require a pressure of 100 atmospheres. The water was therefore yielded by the substrate. Hence the slightest evaporation from the leaves is adequate in itself to produce a transpiration stream of pure water derived from the sea water.

The Semipermeable Membrane

The pressure-bomb experiments on leaves demonstrated that we are dealing with a semipermeable system which has various exceptionally well-known parameters, most strikingly displayed perhaps in halophytes (Fig. 12).

The cell wall is generally considered a direct flow extension of the xylem system, and as such it carries a sap which is practically pure water and permanently under high tension, -40 to -60 atmospheres, or even -100 at wilting. The high negative pressure within the wall is made possible by a crushproof micellar structure and by the mechanical strength of the limiting membranes, the outer being the surface tension of water and the inner being the plasma membrane of the parenchyma cell.

When the turgor pressure of the cell is zero (at 1 atm) the intracellular freezing point reveals a water activity that closely matches that of the tensile water in the cell wall—that is, there is a near diffusion equilibrium across the membrane with respect to water. At 50 atmospheres balancing pressure the measuring sensitivity may easily be within 0.5 atmosphere, which corresponds to a diffusion pressure difference of less than 0.01 mm vapor pressure. So at equilibrium the plasma membrane and/or the cytoplasm, although exquisitely sensitive to a diffusion unbalance, neither passes water nor solutes even in the face of a hydraulic differential of 100 atmospheres. Formally we have interpreted this to mean that the *activity* of the water is the same throughout the system.

Informally one may observe that the osmotic-hydrostatic relations become less round-about by stating that the solute molecules behave *as if* they exert an expanding force upon whatever barrier retains them. If the barrier is simply the surface of the solution, the

solvent water would be expanded to -22.4 atm/mol, which agrees with the observed lowering of the vapor pressure. If the retention is made by a semipermeable net or membrane this alone would bear the solute force, leaving untouched the hydrostatic pressure of the solvent water, which conforms with the observed vapor tension. There would be no hydrostatic solvent gradient through the membrane. In Fig. 1 all components, sea water included, behave *as if* the pure water were expanded to -30 atmospheres. The mechanical support for the negative pressure ranges in dimension from capillary in the xylem, to quasi colloidal in the cell walls, and changes to solute kinetics in the sea water and intracellular fluids. The mangroves must simply match the negative pressure of the solvent water in the sea.

The pressure-volume curves were routinely obtained by pressure from a nitrogen cylinder. There was no indication that the results were different whether the original oxygen tension from the air was left in or flushed out. In one case the leaves of an *Avicennia* twig were soaked in a saturated solution of dinitrophenol for 30 minutes before testing in the pressure bomb. The curve was perfectly normal and the expressed fluid had as little chloride as usual. We do not know, however, how much of the poison penetrated into the cells (Fig. 9, open circles).

Summary

A method is described which permits measurement of sap pressure in the xylem of vascular plants. As long predicted, sap pressures during transpiration are normally negative, ranging from -4 or -5 atmospheres in a damp forest to -80 atmospheres in the desert. Mangroves and other halophytes maintain at all times a sap pressure of -35 to -60 atmospheres. Mistletoes have greater suction than their hosts, usually by 10 to 20 atmospheres. Diurnal cycles of 10 to 20 atmospheres are common. In tall conifers there is a hydrostatic pressure gradient that closely corresponds to the height and seems surprisingly little influenced by the intensity of transpiration. Sap extruded from the xylem by gas pressure on the leaves is practically pure water. At zero turgor this procedure gives a linear relation between the intracellular

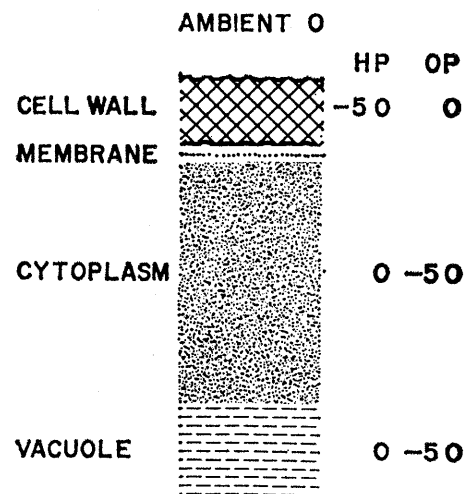


Fig. 12. Schematic section of leaf parenchyma cell bordering a gas phase. The gas interphase is symbolized with concave menisci. HP, hydrostatic pressure; OP, osmotic potential.

concentration and the tension of the xylem.

From this pressure-volume curve one may extrapolate the intracellular water volume. The osmotic equivalent of the intracellular freezing point matches closely the xylem pressure when the turgor is zero. The sap pressure in mangroves, balanced by a similar osmotic potential in root and leaf cells, is low enough (-35 to -50 atmospheres) to diffuse fresh water out of the sea and into the root by simple reversed osmosis. The pressure-volume curve gives a striking picture of the water stress of a plant and reflects with fair accuracy the turgor of the leaf cells. The semipermeable membrane separating the micellar wall from the cytoplasm is subjected to a very high (up to 80 atmospheres) hydrostatic-pressure difference.

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and D. C. Bingham at Longview, Washington; the Arcata Redwood Company, represented by E. A. Hofsted in Humboldt County, California; the Natural History Museum in San Diego and its director, Dr. E. Yale Dawson; and the staff of "Serenidad," in Mulege, Baja California. Plant identifications were provided by Dr. Reid Moran of the Natural History Museum in San Diego, and stimulating discussion by Dr. George G. Laties from the University of California at Los Angeles, Dr. Anders Kylin from Riverside, and Dr. Andrew A. Benson and Dr. Theodore Enns at San Diego.

NEWS AND COMMENT

Crisis at Berkeley: (II) The Second Front

A few months after the student uprising last December, it appeared that the University of California had resolved some of its problems and would return to normal pursuits. At the beginning of March, the Berkeley campus appeared pacified. Many people, to be sure, particularly in the administration, felt that the fall's events had seriously eroded the regard in which the people of California held the university, and that the damage to fund-raising, appropriations, and the university's general reputation was likely to be irreparable. Many others, however, among both faculty and students, felt that the crisis had been productive, not only in affirming a principle of political freedom but in refreshing an academic atmosphere that some felt had gone somewhat stale. It was common, in interviews with students, to hear variants of the sentiment expressed by one undergraduate involved with the Free Speech Movement, who commented, "That was the first time I felt that faculty members took students seriously." Many faculty members seemed almost grateful to the students for having jogged their political consciences. "We had a lot to learn from them," one physicist remarked, and several faculty members expressed views similar to that of the sociologist who stated that he was "deeply impressed by the earnestness, dedication, and basic moral enlightenment" of the students he encountered. As for the administration, many tensions remained, but Acting Chancellor Martin Meyerson was proving almost magically popular, gaining the confidence of students

and faculty alike, not only for his liberal approach to the problem of campus politics but for his interest in educational reform.

Then came the cataclysm. Although the obscenity controversy has been treated as a major demonstration, the key episodes actually involved only nine individuals, only three of whom were students. A young boy, a nonstudent, sat on the steps of the student union one day holding a placard containing an obscene word. When he was turned over to the police, a handful of his acquaintances (students and nonstudents) set up tables to collect money for his defense, marking the tables with signs saying "F. . . Defense Fund," and making speeches using the word. When they too were arrested, still another boy became involved, reading to the police from the last page and a half of *Lady Chatterley's Lover* (in which the word occurs several times), a work which is protected by court decision and is further sanitized by a preface by Berkeley English professor Mark Schorer. This boy was arrested also, and his copy of *Lady Chatterley* temporarily confiscated.

On the campus, the events provoked little response. There was little enthusiasm for the issue, little inclination among either students or faculty to defend the obscenity, and almost no objection as the administration prepared to initiate disciplinary proceedings. Elsewhere in the state, however, in Sacramento, within the Regents, among alumni, and within the population generally, there were serious reverberations.

"Public opinion" is usually a tricky and amorphous thing to measure, but in this case there could be no doubt: it turned against Berkeley with incredible passion.

Why the reaction was so severe is by no means certain. One reason is that, although many students take a fairly relaxed view of obscenity, it makes many adults apoplectic. As the *Lady Chatterley* decision suggests, the students are products of a time when public standards of morality are very much in flux. They are not really sure what is allowed and what isn't, and they take an experimental view of trying to find out. Many adults, on the other hand, grew up in a period when obscenity was confined to the barracks, and are genuinely alarmed to see it invading the ivied halls. The rising political fervor of the Berkeley students had been troubling enough, and contributed to an uneasiness in the relations between the university and the outside community that had been deepening even before the Free Speech Movement came along to exacerbate it. But to many influential Californians the obscenity incident—quickly dubbed the Filthy Speech Movement—seemed the final step on the road to anarchy and depravity. Attacks on the university from outsiders became so hysterical, pressures on the administration for arbitrary action against the offending students so intense, that, as President Kerr described it in an interview with *Science*, "the whole thing just burst open."

"There were tensions before," Kerr commented. "Underneath the great public support for university expansion under the master plan there were always political resentments. On a wide variety of issues, running from the lifting of the ban on Communist speakers to the abolition of compulsory ROTC, we were usually able to persuade the Regents to go along—usually on the argument that it was best for the university. But the sit-ins and the strike really provoked the public, and the