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THE RISE OF SAP IN A TROPICAL LIANA [1,2]

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It was discovered in a Palestine orchard that citrus trees do not necessarily wilt when the trunk is cut from opposite sides at different levels so that every vessel is severed (2). Similar observations have been made on several other species of trees (3). Furthermore, it is known that every transpiration column throughout the cross section of a tall grapevine can be broken by air, without retarding the water uptake. When the air breaks are too extensive the transpiration slows down considerably, but it still may be sufficient to prevent wilting or even to permit a wilting plant to recover (4).

It is common to these cases that air breaks existed in all or most of the active vessels throughout a full cross section of the stem, so that the transpiration stream for some distance, at least, must have run only through the interstices between the vessels.

These phenomena have an important bearing on the cohesion theory, as well as on the relation between vascular and interstitial sap flow in the stem, and it has been our endeavor in the present investigation to elucidate the situation by experimental studies of hydrodynamic conditions in a liana.

THEORETICAL CONSIDERATIONS

Prior to the present investigation a simple concept of the hydraulic system in a vine was developed, which proved useful as a working hypothesis. The ideas were based on the following data from the grapevine (4).

In the first place, when a short piece of stem was trimmed from the upper end of a long excised grapevine section, only a small amount of sap ran out at the lower end. If another such piece was trimmed from the top, more sap ran out. Consequently the sap must have been hung up at the upper end, very likely because the pits in the vascular walls would not allow an air-water meniscus to pass. Secondly, in a piece of stem one decimeter long the sap in the vessels could be easily shaken out, but the sap in the interstices (tracheids and walls) could not be dislodged by centrifugation even at 1700 × g. This sap was freely motile, however, because it could be squeezed out at the ends by pressing the wood. We may interpret this to mean that the sap is freely movable within the fixed volume of the rigid interstitial framework, but cannot be dislodged from it because micromenisci in pit membranes and micropores effectively prevent air from entering the finer structures. In the course of these investigations it was also established that the main part of the transpiration stream runs in the vessels, that there is no low pressure gas phase in or near the conducting vessels, and that there are no metabolic pumps in the stem responsible for the sap ascent.

The data taken by themselves suggest an hypothesis which runs along classical lines, i.e., that the water-conducting xylem in the grapevine stem is essentially a flooded, continuous, micropore system, scattered with elongate macrocavities (vessels). The stem may accordingly be compared to a pipe filled with a sinter of fine sand, throughout which large longitudinal cavities are dispersed (fig 1). If water fills such a system and flows through it, the cavities will offer the paths of least resistance, and through them most of the water will flow. If the hydrostatic pressure is below atmospheric and outside air enters a cavity, this will press the water out of the cavity, but no farther, as the air-water menisci will hang up in the micropores of the cavity walls. The stream of water must now flow past the air-blocked cavity, and the resistance to flow increases. Full flow can then be maintained only at the cost of an increased pressure drop across the resistance (fig 1 c).

It is the purpose of this paper to report our experimental tests of the above hypothesis.

MATERIALS AND METHODS

MATERIAL: Lianas of many different genera grow on Barro Colorado Island in Gatun Lake, Canal Zone. Sterile vines *Tetracera* sp. belonging to the Dilleniaceae were especially well suited to experimentation because they have large vessels and, unlike the grapevine, produce little, if any, gelatinous exudation from the central xylem. In Central America at least one species of Tetracera is referred to as "bejuco de agua" or "water vine" (5) because quantities of potable sap run out of a stem section when this is rapidly severed from the plant by two slashes with a machete.

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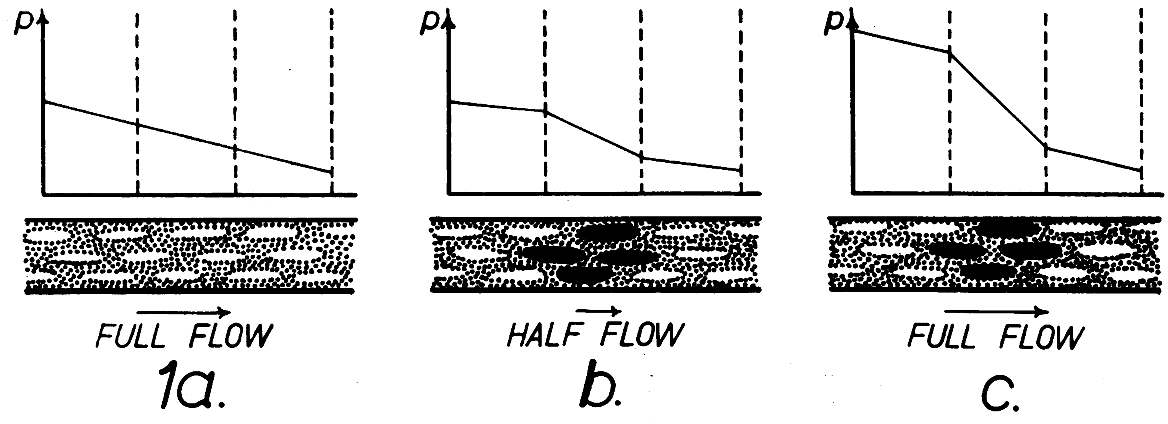


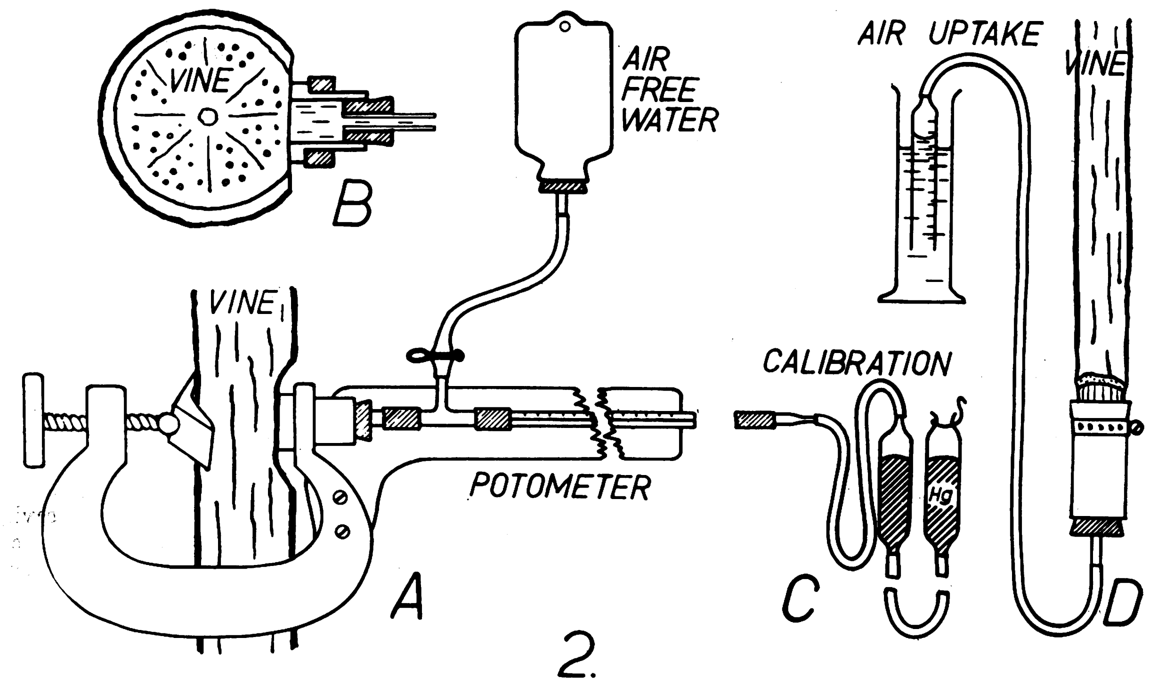


Fig. 1. Flow model of a microporous matrix with longitudinal cavities. Water flow in direction of arrow. a. All cavities water-filled. b, c. Some cavities blocked by air. The curves above show the pressure changes along the tubes.

Fig. 2. A. Potometer assembly mounted on a C-clamp. B. Plastic contact cup on exposed xylem. C. Mercury levelling bulb for pressure calibration of potometer. D. Measurements of air uptake by cut stem. When water uptake is measured the rubber tubing from D draws water directly from the measuring cylinder (cp fig 5).

Some Xylem Dimensions: A cross section of a small (1.5 cm thick) Tetracera stem is reproduced in figure 3. Most vessels are between 0.2 and 0.4 mm in diameter. They end blindly after reaching an average of some 1.5 m in length, determined according to the procedure used for the grapevine (4). The vessels are held in a meshwork of tracheids some 10 to 40 microns wide and ranging from less than a millimeter to a few millimeters in length. The walls of vessels and tracheids are richly studded with pits.

Methods: To test the proposed hypothesis the following measurements were needed: 1) Water and air uptake by the cut stem. 2) Hydrostatic pressure both in vessels and microporous structures.

The total water uptake of a vine cut under water was determined by clamping a hose to the submerged

lower end and connecting it with a measuring cylinder (fig 5). Air uptake (fig 2) was measured by emptying the hose at D and connecting it with an inverted calibrated glass cylinder, which fitted into the water-filled cylinder.

Positive pressures in vessels down to 0.2 atmosphere were estimated with the manometer punch (4).

A record of pressure changes in the microporous structures was obtained by means of a potometer arrangement (fig 2 A, B, C). To apply this, the xylem was exposed and the surface cut flat with a sharp knife. A paste of tooth powder and water was rubbed onto this surface, filling the exposed and opened vessels and providing a microporous contact with the vessel walls which helped to immobilize the air trapped in the vessels. The surface was then covered with vaseline to make it air tight, except for a circle 0.5 cm in diameter over which the plastic contact cup (B) of the potometer was clamped. By loosening the cup stopper the potometer system could be filled with boiled air-free water from a rubber bag without trapping any air bubbles.

The rate of water absorption was measured on the potometer capillary. Assuming the water uptake through the exposed xylem to be a simple process of filtration, i.e, where rate of filtration is proportional to the pressure difference, it should be possible to calibrate the potometer rates in terms of absolute pressure by adding to, or subtracting from, the atmospheric pressure a known pressure, ΔP. The increase or decrease in filtration rate, ΔF, would give the absolute filtration pressure (P) according to the equation $P = \Delta P / \Delta F \times F_1$, where F_1 is the filtration rate at ambient pressure. For each experiment $\Delta P / \Delta F$ would be constant.

In a series of experiments various pressures (ΔP) were applied to the same vine, using a simple mercury calibrator (fig 2 C). The correlation $\Delta P / \Delta F$ was found to be quite linear for each experiment (fig 4). However, when absolute pressures derived by this calibration were compared to those obtained with the manometer punch, the results of the two methods were found to deviate increasingly from one another as the pressure fell below 1 atmosphere. At a pressure in the vessels of about 0.2 atmosphere, recorded directly by the manometer punch, the potometer calibration usually indicated a much higher pressure, i.e, around 0.6 atmosphere.

A similar discrepancy was found independently by another test. In this case the lower end of a cut-out vine section 6 m long was held at different heights, while potometer measurements were made at the upper end. Again the pressure changes indicated by the potometer fell short of the true hydrostatic difference.

These discrepancies cannot be disregarded. They mean either that the postulated free communication between the vessels and microporous structures does not exist, or more likely that the potometer method gives results encumbered by a proportional error.

Results

Effect of Air in the Transpiration Stream: In earlier experiments on tall grapevines, when a cut

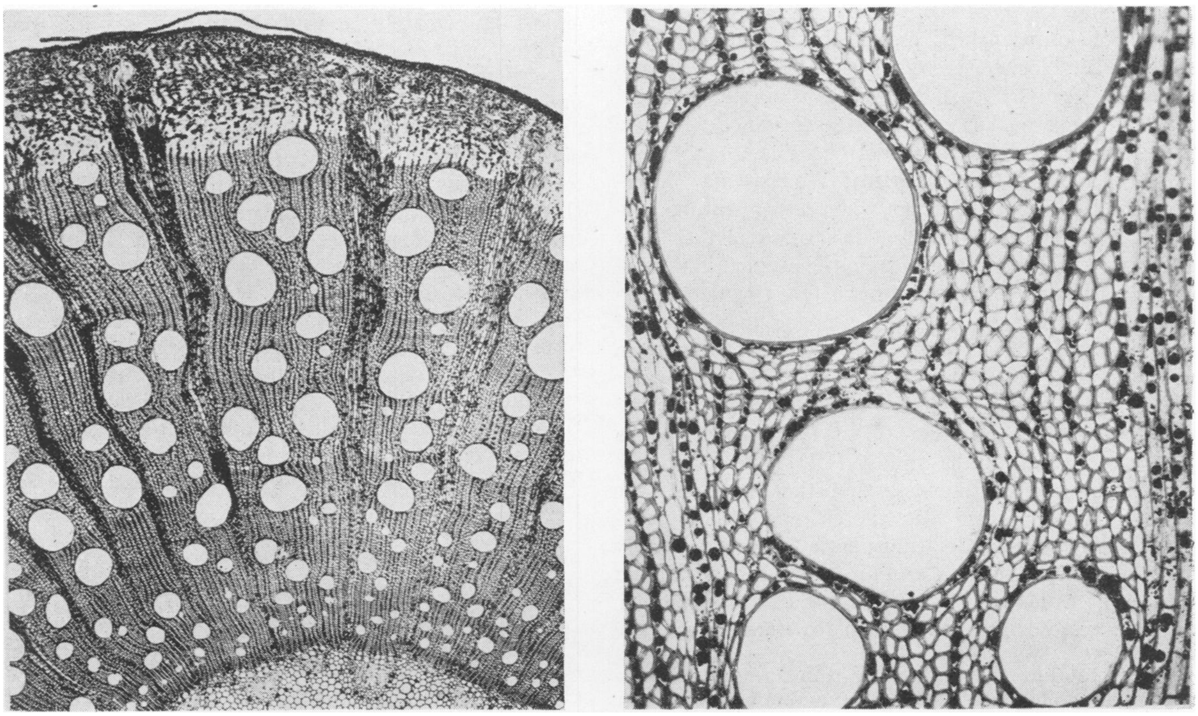


Fig. 3. Cross section of stem of Tetracera liana. Magnifications 20 times and 100 times.

stem was given a sequence of water-air-water the rate of uptake was in all three steps the same, i.e, the water uptake remained unchanged in spite of gross air embolism in the vessels (4). The experiment was repeated on Tetracera lianas with the same results. In this case the events were subjected to closer study by measuring 1) the rate of water intake, 2) the rate and amount of air taken in, 3) the rate at which water absorption was resumed, and 4) simultaneously the pressure in the microporous structures as indicated by a potometer. The result of a typical experiment is plotted in figure 5.

At B_1 the vine was cut under water, resulting in a reduction of the potometer rate from A_1B_1 to B_1C_1, as the vine now received water at a pressure of 1 atmosphere. The cut vine was provided with a tube and the water uptake was registered. At CC_1 the stump received air, and it will be seen that the air, following the receding water columns, disappeared into the vine at the same rate as the water (BCD). After a few minutes, however, the intake of air suddenly stopped (D), and at the same time the potometer rate increased four times (D_1E_1), indicating a pressure drop of similar magnitude. This can only mean that the menisci of the receding water columns in the vessels were stopped by the microporous pit membranes in the walls of the blindly terminating vessels. The continued evaporation from the leaves could now exert its full force on the blocked water, producing the pressure drop at D_1.

At EE_1 water uptake was permitted to resume and it proceeded at a near pre-air rate (EF), but with a potometer rate (E_1F_1) now three times higher than before the admission of air (B_1C_1). Since the water consumption was essentially undiminished, in spite of air-blocked vessels, the rate of flow in the micropores must have increased, causing the observed drop in pressure, i.e, exactly in accordance with the predictions based on the model (fig 1 c).[3]

Effect of Simple Cutting: We may now interpret the potometer readings when a transpiring vine is cut (fig 6 I). As the stem is severed (B) the low pressure (AB) near the cut in the upper section of the vine rises to near atmospheric (BC) while the sap columns in the vessels recede drawing in air behind them. When the air-water menisci reach the pits in the vessel end walls they cannot pass, and the water movement is now completely blocked throughout the cross section of the stem (C). From then on the pressure in the sap falls rapidly (CD), due to the pull exerted by the continued evaporation loss from the leaves. When applied near the cut end the manometer punch registered atmospheric pressure simply from hitting the severed and air-filled vessels. Higher up, i.e, at a distance above the cut of more than an average vessel length, the punch registered nearly the water vapor pressure from hitting only sap-filled, unsevered vessels.

[3] The total amount of air drawn into the stem corresponds in volume to the maximum amount of water which is discharged from the lower end of a long vine section when a piece as long as the average vessel length (ca 1.5 m) is trimmed from the upper end (4).

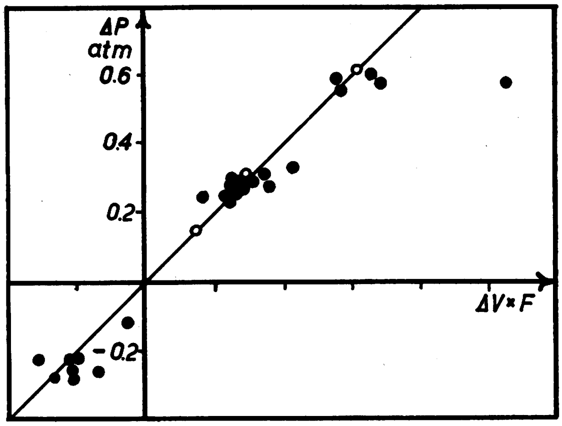
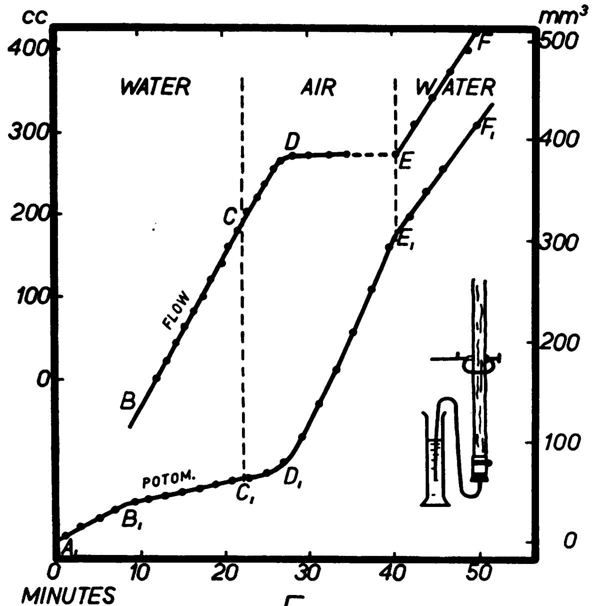


Fig. 4. Relation between calibration pressure (ΔP) and the corresponding change in potometer filtration rate (ΔF). Open circles. Filtration rate obtained by hydrostatic weight of water. Abscissa in arbitrary units which varied for each set of determinations.

In the lower stump we find initially a pressure rise towards atmospheric as the water recedes into the vessels due to the elastic rebound of the stem and root system. When the menisci are stopped by end walls, the pressure typically drops, only to rise again through refilling from the roots until the stump starts bleeding. In one vine used for such an experiment (fig 6 II) the pressure was high due to prolonged rains, and bleeding from the lower stump started almost immediately so that sap flowed into the potometer and reversed the curve.

Effect of Double Cut: In one series of experiments cuts were made at different levels with a saw on opposite sides of the stem (fig 7). Such treatment does not usually produce wilting (cp above). When the first cut was made half way through the vine (A) there was a marked drop in pressure above the cut, indicated by the higher potometer rate. With the next cut (B) the pressure dropped further, as most vessels between A and B had now been opened to air and between the cuts the transpiration stream was forced to run mainly through the microporous structures. When the distance between the cuts was decreased by the third cut (C) the area through which the water could travel in the micropores was greatly diminished, and the pressure dropped even further. The minimum was reached when the vine was cut through completely.

In a vine with a double cut only those vessel elements which are severed by the saw become inoperative. Below and above this the vessels are full of sap with conduction intact, figure 8 (cp (1), figs 17 and 18). The fact that wilting does not occur means simply that the transpiration stream has force enough to overcome the greatly increased resistance by developing an increased pressure gradient across the region of inactivated vessels, such as recorded by the potometer.



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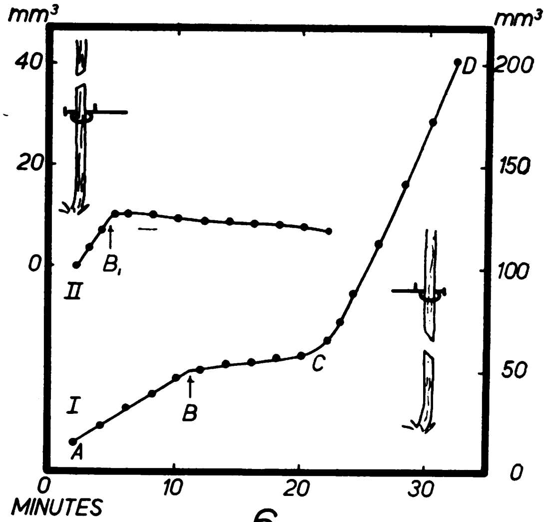

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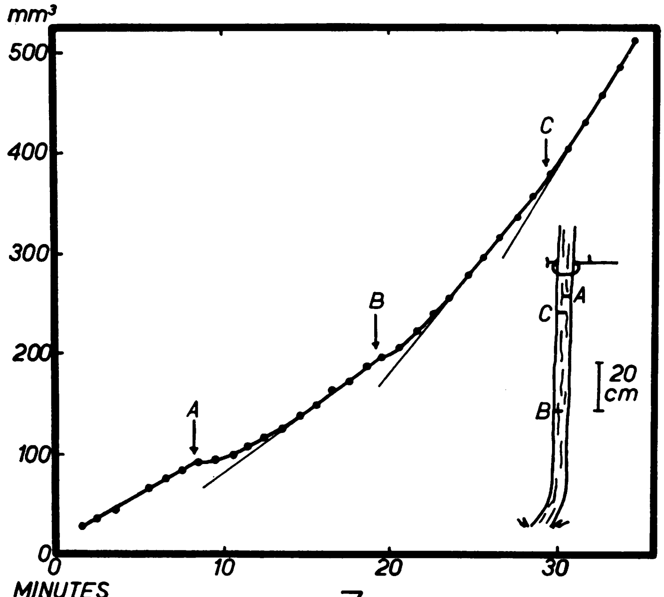

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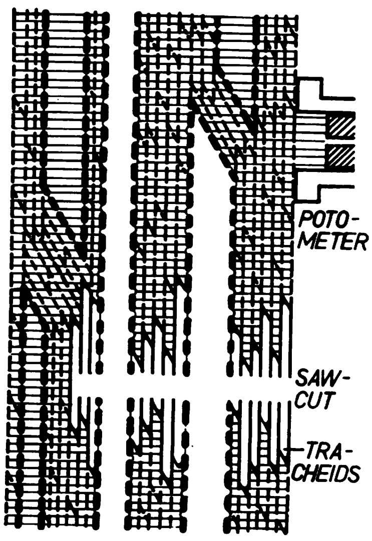

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FIG. 5. Measurement of water-air-water uptake by cut vine and simultaneous measurement of potometer filtration rate. The rate of water uptake of the vine is nearly the same before (BC) and after (EF) the air plug (CE), but the potometer rate (B_1C_1) increases fourfold (E_1F_1), indicating a similar pressure drop.

FIG. 6. Changes in potometer filtration rates produced by cutting the stem in air (at B and B_1). I. Potometer on upper section of cut vine. II. Potometer on lower section of cut vine.

FIG. 7. Increase in potometer filtration rate produced by cutting the stem half way through at different levels (A, B, C), indicating a similar drop in pressure. Location of cuts drawn to scale in lower right-hand corner.

FIG. 8. Diagrammatic representation of the effect of a saw-cut in a stem with sap pressure below one atmosphere. Water-filled structures shaded horizontally. Large channels are vessels.

Discussion

We have demonstrated in the present investigation that air introduced into the transpiration stream of a liana stays confined to those elements which are severed (vessels, tracheids), and does not spread into other compartments through pits or micropores in the walls. This verifies experimentally a basic assumption made by Dixon (1).

When gas is admitted to vessel compartments containing sap at subatmospheric pressure the sap is sucked out of them and they are eliminated as water conductors. This produces a local increase of resistance, as the transpiration stream is now denied channels of easy flow and must pass around them in the microstructures. Normal flow can then only be maintained at the cost of an increased pressure drop across these breaks. Such a drop has been demonstrated in every case of experimentally produced gas breaks.

Potometer experiments on transpiring vines have shown that the pressure gradient to the outside often increases three to four times when the vine is cut or when air is given to an already cut vine. In many cases we know from direct measurements with the manometer punch that the vessel pressure before the cut was, say, 0.2 or 0.8 atmosphere and hence, assuming the same pressure in the vessels as in the microstructures, several atmospheres' tension must have developed in the stem above the break. As this was measured at ground level one might be tempted to extrapolate it to reach some -10 atmospheres at the top of a liana 40 meters tall. It is true that accurate, positive hydrostatic gradients have been measured in grapevines in the spring and at night, but we failed then, and have failed also in our present Tetracera vines to show that such a gradient exists during transpiration. In either case, however, one may suspect that such will be found when a proper technique is applied. It should also be emphasized that there is no direct demonstration so far of equality of pressure in vessels and microstructures, no matter how likely this may also seem to be. One may temper rash conclusions by pointing out the fact that experimental evidence for the stability of the presumed cohesive columns in the vessels is rather negative and that no mechanism is known which could repair breaks high in the vine (4). Even in the wet season at Barro Colorado, when measurements were taken at night in pouring rain, the manometer punch failed to give high enough pressures at ground level to account for the repair of vascular gas breaks 20 meters up and higher.

One seemingly basic obstacle to the concept of the cohesive lift of water in the vessels has now been overcome, however, by demonstrating that in vines air breaks stay confined, and hence they will not seriously damage a cohesive system.

Summary

Pressure-flow relations have been studied in the stem of a tropical liana (*Tetracera* sp.). It was shown by potometer measurements that whenever an air break is introduced into the vessels of a transpiring vine, e.g, by a double cut, or by cutting it off completely, the pressure above the cut always drops drastically.

When a cut liana takes up water from a burette and then is given air the air is drawn in at the same rate as the water, but soon stops abruptly, i.e, the receding water columns hang up. From this point on we observe the above-mentioned pressure drop. The air which enters the severed vessels is evidently stopped by the pit membranes in the vessel walls which do not allow an air-water interface to pass. As the vessels are of limited length, the air does not spread. The vessels represent the paths of least resistance to the transpiration stream, and whenever vessels are severed a subatmospheric hydrostatic pressure will empty them, thus rendering them inoperative for water conduction. This means a locally increased flow resistance which results in the recorded pressure drop. There are good indications that the drop may reach cohesive values.

The results demonstrate that air breaks in the vessels and tracheids produced by various cuts stay confined in the severed units and that the transpiration stream simply moves around these obstacles in the intact units, as postulated by Dixon. Hence the idea of cohesive lift is not incompatible with air breaks in the transpiration stream.

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