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## On the Ascent of Sap

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XII. *On the Ascent of Sap.*

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MANY theories have been formed to account for the ascent of sap in high trees, when root pressure is not acting. All have been found, on careful examination, unsatisfactory. Our attention was particularly directed to the problem as we were together in Bonn, in the Summer of 1893, when Professor E. STRASBURGER was kind enough to show us some of his experiments on the question, and since then we have, at intervals, occupied ourselves with some considerations as to the cause of the ascent of liquids in trees. It was not, however, till late last Spring that we had leisure to enter definitely on the research.

We wish to acknowledge the kindness of Professor E. PERCEVAL WRIGHT in giving us the benefit of his advice on all occasions, and also the advantage we derived from Professor G. F. FITZGERALD'S suggestive ideas.

At the outset we will describe the theory which we venture with great diffidence to advance, as to the nature of the phenomena of the ascent of sap.

The '*Saugkraft*' of the leaf, or its suction force, has been appealed to by many botanists, as drinking away the sap at the top of the conduits, or aiding its elevation by establishing a difference of gas-pressure. Our theory is that this is the all-sufficient cause of the elevation of the sap, not however by establishing differences of gas-pressure, but by exerting a simple tensile stress on the liquid in the conduits. We may compare this action to the action of a porous vessel drawing up a column of liquid to supply the evaporation loss at its surface. A porous pot, in which the pores were so exceedingly fine that the water meniscuses formed in them would be able to support a tension equivalent to many atmospheres pressure, and supplied below with water in a state capable of standing this high tension, would represent (according to our views) the arrangement obtaining in high trees. The meniscuses are formed in the membranous '*réseau*' of the evaporating cell-walls, while the columns of liquid supplying their evaporation-loss exist in the functioning conduits. We cannot of course pronounce upon the complete identity of the actions, for there may be osmotic actions in the leaf, exerting considerable tensile forces upon the raw sap in the bundles. And, again, the influence of the stomata in opening and closing is, of course, peculiar to the leaf. From what is known, however, as to the conditions

favouring transpiration, we think that the suction force is, with most probability, referable to surface-tension phenomena, having the same thermal energy relations with the surroundings as obtain in the case of the damp porous vessel; that is, the action progressing at the evaporating surfaces in the leaf during transpiration, and establishing a tensile stress in the sap, is of a "sorting-demon" description (*i.e.*, a sorting out of the more quickly moving molecules) common to spontaneous evaporation and leads to an inflow of heat from surrounding objects.

This hypothesis has recommended itself to us, after much consideration, as the only one which is agreeable to all the known phenomena connected with transpiration, as well as affording a rational explanation of the curious structure of the conducting tissues of trees.

In support of the theory we will show, 1st, that the transpiring surfaces in the leaf are capable of exerting a tension which is sufficient to account for the raising of exceedingly high columns of water; 2nd, that the conditions necessary to maintain the stability of such columns of liquid are not only fulfilled in the conducting tissues of trees, but that the state of affairs in them is such as to involve the necessity of the liquid they contain being in tension.

Firstly, with regard to the adequacy of the leaf to generate the necessary tensile stress upon the sap; this we demonstrate by experiments, in which the leaf is caused to transpire against a pressure higher than that of the atmosphere; that is in which the meniscuses within the 'réseau' of the evaporating cell-walls of the leaf are compelled to bring forward the transpired liquid against high external pressure, unbalanced by forces from within. An accident to the apparatus which we used limited our observations to pressures of 3 atmospheres.

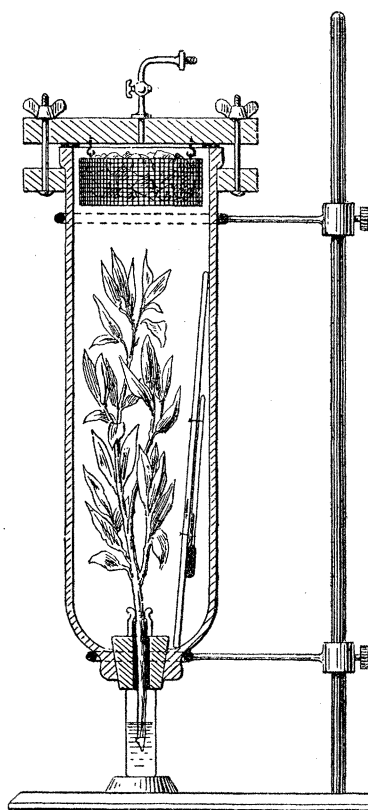
The accompanying figure (fig. 1) shows the arrangements adopted. The vessel used was a thick glass receiver, closed at top by a rubber ring and strong lid of wood. The branch is inserted as figured, its cut extremity being exposed to atmospheric pressure only and dipped in a weighing tube containing water. This tube is weighed accurately before and after experiment, and during the time of experiment is held pressed against the rubber stopper surrounding the stem of the branch. Pressure is got up in the receiver by pumping dry air into the receiver from above. Within, at top of the receiver, hangs a wire basket containing broken pumice carrying phosphoric anhydride to absorb water transpired by the leaves. The receiver being some 45 centims. in length can readily be transported into sunshine when desired. To measure the pressure and temperature obtaining in the receiver a manometer and thermometer stand within. The manometer is simply a straight glass tube, closed at one extremity, and containing a small column of mercury as an index. The length of the tube occupied by air above the index is divided to one half, one third, one quarter, &c., thus indicating the pressure in atmospheres directly.

A branch of maple (*Acer macrophyllum*) with six fully developed leaves was chosen for experiment (April 18th). This was left standing some hours after cutting, thus

avoiding any possible effect of initial negative gas pressure in the tissues, as recommended by STRASBURGER. It was then placed in the receiver with cut stem protruding, and the pressure within raised to 2 atmospheres, *i.e.*, one additional atmosphere. The thermometer within read  $15^{\circ}$  C., rising to  $16^{\circ}$  C. On re-weighing the water tube after 1 hour and 20 minutes a loss of 0.050 gram was observed. This was in the afternoon, 4.45 to 6.5.

A maple branch (*Acer macrophyllum*) was exposed to a pressure of 3 atmospheres, and the whole placed in the sunshine. In 1 hour water was collecting within upon the glass, and streaming down the walls, although fresh phosphoric anhydride had

Fig. 1.



been placed above. The water was visibly lowered in the weighing tube. An accident to the apparatus (the stopper beneath being blown out) during the second hour prevented a weighing being made. At this pressure of 2 atmospheres in excess of the normal, minute air bubbles were slowly evolved at the cut surface of the stem.

Another maple branch was exposed to the pressure of 3 atmospheres, and placed at a northern window from 6.20 P.M., April 24th, to 10.50 A.M., April 25th, temperature varying between  $11^{\circ}.5$  and  $15^{\circ}$ . This was  $16\frac{1}{2}$  hours. Loss from weighing tube was 0.623 gram. Leaves within somewhat flagged. Air, as before, slowly evolved at cut surface.

The same branch of maple as in the last experiment was put under a pressure of

3 atmospheres from 11 A.M. to 5.30 P.M., April 25th, in bright light at a south window. Loss from weighing tube 0.290 gram. in  $6\frac{1}{2}$  hours; temperature varied from  $11^{\circ}5$  to  $13^{\circ}$ . Leaves very flaccid at conclusion of the second experiment. A measurement of the surface area of the leaves of this branch was made by cutting out in paper and weighing. The total leaf surface, both upper and lower, was 1126 sq. centims.

A sycamore (*Acer Pseudoplatanus*), with less leaf surface than the previous branches but more loosely arranged in the receiver, put under pressure of 3 atmospheres from 11.15 A.M. to 5.20 P.M., April 26th, in south window, having sunshine at intervals, gave 0.916 gram. as the amount taken up for transpiration. This was in 6 hours. Temperature varied from  $13^{\circ}$  to  $20^{\circ}$  within receiver.

The same branch as foregoing was left over night in the north window under 3 atmospheres, 5.40 P.M., April 26th, to 10.50 A.M. on the 27th. Temperature varied from  $13^{\circ}$  to  $11^{\circ}$ . Pressure fell during night, by leakage, to 2.3 atmospheres. Loss from weighing tube 0.802 gram. in 17 hours. Total leaf area of this branch was then found to be 608 sq. centims.

Lime (*Tilla europæa*); pressure, 3 atmospheres; 1.15 P.M., April 27th, to 4.15 P.M.; 3 hours; temperature fairly steady at  $14^{\circ}$ . In south window; cloudy. Loss 0.301 gram.

Same branch as above; 3 atmospheres; from 5.40 P.M., April 27th, to 10.50 A.M., April 28th; temperature  $14^{\circ}$  to  $23^{\circ}$ . Pressure fell to 2 atmospheres by leakage. Leaves flagged at conclusion. Loss from weighing tube 0.508 gram. in 17 hours. Total leaf area 316 sq. centims.

No further experiments were made with this apparatus, as it unexpectedly burst in the course of the next experiment; fortunately doing no harm, but putting a stop to further experiments. It was intended to continue the experiments, using higher pressures and with a control or differential arrangement; two receivers being employed and two branches; one in a receiver under pressure, the other at normal pressure. The apparatus was not completed in time for this paper. These experiments, as they stand, however, show that the capillary surfaces at the seat of evaporation in the leaf are capable of functioning at a pressure equivalent to the hydrostatic pressure of 20 metres of water. That is, they continue to give off water vapour and maintain their position so that a continuous flow of water must rise into the leaf to supply the loss by evaporation. We may fairly assume that they will similarly function with 20 metres of water hanging upon them within the conduits of the tree; or, what is the same thing, they can lift this column of water. There was nothing revealed in the course of our experiments to cause us to suppose any particular limit to the power of the leaf to withstand pressure. We find, in fact, capillary forces (if, indeed, they are altogether of this nature) capable of sustaining and exerting tensile forces certainly sufficient to lift the raw sap into tall trees.

These experiments are in perfect agreement with BOEHM'S\* laborious researches, in

\* 'Berichte der Deutsch. Bot. Ges.,' 1893, p. 208.

which that author, after very many trials, succeeded in causing a transpiring branch to raise a column of 90 centims. of mercury. The precariousness and difficulty, however, attending the carrying out of this observation, has precluded other experimenters from repeating it.

Although osmotic actions may be concerned with the evaporative function of the leaf, *i.e.*, in the transference of water into the protoplasm-filled cells; still it is very probable that surface tension forces developed upon the surfaces of walls coming in direct contact with air diffusion currents are responsible principally for the tensile forces displayed by the leaf. The fact that transpiration is not only accelerated by direct sunshine but even more influenced by warm dry winds, supports the view that evolution of vapour at the leaf obeys the general laws of evaporation from a moist surface.

It has, we believe, before now been pointed out that spontaneous evaporation at the surface of a liquid into an unsaturated gas, such as the atmosphere, is of the "sorting demon" class of molecular actions. For the more energetic molecules at the surface of the liquid, or approaching it from beneath, have the greater chance of freeing themselves from the sphere of molecular attraction of their fellows, and escaping into the air. This involves a cooling of the surface layer, for this is continually tending to a state of decreasing mean *vis viva*, which would at length result in the freezing of the remaining liquid if heat did not flow in, radiated or conducted from surrounding objects. Hence the evaporating layer becomes a sink of energy, depending upon the sorting of molecules there progressing, a place where heat is being converted into the molecular kinetic energy attending the change of state. Under certain conditions of saturation of the atmosphere, it will even show an action reversed in direction; vapour from the atmosphere will condense upon the curved surface or meniscus, and the flow of heat will be *from* the surface film. Or, finally, there may, of course, be a state of equilibrium, owing to equality in the amount of vapour evaporated and condensed. We remark here, as a suggestion, that, under some conditions, such reversal of the action may occur in tall trees. Nor is it improbable that when, as sometimes happens, a cut branch which has flagged for want of water revives in a damp place, the action is of this nature; a change from evaporation to condensation occurring in the leaf. The state of equilibrium is, probably, not uncommon, and appears often attained under the artificial conditions prevailing in hot-houses.

The doubt as to whether the sap in the conducting tissues is in a state capable of taking up and transmitting the tension imparted to it by the loss of water from the evaporating surfaces in the leaf is set at rest, not only by the important experiment of BOEHM'S (referred to above), in which a transpiring branch supported at its base a column of mercury 90 centims. high, but also by the consideration that the conditions in the conducting tissues of trees are exactly those under which liquids are stable when exposed to tensile stress.

As it has been either tacitly assumed or avowedly stated that the presence of air or gas dissolved in a liquid is detrimental to the stability of the liquid under tension, or prohibits completely the establishment of tensile stress in it, one might naturally conclude that the sap, which is probably not completely air-free,\* would rupture in every lumen owing to the development of gas-bubbles when exposed to tensions sufficient to raise it in high trees. And, of course, under the stress, a lumen in which rupture has occurred at once becomes water-free and useless.

The question of the stability under tension of water containing dissolved air being therefore involved, we made some experiments to settle the matter one way or the other. We found that the presence of dissolved air did not interfere with the attainment of high tensions; in fact, when all solid objects present had been wetted by preliminary boiling the presence of considerable quantities of dissolved air seemed in no way to interfere with the success of the experiment. Air-free water gave no better results, nor (whether from chance or not) gave results quite so good. In most cases rupture appeared ultimately to occur upon the wall of the tube. Professor FITZGERALD, and, in a written communication, Professor WORTHINGTON, suggested that solid objects in air-containing water might, when this was under tension, collect air upon their surfaces and so bring about rupture. Even if this was so for hard solids, such as glass—and the results of our comparative experiments did not point to it—it appeared most improbable that it could apply to a substance so permeated and little differentiated from the water as woody cell-wall. To test the behaviour of this material in presence of air-containing water under tension, we enclosed chips of the wood of *Taxus baccata*, which had been boiled in water to ensure complete wetting, in tubes and subjected them to tension by cooling. In not one experiment of many did rupture occur at the chips, the liquid appeared, in fact, to break preferably anywhere else. We add particulars of the experiments.

(1.) A cylindrical glass vessel of 328 cub. centims. capacity was washed first with potassium hydrate and secondly with dilute hydrochloric acid, and finally boiled for an hour about half filled with water. A beaker of water was also boiled for about an hour, and then let cool to the air temperature, while only covered with a sheet of filter paper to keep out dust. The vessel was inserted into this while ebullition was going on within it, so that it drew up sufficient water from the beaker to complete its filling. In sealing, a bubble of air was permitted to remain in the tubulure. The volume of this bubble at atmospheric pressure was estimated at about 0·05 cub. centim. In this vessel the tension obtained by heating till the bubble disappeared and slowly cooling, was estimated at about 2·3 atmospheres. There was no

\* The actual state of the transpiration water is not, so far as we are aware, known; still, from the fact that sap forced up by root-pressure contains some dissolved air, it may be inferred that the transpiration sap will not be air-free. A qualitative experiment on the sap forced up by the root-pressure of *Cordyline rubra* showed that it contained a small quantity of dissolved gas.

doubt whatever as to the presence of air and the establishment of a state of tensile stress appeared unattended with special difficulty.

(2.) As previously mentioned, the behaviour of water mechanically stretched in presence of wood appeared a matter of much interest. A smaller tube, having a capacity of about 60 cub. centims., was filled with water as before, which had been cooled while freely exposed to the air in a wide beaker. Four chips of the wood of *Taxus baccata*, which had been boiled in water to ensure their complete wetting, were inserted, and, in sealing, a bubble of air was designedly enclosed.

The water would in no case break at the chips, but generally at the wall or somewhere in the liquid. Estimating as before, by observation of the diameter of the bubble formed on breaking, tensions of between 3 and 4 atmospheres were attained.

(3.) A tube of the same dimensions as the last, *i.e.*,  $13 \times 2.7$  centims. about, was filled with water, which had been boiled the previous day and allowed to stand, to a depth of 6 centims., in a wide beaker 10 centims. diameter, for 20 hours, with no other covering than a filter paper. Chips of *Taxus* and some more air were sealed up in this tube. This indeed contained so much dissolved air that no clinking sound could be produced by striking it upon the hand; while a second similar tube, sealed up with air-free water, clinked loudly. It was found that higher tensions were obtained in the tube containing air and the chips of wood than in the air-free tube. A more careful estimate than the previous ones was made of the actual amount of tension attained. This was effected as follows: immediately upon rupture a spring hair divider was applied to measure the diameter of the bubble. Several observations afforded 5 millims. It was necessary to find out what volume this represented. Accordingly, an observation was made, by warming the vessel slowly in a large mass of water, till such a temperature was reached that the bubble was of this dimension. This was found to be  $35^{\circ}.5$ . The bubble was then jerked into the narrow tubular-neck of the vessel and the whole again brought to the temperature of  $35^{\circ}.5$ . While at this temperature, the length the bubble occupied in the neck was measured. It was found to be 23 millims. A portion of this neck, which had been removed in sealing, was now used to determine the bore, by weighing it when filled with mercury. It was found that the volume represented by the 23 millims. was 0.041 cub. centim. This, however, is due not only to the strain experienced by the water, but to the distortion and yielding of the vessel under the stress. All calculations of these effects were, however, set aside in favour of two direct experiments, as follows: Two vessels of similar dimensions to the foregoing, being indeed made of the same tubing, were filled with air-free water and their tubulures attached to an air pump, so that the pressure in them could suddenly be lowered by one atmosphere while the movement of the meniscus of water in the neck could be observed. Each vessel gave an identical result; a movement of 3.3 millims. for the one atmosphere, or a displacement through 0.0058 cub. centim. We may, without lowering the degree of accuracy of this rough method, assume that this is the total effect of one atmosphere



of tension in diminishing the volume of a free space in the vessel. The stress in atmospheres that prevailed will then be obtained by dividing the observed strain by this number representing the strain per atmosphere; the result is to afford something over 7·5 atmospheres, and although this number is probably not very reliable, it is, we think, safe to conclude that the stress was probably close to 7 atmospheres.

These experiments, we think, proved conclusively that water containing considerable quantities of air—in the last experiment the condition must be approaching saturation—can sustain very high tension; and they further show that the cell wall will probably act to preserve it in this state and enable higher tensions to be reached than can be obtained experimentally in glass vessels. A tension of seven atmospheres is of course adequate to sustain the transpiration sap in a tree 70 metres in height. Our rough experiments in glass vessels cannot be supposed to indicate any particular limit to such stresses.

It occurred to us to seek direct evidence of the tractional force which the leaf, when transpiring, is able to exert, by observing whether choked branches exhibited a diminution in diametral measurement. G. KRAUS\* has made similar observations with positive results.

Our experiments were upon *Morus alba* and upon *Pelargonium zonale*. These showed that choking with mercury or with air was attended with considerable shrinkage of the stem. In the case of the first plant, a hard woody stem, 1·3 centim. in diameter, diminished by 0·4 millim. in the course of 20 hours after choking with mercury, although the cut stem had been restored to water and the measurements were taken but 5 centims. above the surface of the water. The *Pelargonium* was 0·9 centim. in diameter and diminished between evening and ensuing morning by 0·34 millim.; the cut end being exposed to the air. This latter made a slight recovery after being restored to water.

The measurements were made with a calipers constructed so as to magnify five times, and capable of having the amount of separation of its legs observed and measured under the microscope.

The nature of this phenomenon is somewhat obscure—it must be confessed. We cannot localise the shrinkage; it appears improbable, however, that it is due to surface drying of the cortex, but rather to the demand of the leaves. If, then, it is due to a drainage of the tissues by mechanical traction exerted upon the contained liquids, the familiar nature of the phenomenon must not blind us to its significance. Although effected with apparent ease upon drying by evaporation, to diminish by mechanical means the water contents of the tissues by an amount sufficient to cause shrinkage of the cell wall probably requires the exertion of very considerable tensile force.

As to observations on record of the gas tension in conduits low down or high up in the tree, we would point out that, upon our view, they refer to quite a different matter from the actual stress in the sap. They simply refer to gas-filled elements, the

\* "Ueber die Wasservertheilung in der Pflanze." 'Abhandl. d. naturf. Ges., Halle,' xv., 1881.

pressure in which probably in no way influences the ascent of sap. It is not safe to conclude even that this gas is derived from the transpiration sap.

According to the foregoing view, such conduits as contain free gas are inoperative in the transport of sap for the time being; for as soon as rupture occurs in any given element of the conducting tissues, the tension prevailing throughout the liquid permeating these tissues draws out the liquid from it and leaves it filled with gas. The peculiar properties of the woody wall (*i.e.*, prohibiting, when damp, the passage of undissolved gas) come into play, and so the rupture is limited in extent to the lumen of the element in which it is first formed.

From this it will be easily understood that the view formerly widely accepted, that the lumina of the conducting tissues during the time of active transpiration for the most part contain gas, if correct, would render our explanation untenable. This view, however, which had never much to recommend it, has been completely disproved by STRASBURGER'S and RUSSOW'S observations.\* STRASBURGER'S method of estimating the amount of air in the wood was the following: He cut branches under water off various trees, and set them standing in water for half-an-hour in a damp, dark room, so that transpiration might be as feeble as possible. In this way the bubbles in the conduits came to have the same tension as the atmosphere, and consequently, when cutting sections for direct microscopical observation of the conduits, the chances of drawing in air were minimised. For the sake of greater security in this direction, he cut the sections under olive-oil, or a mixture of gum and glycerine. His results show that the part of the wood which is most active in conveying up the transpiration-sap (*i.e.*, outer portions of sap-wood) are most free from bubbles, while the percentage of lumina containing air increases as we pass inwards from the outer parts of the wood. The following are the details of his observations, which were carried out in the summer:—

*Picea excelsa* (*Fichte*).—A branch 3 centims. in diameter, examined as described above, showed almost no bubbles in this year's wood. In the autumn wood of the previous years there were bubbles, while the spring wood was found to contain bubbles in noticeable quantities only in the fourth ring from circumference and inwards.

*Pinus Laricio* showed bubbles in autumn tracheides of outermost ring, while in the spring wood there were only very few bubbles in any ring. The branch was 6 years old.

*Larix europæa*.—Bubbles few in the last two rings, more numerous within. The branch was 3 years old.

*Abies pectinata* (*Edeltanne*).—A branch 8 years old had air bubbles almost only in the inner rings of the upper side, while in the under side where the wood was composed of brown-walled tracheides there was a considerable quantity of air which increased inwards. The outermost ring was the only one which was almost free from air.

\* "Botan. Centralblatt," vol. 13.

*Tsuga canadensis*.—A branch 10 years old; had no bubbles in last ring; few in the next. The number increased inwards.

*Robinia pseudacacia*.—3-year old branch, had the elements of the outermost ring almost air-free, the bubbles being confined to wide vessels. Of the previous year's growth all the wood-fibres and larger vessels contained air, while only the narrow vessels of the autumn wood were without air.

*Wistaria sinensis*.—Bubbles few in last ring, occurring here and there in large vessels, and very occasionally in the narrow vessels.

*Quercus*.—Last 2 years' growth showed scattered bubbles in the vessels, none in the large vessels surrounded with tracheides; the narrow fibres contained air even in the last year's growth. Towards the interior the air-contents of the elements increased rapidly, the wide tracheides being the last to lose their water.

The results, however, most strikingly favourable to our hypothesis are those in which the percentage of gas was estimated in trees after the passage of the transpiration current had been marked out by some coloured fluid. In an example of *Picea excelsa* (*Fichte*) which, after it had been severed from its roots, was supplied with a solution of copper sulphate, the conduits at a height of 11·3 metres, in which the copper sulphate rose, were found to contain only a few air bubbles, while the uncoloured central part of the wood contained relatively little water and was rich in air. His examination of the large oak, nearly 22 metres high, which first took up picric acid and then fuchsine, gave similar results, and he states, further, that the lower conduits of this tree, which must have been injected by water under atmospheric pressure, were scarcely richer in water than those situated higher up in the tree.

In winter, especially after dry, clear weather, the amount of air in the wood of the trees examined was greater. The highest percentage of water was found in trees at the beginning of the unfolding of the bud in spring.

The fact that gas bubbles do occur in the region of the wood which transmits the ascending current indicates an important function of root-pressure, *i.e.*, to dissolve up and clear out the gaseous contents of such conduits as are occupied with bubbles. In the autumn time the gaseous contents of the tree increase in amount, and in the spring the young buds are provided with sap, and at the same time continuity in the watery contents of many of the conduits is re-established, so that at the beginning of active transpiration there may be a water column of as large a section as possible existing in the conducting wood.

This view, namely, that the functioning conduits must necessarily have their lumina swamped with water, is supported by another observation of STRASBURGER'S, of a different kind. He found that, in order to make air-dried wood capable of conducting water, it was necessary, in addition to thoroughly soaking the walls, to inject the lumina also with water, which would, of course, have the effect of establishing continuous water-columns in the wood.

The marvellously subdivided structure of the wood finds full explanation in the existence of a stressed liquid within it. Rupture of the sap-current never can be complete; but each chance rupture is confined to the minute dimensions of the tracheal element in which it is formed by the fact that the woody walls, though freely pervious to water, are impervious to undissolved gas. The endeavour of the tree will be to develop, so far as this circumstance alone is considered, a tissue as minute and at the same time as porous as possible. The provision of the bordered pits appears to be directed to this end. These give the very maximum of permeability in their closing membranes, which preserve their median and least obstructive position so long as water alone surrounds them. But closing and bringing the thickened torus against the covering dome, they prevent the passage of free gas. Very minute perforations of the torus will not, in this connection, prove a source of danger; for there is—theoretically at least—the possibility of free gas bubbles existing in a stressed liquid if these are sufficiently small to exert surface forces adequate to resist the tension tending to enlarge them. But while the gaseous pressure in the conduits cannot exceed the pressure of one atmosphere (for a small bubble forming within them is expanded to fill the cavity in which it arises), yet the water pulled outwards from the wall will exert a distending tension upon it which will act to close the pit membrane against the dome. The necessary provision of surface forces adequate to resist this tension and preserve the wall from being drained of water will set a limit to the dimensions of distinct perforations in the torus, if indeed such exist.

It would appear from the unsymmetrical development of the pits, by means of which the cells of the medullary rays and wood-parenchyma communicate with the conduits, that the tension established by transpiration is not transmitted in full through them. That their contents are often influenced by this tension is, perhaps, indicated by the fact that the closing membrane of the unilateral pits is very usually bulged into the lumen of the adjoining conduit.

There is one other argument in favour of the existence of that state of tension of the sap which we assume in the foregoing, and that is the difficulty of explaining the *evasion* of such a state. For the conditions inevitably lead to it. What are these conditions? Minute cells provided with inter-communication for liquid, but not for free gaseous motion; their walls completely wetted and indeed eagerly retentive of water. Such cells periodically swamped by a dust-free liquid containing no free gas, for such cannot move in the tracheides. What now must ensue upon the ebb in the tide of root pressure? Our experiments indicate that the air containing sap will not break because of the presence of the dissolved gas before many atmospheres tension are reached, and that contact with the wetted wall introduces no instability.

There will be, in fact, a state of mechanical stress naturally induced. It appears as if this result was inevitable.

The capability of the leaf to withstand the stress and continue its function of

transpiration is also indicated by experiment. There will thus be brought about a slow lifting of the sap column attendant upon the discharge of water at the leaf and its supply at the root.

How far a mechanical stress in the sap is transmitted into the roots must at present be matter of speculation. But an interesting possibility suggests itself in this connection. If the tension is transmitted to the surface of the root, it will result in the precipitation of aqueous vapour from the soil upon the root surface. This simply follows from the difference in the hygrometric state of the air around the leaves and the air around the root. In dry weather, the meniscus, still actively evaporating above, will probably be able to support not only the weight of the sap but to establish a meniscus upon the root surface, having a lower equilibrium vapour tension than the vapour tension in the soil. This possible mode of supply can be illustrated by a simple experiment.

Two porous pots ( $13 \times 3.5$  centims.), one in the air, one beneath in damp sand and earth, and communicating by a tube, 90 centims. in length, of narrow bore (0.15 millim.) are both filled with water. An index of mercury in the narrow tube will be pulled up from below into the upper pot in some 4 or 5 hours, when the conditions are those of a fairly dry room. This experiment we prolonged for 8 days; at the end of which time examination showed that the pots were still quite full of water, and that the earth had been considerably dried, which was due only to the transpiration and condensation going on in "leaf" and "root"; for the surface of the earth was covered by a close-fitting metal plate. On lifting the "root," the difference in temperature of this and the "leaf" was so well marked as to be easily appreciated by touch.

It is at present impossible to advance this as more than a suggested explanation of the otherwise rather mysterious action of the root in dry weather, in supplying the large quantities of water needed by the leaves.\* That the root possesses some power of occluding or absorbing water in the vaporous state, may be shown by exposing the carefully-washed root to a damp atmosphere, using controls whose roots are enclosed in a dry atmosphere. The experiment is made by encircling the stem with a split perforated cork, and inserting this into a wide-mouthed bottle con-

\* It is simply matter of observation that fine-grained organic materials such as fibres of linen, oatmeal, &c., when dried, will again rapidly condense water-vapour in their pores when exposed to damp air. It is also matter of observation that such bodies, if exposed when wet or very damp to dry air, will give up a portion of their moisture. It would be better, perhaps, to speak of such phenomena as "continuous" with those of precipitation and evaporation at capillary surfaces, as Lord KELVIN has done in his exposition of the laws governing the latter actions. We do not wish it to be understood that in leaf and root we postulate evaporation phenomena identical with the actions of the porous pot. Whatever the precise nature of the molecular actions involved in bringing forward the water in the leaf, thermal energy to make good the cooling by evaporation will be required to preserve those molecular actions in activity; and in the root the mere drying of the surface layer by the demand of the leaf will result in the precipitation of water upon it from the damp atmosphere of the soil.

taining a little water, or empty. Examples of *Senecio vulgaris* gave good results. One specimen retained a considerable amount of turgescence, although drooping, from the 9th to the 15th of October; while a control with root enclosed in a dry bottle became completely shrivelled. Again, of four specimens of the same plant, two with roots over water, two with roots in bottles containing only air, the former showed a marked advantage over the latter. This experiment lasted from the 10th to the 15th of October.

We tried also the exposure of the root in a vessel, to a great extent, exhausted of air, but containing water. The results indicated that the gain over exposure to damp air is not great.

We also experimented with roots exposed over water kept at a temperature of about 30° C. by means of an immersed platinum wire warmed by a current of electricity. This latter method gave very marked results, but the method is open to objection on the score that there may be direct precipitation by cooling, and supersaturation of the air in the upper part of the vessel.

Of course, the removal of the plant from the earth cannot be effected without injury to and removal of root hairs and fibres, and this is probably one reason why the state of turgescence is not better maintained. Again, in the earth the proximity to damp surfaces is very close. Sometimes, indeed, plants are found spreading their roots into vapour-filled spaces, as between large stones, slates, or beneath flower-pots, when it is very probable that this part of the root takes moisture in the fashion of an aerial root.

The explanation of the functioning of aerial roots is not improbably to be found in a difference of temperature, maintained by the more active metabolism of the leaf on the one hand, and on the other by the silky surface and pale colour of the root.

The question as to how far the cell walls participate in transmitting water admits of definite consideration only in the case when they expose free surfaces to the lumen; for in this case, according to the foregoing views, certain surface forces are developed upon the walls, the intensity of which will depend upon the stress in the sap. At any level in the tree this has a minimum known value due to the gravitational pull of the underlying liquid. The existence of these surface forces, however, involves a certain fineness of grain, upon which an estimate of the viscous resistance may be made according to received principles. The assumption most favourable to the freedom of the wall will be to assume that it behaves towards these surface forces somewhat as a hank of wet flax suspended from one end behaves; that is, above, where the tension is greatest, the grain adjusts itself under the surface forces. There is some reason to expect this from the property of swelling or shrinking displayed by the cell wall according as it is fed with or deprived of water.

Of course, where the cell wall is swamped its freedom may be very considerable in a longitudinal direction. Some experiments of our own in which coloured water was forced under pressure into a small area upon the cross-section of a piece of *Taxus*

*baccata*, proved in agreement with the observations of others as to the comparatively feeble permeability in radial and circumferential directions. The swamped condition obtains, it may be assumed, in experiments upon small cut branches; or when the action of root pressure fills the tree.

It is probable, however, that the development of cells having very much thickened walls, such as both the wood and bast fibres exhibit, may be beneficial to the plant as reservoirs offering such considerable resistance to yielding up water as to afford a slow supply in times of drought.