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Cohesive Lift of Sap in the Rattan Vine

The problem of how sap rises lies stranded for lack of means to measure negative pressure in liquids.

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The rise of sap in tall trees has puzzled plant physiologists and laymen alike for more than a century. The cohesion theory of Dixon and Joly (*1*) and Askenasy (*2*) is generally accepted as the principle involved, and, indeed, no other likely explanation has been forthcoming. It is postulated by this theory that evaporation from the leaves pulls the transpiration stream through the tree by virtue of the cohesive property of water. If this is true, the sap pressure in the top of a tree 100 meters tall should be some −20 atmospheres, for, in addition to the hydrostatic gradient of 1 atmosphere per 10 meters, one needs a similar pressure drop in order to sustain the transpiration flow (*3*).

This "wick theory," as it has also been called, carries a special fascination in that it seems incredible that water, which cavitates so readily when evacuated in a flask, should flow with impunity through intricate channels at a pressure which is negative by many atmospheres. And yet, it is easy to show that water possesses this elusive potentiality, provided it is confined within capillary dimensions. This was already indicated by the classical experiments on the cavitation pressure in fern sporangia (*4*) but was given a firm quantitative foundation by the direct and elegant centrifugation technique introduced by Briggs (*5*). By spinning boiled water in *Z*-bent capillaries at ultrahigh speed (Fig. 1*A*), he found that it would withstand −260 atmospheres before rupturing. Using an ordinary laboratory centrifuge, one may produce −20 atmospheres, but even air-saturated tap water will not cavitate at this tension, provided the capillary is no wider than half a millimeter.

What then is the evidence that negative pressures of such magnitude may occur in plants? The most convincing support was contributed by the noted German plant physiologist Otto Renner in 1911 (*6*). He connected a leafy twig to a burette and, by compressing the stem with a screw clamp, forced the leaves to exert their maximal pull (Fig. 1*B*). When the leafy top was cut off and a vacuum line was attached in its place, the rate of flow decreased to one-tenth. The conclusion from this beautifully simple experiment seems inevitable—namely, that the leaves must have imparted a pull of 10 atmospheres on the sap. By a slight modification of technique Renner was also able to show that a few atmospheres negative pressure may well obtain in a twig still attached to the tree (*7*). Using in principle the same line of approach, many later authors have confirmed and extended these findings.

If liquid under tension prevails in the stem, what prevents the sap from cavitating? If the sap cavitates, what prevents the vapor lock from spreading? Both of these questions seem answerable in terms of the anatomical design of the conductive system. Basic to all trees is the tracheidal structure, which forms a continuous tissue of minute spindle-shaped chambers 20 to 80 microns wide. In conifers this is the only system, but in hardwoods the flow is aided by vessels, which in some species (especially vines) may be as much as half a millimeter wide. These tubes are partitioned by cross walls, which may be a few centimeters to several meters apart, according to species. The walls of all structures are studded with microscopic perforations (pits), and the sap flows through the various compartments in a continuous capillary meshwork. Should negative pressures develop, nucleation would be inhibited simply by the fine dimensions of the channels. It is of particular interest that the pits are closed by a water-pervious membrane of such fine porosity that a gas interphase cannot pass—that is, the flow system is completely check-valved from one compartment to the next with respect to gas passage. The problem of transporting water at high negative pressure over a long distance has thus been solved by combining capillary dimensions with check-valved compartmentalization; in fact, we doubt that any other solution is even theoretically possible.

One may test the function of these structures on a cut liana taking up water from a burette. When the stem is suddenly removed from the water, the air at first follows the receding water columns but soon comes to a complete stop—that is, when the menisci are caught in the membranes of the first cross walls. It is quite obvious

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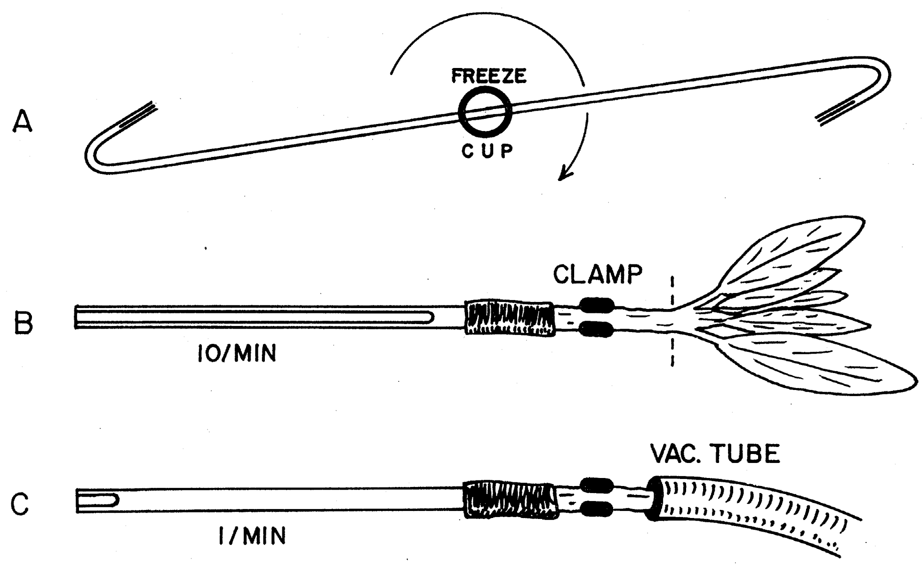

Fig. 1. *A*, Water-filled capillary spinning in a centrifuge to produce tensile water (*5*); *B*, leafy twig with clamped stem, taking in water from a capillary at a rate of 10 volume units per minute; *C*, vacuum tube drawing water through the same stem at a rate only one-tenth that of the leaves (*6*).

that, when a twig or branch breaks off, air does not penetrate beyond the wounded area, for none of the adjacent structures wilt. Nevertheless, Bailey (*8*) found that fresh xylem, when removed from various conifers 25 meters above ground, would let air through at a pressure of less than 3 atmospheres. Does this mean that the air penetrated through nonfunctional channels, or could it be that the sap pressure in the top of the tree was nowhere near the predicted −5 atmospheres? Another discordant finding was that of Ursprung (*9*), that leaves from locust trees wilted when the twig was forced to draw water maintained under reduced pressure. What was the reason?

When the cross-section area of a stem is drastically reduced by cutting, the rate of water uptake may remain practically unchanged. This may seem to be a case of lavish overprovision of flow channels, but it is evident that the compensation takes place only at the cost of a pressure drop above the restricted area, which may amount to several atmospheres (*10*). So, although the evaporation pumps are powerful enough to restore normal flow, the entire system must suffer stress in terms of abnormal tension.

It is inherent in any simple static cohesive system that there must be an exact hydrostatic gradient throughout, but, inasmuch as we still lack a method for measuring negative pressures with any accuracy at all, this, the most fundamental parameter of cohesive lift, remains unverified. At positive pressures, however, such as exist in the grapevine in the springtime before the leaves unfold, direct manometric measurements are easy to make, and these have revealed an exact hydrostatic gradient from the ground level up, irrespective of the general pressure level (*11*). So in this case, at least, we are dealing with a simple hydrostatic system, and we need not invoke any unknown lifting force in the stem. If this situation is extrapolated to negative pressures, which seems a reasonable enough step, it must be taken into account that such a system would be badly damaged if extensive cavitation were to occur. If, for instance, the entire cross section of a stem could be artificially cavitated in a region of negative pressure, the transport system should become vapor-locked, and sap flow should cease.

Vapor Lock Produced by Freezing

When water freezes into ice cubes in the refrigerator, the dissolved gases are dispelled as bubbles, for ice has no perceptible solubility for gas (*12*). Similarly, when water is frozen in a glass capillary and thawed, a string of bubbles is left in the capillary, and it takes days for these to redissolve into the water. Finally, if a capillary bent into a *Z* is filled with water and set to spin in a centrifuge, according to the method of Briggs, the water cavitates immediately when the midsection is frozen by a piece of Dry Ice (Fig. 1*A*) (*13, 14*). Freezing, therefore, offers an opportunity to cavitate the sap within an intact vine (*15*).

During an expedition of the Scripps Institution of Oceanography to the Torres Strait area in 1960, an opportunity developed to perform a series of experiments on rattan vines (*Calamus*) growing in the jungle near Cairns, Queensland. The rattan cane of commerce is the climbing stem of several species of palm. The stems originate in a basal leaf rosette, and, climbing through the foliage by means of hooked flagellae, they commonly reach the canopy of the tallest jungle trees, some 30 to 50 meters aloft. Evidently the stem grows faster than it climbs, for loops 10 to 20 meters long are regularly found lying on the ground. This feature, among others, made the rattan an ideal material for a crucial test of the embattled cohesion theory. The plan was to cavitate such a ground loop by freezing. The loop would then be elevated 11 meters, and when it thawed it should remain vapor-locked, so that sap could not pass. Several experiments were performed, all with similar results. We shall here describe only the latest and most complete of these.

A loop of vine was put into a basin, and the stem was cut off under water with pruning shears. While under water, the vine was connected with a graduated glass tube through a rubber hose, and the assembly was clamped to the base of a small tree. The vine (1.5 to 2 cm thick) was then taking up water at the rate of 12 milliliters per minute. The stem was fitted tightly between two grooved pieces of Dry Ice, but whatever peripheral freezing took place did not even slow down the rate of uptake. Neither did the rate slow down when the burette was filled to the brim with water and stoppered; the water simply vacuum-boiled and disappeared at undiminished rate (*11*). From this it was already clear that we were dealing with tensile forces in the stem. By letting air into the stem, the flow was finally stopped, and the vine froze solid. A section 2 meters long, containing the air, was excised under water, and the vine (with its frozen section) was reconnected with the burette.

The experimental results are shown in Fig. 2. The normal drinking rate before freezing was 12 ml/min (*A*). With the stem frozen across, it was zero (*B*). When the loop with the frozen section was hoisted 11 meters in the air, the burette gained 26 milliliters, and no drinking ensued when the section was thawed (*C*) (*16*). Clearly, therefore, the freezing had cavitated the sap, which was then free to drain down by gravity until balanced by barometric pressure. From the experiment with the stoppered burette mentioned above, we must assume that the nearest vessel compartments above the ice were likewise emptied and vapor-locked, in this case by the transpiration pull; that is, the vine was vapor-locked through the gravity pull from below and through the transpiration pull from above. When the loop was lowered to the ground (*D*), water consumption was promptly resumed, and, after an initial excess intake of 20 milliliters, the rate settled down to a steady 20 percent of the initial rate. The excess intake is a measure of the collapse of the lower vapor lock, and the reduced steady-state rate signifies that the vapor lock did not collapse completely. The latter finding may readily be explained as a result of the flow resistance in the 15 meters of vine which separated the burette from the cavitated section. In any event, when the burette was elevated 11 meters, the vapor lock evidently collapsed, for full drinking rate was resumed (*E*). When finally the cavitated section was excised, the drinking rate remained unchanged.

These experiments furnish evidence for cohesive lift and a normal hydrostatic gradient in tall rattan vines, for such vines take up water at an undiminished rate from an evacuated vessel and, when a bubble-seeded section of the vine is elevated above barometric pressure (10 m), the sap columns vapor-lock and transpiration flow stops.

Freezing of Northern Forest Trees

If the ascent of sap in tall trees is caused by cohesive lift of liquid under tension, cavitation of the sap could be utterly destructive to the transpiration flow. But if freezing is so devastating to the rattan vine, one must ask: What happens then to the northern trees in the wintertime? Do they freeze, or do they become supercooled? If they remain supercooled, why are they not triggered into freezing by ice and snow?

Calorimetric determinations of freezing in the xylem of several species of northern trees showed that, without exception, they regularly froze, even at very moderate temperatures. Thus at $-6°$ to $-10°C$, all free water was frozen, with only a small fraction, corresponding to 30 to 40 percent of the dry weight, left unfrozen and bound to the cellulose (*14*). In other words, all free water in tracheids and vessels freezes regularly and, hence, triggers gas seeding throughout the tree. Since freezing and thawing take place repeatedly during the winter season, it is clear that cohesive tension cannot exist at this time. Only a few species of hardwoods and lianas, such as birch and grapevine, respectively, are known to have, in the springtime, a short period of stem pressure high enough to mend gas breaks. Isolated roots of conifers develop positive sap pressure, but this seems to build up too slowly to be of much help (*17*). Undoubtedly, our knowledge on this problem is very incomplete.

Sap Flow in the Sugar Maple

We found in the rattan vine that cavitation, induced by freezing above 10-meter elevation, caused sap to flow out at ground level. It is natural to link this translocation with the flow of sap from maple trees when these are

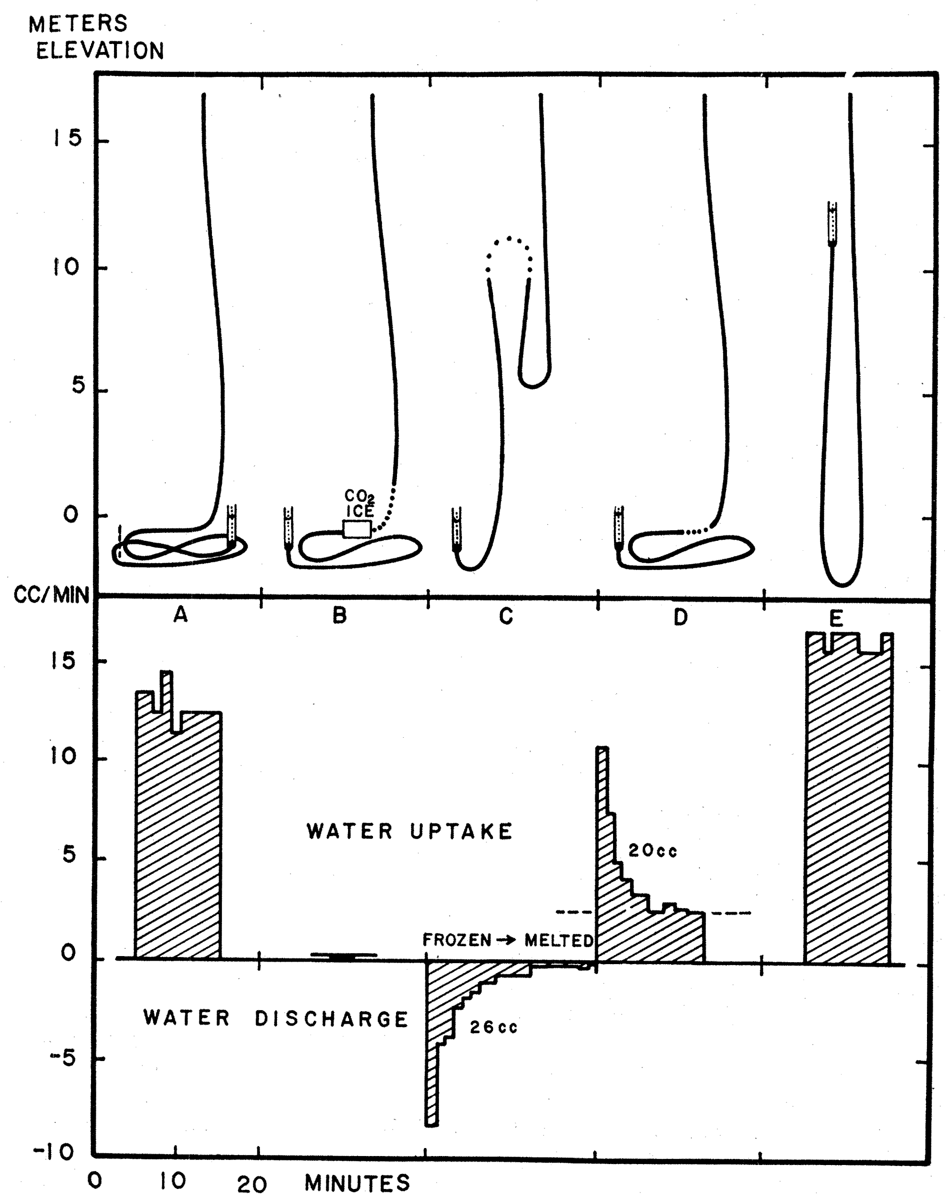

Fig. 2. Water intake by a rattan vine: *A*, before freezing; *B*, frozen; *C*, with nucleated loop elevated 11 meters; *D*, with cavitated section on ground; *E*, with burette elevated 11 meters. Dotted line, cavitated section.

punctured during the first thaw after winter freeze. The sap is then bubble-seeded throughout the tree and is, accordingly, free to drain down from the upper parts sufficiently to build up a positive hydrostatic gradient in the lower parts of the stem. There can be little doubt that this sort of situation exists in maples and other trees when the frozen sap melts in the spring. But the mere fact that so few species display a "sap run" indicates that this controversial old problem is more complex than it appears (*18*).

Sap Cavitation and Cosmic Radiation

Another interesting implication of the sap-rising problem is the possible detrimental effect of cosmic radiation upon sap under cohesive tension. Glaser's bubble chamber for the study of elementary particles was developed upon the principle that ionizing radiation will nucleate a superheated liquid to form bubbles, analogous to the condensation tracks formed in supersaturated water vapor in the Wilson cloud chamber (*19*). Now, especially during drought, tall trees and other vascular plants are supposed to develop sap pressures of −10 atmospheres or less [−143 atmospheres has been claimed for a desert shrub (*20*)]. The vapor tension is, at the same time, positive, of course, so that technically the sap is in a highly superheated, explosive state. If these tensions are really normal for tall trees and dehydrated plants, what happens when the sap is hit by cosmic radiation? Is it triggered into cavitation or not? This possibility was tested by irradiating thin-walled glass capillaries spinning in a centrifuge. In a series of such experiments, where water was subjected to pressure of −20 atmospheres, it was demonstrated that sodium-22, dissolved in the water and giving approximately 10 disintegrations per second at the central part of the capillary, did not promptly cavitate the water. Neither did the vastly more powerful ionization from a close-range therapeutic x-ray tube, nor ionization from a therapeutic cobalt-60 source. So there seems to be no obvious contradiction between tall trees and cosmic radiation.

Life under Metastable Conditions

The condition of superheated sap in plants represents the most striking instance known of the invasion by evolutionary processes of a region of physical metastability. It is not the only case, however, for a few years ago a population of supercooled fish was found living at the bottom of Hebron Fjord in Labrador, 100 to 200 meters deep. The temperature of the bottom water in this fjord remains constant the year round at about −1.7°C and the freezing point of the blood of fishes living in this water is near −0.7°C—that is, the fishes are supercooled by nearly 1°C. If they are brought to the surface and touched with a piece of ice, freezing is triggered and ice propagates readily through their bodies and kills them. They can flourish where they are solely because there is no ice at the bottom, which could seed them into crystallization (*21*). In contrast to these fishes, plants are less vulnerable with respect to their metastable condition, for they have built-in protection against both nucleation and gas propagation.

Conclusion

It is clear that the bioengineering of a tree is amazingly suited to deal with liquid under tension. However, the mechanism by which the plant copes with certain situations is incompletely understood. Nucleation and cavitation are a regular part of the life cycle of northern forest trees. How is this massive gas seeding mended, and is it really true that a redwood or eucalyptus 100 meters tall maintains a sap pressure at the top of −20 atmospheres? We do not know by direct measurements what hydrostatic pressures the transpiring plant must buck in the soil, nor can we, with any accuracy, measure negative pressures in the trees. So, we have no direct knowledge of hydrostatic gradients in these structures. There is little reason to doubt that a variety of microporous structures, such as clay, soil, xylem, or gelatine, may become squeezed by the cohesive forces of the enclosed water, but the empirical study of all of these phenomena is deadlocked by lack of accurate measuring techniques.

The free-for-all, charming old problem of how sap ascends tall trees still presents a wealth of unsolved questions to challenge the experimental ingenuity of future workers (*22*).

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