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The Ascent of Water in Trees. (Second Paper)

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VIII. *The Ascent of Water in Trees.* (*Second Paper.*)

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[Plate 30.]

Contents.

Section 1.—Introduction.

In a previous paper an account of certain investigations into the physics of the flow of water through wood has been given.*

These experiments showed that in the wood of actively transpiring trees the total pressure required to maintain the transpiration rate of flow might amount to a head of water of from five to seven times the height of the tree. The factors which produce this resistance are the friction against the sides of the vessels, the passage

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* 'Phil. Trans.,' B, vol. 198, 1905, p. 41.

through the end walls, and the special highly variable resistance due to the presence of air bubbles in the vessels. Other things being equal, the resistance to flow is strictly proportional to the length of the stem, provided that the conducting tract is approximately similar in character and in sectional area throughout the length of the piece of stem tested. Hence it is difficult to see any reason for CURTIS's statement* that the resistance offered by a stem to the flow of water is not proportional to the length of the stem, unless this observer worked with partially blocked stems. This author also states that the same force is required to overcome the resistance to a definite rate of flow, whether applied as a pressure or as a tension. This is, however, only the case when the conducting elements are completely filled with water, and even then the resistance to flow is two or three times greater than would be expected from a viscosity calculation. The latter fact is partly due to the internal thickenings on the vessels, which reduce their effective radius, and partly to the existence of transverse partitions in long pieces of stem, which add to the resistance to longitudinal flow. The average resistance to flow through the side wall of a vessel or through that of a tracheide of a Conifer may be from 2 to 10 or more times the resistance to flow through the entire length of the same vessel when filled with water, although when large numbers of air bubbles are present the tendency to lateral exudation from a given longitudinal path is much increased. In this way water can be transmitted rapidly and with but little lateral exudation through tracts where the supply is abundant and the local demand small, so that the vessels are filled, whereas in a region where the loss by transpiration is excessive, the appearance of air bubbles in the vessels partially blocks the upward flow and increases the lateral exudation until the local needs are supplied. STRASBURGER attempted to show that the flow of fluids through the vessels of wood was dependent upon their viscosity, by driving such liquids as water, turpentine, alcohol, ether, and benzole through short lengths of stem under similar heads and noting the time of formation of a drop in each case. STRASBURGER's method is vitiated by his assumption that the drops of the different liquids were of the same size, which is not the case, and he also forgets that the different densities of the liquids cause the weight of the columns in the vessels to vary. Nevertheless he found that the number of drops passing through in a given time was approximately proportional to the viscosity of the liquids used. As a matter of fact, the values obtained for the viscosity by this method depend largely upon the order in which the different liquids are passed through the stem, even when the actual volume escaping is measured. Thus water preceding turpentine or benzole gives absurdly different results to water following these liquids, and to a less extent the same applies with alcohol and ether. The relation between flow and viscosity can be best shown by comparing the flow of water at different temperatures, as has already been done.†

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* 'Bull. Torrey Bot. Club,' 1901, p. 335.

† 'Phil. Trans.,' B, 1905, pp. 44, 67.

Many other observations of STRASBURGER'S are open to physical criticism. Thus he records that through two similar pieces of Æsculus stem 2 per cent. solutions of $CuSO_4$ and $ZnCl_2$ flowed in exactly the same volume (250 grammes) while the head fell from 120–40 centims., whereas from 220–240 grammes of water flowed previously through the same stems, the pressures falling from 130–45 centims. in the same time. STRASBURGER considers this to be due to the stems becoming more fully injected with water, whereas apart from the errors due to the unequal fall of pressure in the two cases, two other opposed factors come into play, the greater density of the saline solutions, and their higher viscosity as compared with water. Under the conditions given and with vessels of the diameter of those of Æsculus, the greater head overpowers the higher viscosity, and hence arises the greater flow of the saline solution.

A knowledge of the hydrostatical conditions existing in the wood vessels forms the first essential to any theory on the ascent of sap, and hence a summary and criticism is appended of what is already known, together with some new observations.* I have already shown that with a moderate velocity the flow through open vessels filled with water takes place in approximate accordance with POISEUILLE'S formula for the flow through rigid tubes, divergences being due to the presence of the internal thickenings and the occurrence of transverse partitions. Precisely the same conclusion applies to the capillary actions exercised by the wood elements, for these obey the usual physical laws in spite of apparent peculiarities. STRASBURGER† found that water rose a less height by capillarity in wood vessels than in glass vessels of similar bore. The height, however, depends largely upon whether the walls are wetted or not. Wetting reduces the angle of contact to nil. The cosine of the angle of contact upon which the rise is directly dependent then attains its greatest value, unity, and hence the rise would be greater in the wood vessel with wetted walls than in a glass tube oiled internally. If the walls are wetted in both cases, the lesser capillary rise in the wood vessel is due to the action of the internal thickenings, which cause the power of capillary elevation to vary at different points, the rise naturally ceasing at a weak point, without attaining the maximal theoretical value.

The simplest mode of showing the capillary ascent of liquids in wood is by floating dry rectangular blocks 2 or more inches in length of any vascular white wood, cut parallel to the grain, on a solution of eosin, with the cut ends of the vessels downwards. The very rapid appearance of the eosin on the upper surface makes this a useful and striking demonstration experiment, and if a fresh block is laid on its side after greasing all but the upper and under surface, the relative impermeability of wood to transverse flow is readily shown. Experiments performed

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* Apart from the literature quoted in PFEFFER'S 'Physiology,' excellent summaries are given by F. DARWIN, 'Proc. Brit. Assoc.,' 1898, and by COPELAND, 'Bot. Gazette,' vol. 34, 1902, p. 166.

† 'Bau und Verricht. der Leitungsbahnen in den Pflanzen,' 1891, p. 810.

in this way always give a greater ascent than would be obtained in glass tubes of bore equal to the vessels, but since it is impossible to disentangle the true capillary ascent in the vessel from that due to imbibition by the walls, and to the influence of the tracheides, the observations have no special value.

COPELAND[*] has recently described experiments with an artificial "tree" made by erecting a continuous column of plaster of paris 12·4 metres high, enclosed in glass tubes, with lateral manometers, the lower end of the apparatus being in water, the upper in an osmotic "cell." COPELAND observed a suction pressure at the bottom of less than half an atmosphere. Admitting his inability to explain his results, he arrives at the conclusion that some mysterious force prevented the full tension of the suspended column of water being manifested at the base. The explanation is, however, a simple one, the tube probably contained at no time a continuous free suspended column of water, but series of columns broken by supporting menisci, and the absorption at the base, with its resultant negative pressure, was due to the continued absorption of water by the plaster of paris, a power which it retains after setting. COPELAND'S tube is merely a modification of that described by JAMIN,[†] and in a similar tube set up by STRASBURGER[‡] the water rose with progressively increasing slowness, requiring 100 days to attain a height of 301 centims. The resistance to flow through a tube filled with plaster of paris is enormously greater than through the vessels of a stem, and the osmotic cell used by COPELAND was incapable of developing a sufficient osmotic force to draw water at an appreciable rate through his tube, even if this enormous tension could have been transmitted through the water (and air-bubbles) in the plaster of paris. In fact, if COPELAND had removed the osmotic cell and the upper 9 metres of his apparatus, he would have obtained precisely the same results as when they were present. DIXON has shown[§] that COPELAND'S tube, under a head of 122 centims. Hg, would not transmit 1 cub. centim. per annum.

As was perhaps first clearly shown by SCHWENDENER,[||] the vessels of actively transpiring wood do not contain continuous water columns, but always contain varying numbers of air-bubbles. This statement has been confirmed by all subsequent observers, and no theory of the ascent of sap is worthy of a moment's consideration which does not take this fact into account. According to STRASBURGER, the channels containing least air are most active in the ascent of sap, but this is the direct physical consequence of the lesser resistance to flow in the vessels more completely filled with water. The fact that the water disappears first from the largest vessels led STRASBURGER to conclude that these are more used for storage than conduction, but here again we have a direct physical consequence of the more

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[*] 'Bot. Gaz.,' vol. 34, p. 161.

[†] JAMIN, 'Compt. Rend.,' 1860, vol. 50, p. 385.

[‡] 'Bau und Verricht.,' p. 800.

[§] 'Proc. Roy. Dublin Soc.,' 1903, vol. 10, p. 48.

[||] 'Sitzungb. d. Akad. d. Wiss. zu Berlin,' vol. 34, 1886, p. 561.

ready flow through the larger vessels. The conclusion that if all the vessels in the intact plant were filled with air, no re-establishment of conduction is possible, is incorrect, as will be shown by the experiments on the Maple, detailed later. Dry dead stems cut and injected with water have their conductivity restored temporarily at least, so long as the vessels are open, and the root-pressure may act in the same way in an intact plant. After transplanting, however, the absorption by the roots may be insufficient to make good the loss by the leaves, etc., in which case a rapidly increasing block is created, which may ultimately prevent any re-establishment of the upward flow. In such cases, injection with water under pressure through a side branch should give the tree another chance of recovery, which practice is worthy of experimental trial in the transplantation of slowly rooting trees under dry conditions.

The whole structure of the wood is such as to allow of the existence of channels filled with water alongside others filled with air, and water is also able to pass air-bubbles in the vessels while the bubbles remain stationary owing to their adhesion at one or more parts to the internal thickenings. It is only when relatively considerable pressure is applied to opened vessels that the series of water and air-columns is drawn out as a whole, the pressure required varying according to the diameter of the vessel, the number, size, and shape of the internal thickenings, and the number of the air-bubbles. The whole phenomenon is capable of simple physical explanation, without invoking any mysterious interactions due to the properties of the walls, as suggested by STRASBURGER.*

Section 2.—CAPILLARY AND SURFACE TENSION ACTIONS IN THE VESSELS.

ZIMMERMANN† found that a JAMIN'S chain, freshly formed in a glass tube, is freely motile, but after standing develops a high resistance. This was correctly explained by STRASBURGER‡ as being due to the spaces between the water-columns becoming wetted, so that the menisci no longer adhere to the walls and resist movement. Before this happens the tube passes through an intermediate condition in which the menisci adhere along portions of their rims only and threads of water pass from column to column, so that a moderate pressure will cause water to pass the air-bubbles slowly while these remain stationary, and stronger pressure will drive the whole chain out. The presence of internal thickenings causes this condition to appear much earlier in the vessels, as soon, in fact, as the air-bubbles attain a diameter at all approaching that of the vessel. Indeed, quite small bubbles may be seen to adhere to the walls when a rapid transpiration current is passing through vertically-placed vessels, and this is of great importance in preventing the immediate accumulation of air-bubbles at the upper ends of the vessels.

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* 'Saftsteigen,' p. 79.

† 'Ber. d. D. Bot. Ges.,' 1883, p. 384.

‡ 'Bau und Verricht. der Leitungsbahnen,' p. 816.

Zimmermann supports Nägeli's conclusion that the high resistance in a Jamin's chain is due to the viscosity of the surface tension membrane being higher than in the interior of the liquid, and is not due to any interaction between the wall and membrane. This is a curiously contradictory statement, since an increase of viscosity can raise the resistance to flow only by frictional interaction with the walls. The fact that Jamin's chains, formed with air and such liquids as alcohol or ether, which keep the walls permanently wetted, do not develop any high resistance on standing, is sufficient to show the true source of this phenomenon. Owing to the ready permeability of the walls of the wood-vessels to water, complete adhesion of the menisci never takes place in living functioning wood-vessels containing water and air-bubbles, and even in vessels filled with air a film of water lines the interior. The slow restoration of conductivity when water is forced into a dried length of a stem is due to the fact that the water enters the closed vessels laterally through the walls, forming a series of broken columns whose menisci at first adhere firmly, but subsequently become more freely motile as the walls become wetter and the air-bubbles smaller (*cf.* fig. 1, A, C, and D).

Zimmermann gives the maximal resistance of a Jamin's chain of air and water in tubes of 0·2–0·02 centim. diameter as being one-quarter to one-sixth of the capillary force for the same tube. The magnitude of both forces depends upon the nature of the tube, of the liquid and of the gas, as well as upon the diameter of the tube, but no comparison such as that given by Zimmermann is possible, since the Jamin's chain resistance also depends upon the number of menisci in a given length of the tube. Strasburger* has, however, shown that slight pressure will drive water through a vessel containing a chain of air-bubbles and water columns, whereas a pressure of more than half an atmosphere may be needed to drive out the chain as a whole from vessels 20 centims. long. This fact holds good in spite of Schwendener's theoretical objections to its possibility, and it is due to the fact that a rapid flow is required to break even the imperfect adhesions of the menisci of the air-bubbles to the internal irregularities of the walls. Strasburger also showed that under the same pressure less water flows through vessels containing air than through ones filled with water. More exact experiments of my own† have distinguished between the rate of flow and amount of flow, and between the different factors affecting them. Strasburger's conclusion‡ that the menisci of the air-bubbles will tend to draw water into the vessels by capillarity is misleading, although he correctly states that capillarity plays no appreciable part as such in the ascent of water. For instance, if the air-bubbles and water in a vessel are all at rest (fig. 1, D), the pressure in the air-bubble FG will be greater than the pressure in the liquid EF by the surface tension pressure exercised by the curved

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* 'Leitungsbahnen,' p. 820.

† 'Phil. Trans.,' B, 1905, p. 44.

‡ 'Ueber das Saftsteigen,' p. 81.

film at F. This pressure depends upon the radius of curvature of the film, and the latter is dependent upon the radius of the vessel and the capillary action of the wall upon the meniscus. In the case of mercury, FG would represent the mercury column, EF the air-bubble. The capillary depression of mercury is so pronounced in a narrow vessel as to cause a backward flow even against the action of gravity after the mercury has been forced in by pressure, and in spite of the firm adhesion of mercury to moist walls. If a continuous column of mercury breaks, however, the separate segments remain stationary, the pressures at F and G balancing, and the pressure in the mercury being correspondingly higher than that in the neighbouring air-bubbles.

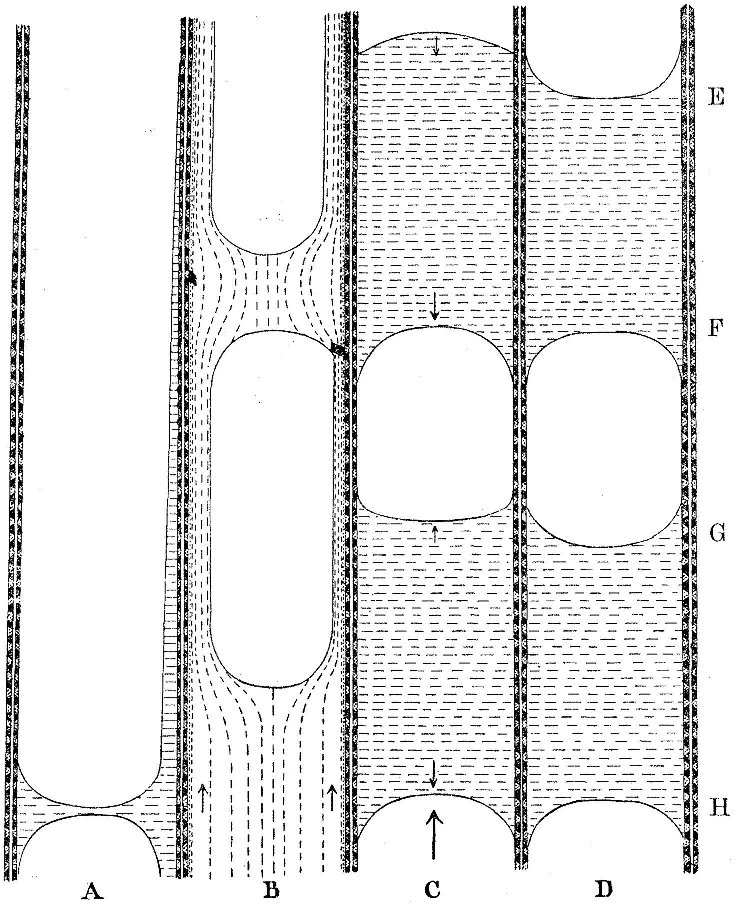

FIG. 1.—Diagrams of Wood Vessels.

A, Emptied vessel, drawing in water laterally; B, Showing influence of walls on distribution of solid matter during upward flow; C, Walls wetted below, unwetted above, showing resistance to flow of menisci; D, Stationary condition.

These conditions are statical only. If flow takes place through the vessel towards E, the partial or complete adhesion of the borders of the menisci will cause that at the level E (fig. 1, C) to flatten or become convex, and that at the level F to become more convex. In this case the pressure in the water between E and F will be less than the pressure in the air-bubble between F and G by the difference between the surface tension pressures exercised by the menisci at the levels E and F, assuming that the same ratio holds good for the points E and F, G and H (fig. 1, D). The fact that the surface tension of a liquid may be raised by the presence of dissolved substances in it in accordance with their osmotic value gave rise to the suggestion that co-ordinated variations of surface tension, produced by the excretion and reabsorption of sugar and other substances from the medullary ray cells, under the stimulus of the gaseous diffusion from the air-bubbles, might induce an upward flow of water, or at least reduce the resistance to onward flow. Although the possibility of the existence of such actions in the wood vessels cannot be denied, attempts to demonstrate their connection with the upward flow of sap have not met with any success, and, in fact, the most active excretion of sugar into the vessels usually occurs in spring, when they are filled, or nearly filled, with sap, so that at most only an osmotic action can be exercised.

There are, however, other ways in which a movement of water columns in the vessels can be produced by influences radiating from the medullary rays. The capillary depression or elevation of a liquid in a tube is directly proportional to the cosine of the angle of contact and to the surface tension of the liquid, and is inversely proportional to the radius of the tube and the density of the liquid. If the angle of contact is less than 90°, the meniscus is concave and the liquid is raised; if greater than 90° it is depressed. The angle of contact depends upon the material of the wall and of the liquid, and is not the same with air above mercury in glass as with water above mercury, nor is the surface tension the same. Water contained in a tube, whose walls it wets imperfectly or not at all, has an angle of contact less than 90°, but when the walls are wetted the angle of contact becomes zero and its cosine unity, so that the capillary elevation attains its maximal value for the given tube. Suppose that at E the wall was wetted, but at F (fig. 1) was not wetted, owing to the presence of a film of oil. Then the cosine of the angle of contact at E being greater than at F, the water column would be drawn upwards until G reached the position F, when the reverse action would be exercised, as in fig. 1, C, where the menisci exercise a total downward pull, unless in the meantime the oil film had floated upwards or been removed. If the wall in front of the meniscus E was kept internally wetted and that at F non-wetted, the column would move steadily upwards, the energy for movement being derived from that requisite to maintain such conditions in the walls of the vessels. The interest of these suggestions is chiefly theoretical, nevertheless they show the possibility of a physical ascent of sap by the aid of vitally controlled energy, which seems at present the only explanation affording a satisfactory hypothesis.

Section 3.—The Influence of Surface Adsorption upon the Sap in the Vessels.

When a solution is drawn through a glass tube, the molecules of the solute in the innermost layers may be drawn to the glass and held back to a certain extent.* If the tube is narrow and long, and the rate of flow not too rapid, this action may become so pronounced that the first portions to escape may be pure water, although a saline solution was driven in at the proximal end. This action continues until saturation point is reached, when the liquid issues of the same strength as it enters. If, however, the molecules of the solute are less attracted than those of the solvent, then the reverse action takes place, so that a mixture of alcohol and water issues at first in greater alcoholic strength. These actions will be shown even if the molecules are merely drawn into the outer more slowly moving layers without being actually held, and in the case of vessels whose walls are permeable to water similar actions take place, but in the substance of the walls as well as at its inner boundary. J. J. Thomson's explanation of this phenomenon, in the case of tubes with impermeable walls, is that if the surface tension is diminished by the addition of a substance to it, there will be more of it in the films than in the central liquid, but less if the surface tension is increased. The surface tension of a solution in contact with a solid diminishes as the strength of the (saline) solution increases, so that in a capillary glass tube the outer layers contain more salt than the central ones, and if the tube is narrow, pure water may at first issue from it when a saline solution is driven slowly through. If, however, a little paraffin oil or alcohol is added to water, the surface tension of the film in contact with the solid wall is increased, and it therefore contains less of the added substance, so that the strength increases in flowing through a fine silica tube.

If the tube contained a series of air-bubbles past which a saline solution flowed, since the surface of a saline solution in contact with air is higher than that of pure water, the film around the air-bubble will contain less of the dissolved substance than the outer layers, so that a steeper gradient of concentration exists between the wall and the bubble than where water only lies between the opposite walls (*cf.* fig. 1, B).

Friction against the surface tension film of the adhering air-bubble will retard the flow of the purest water somewhat, the main flow being in the medium layers between the bubble and the wall, and this partly neutralises the additional surface-tension separation effected by the presence of the air-bubbles.

Evans† has recently investigated the surface adsorption of various substances caused by cellulose fibres, by placing 5 grammes of filter paper in 100 cub. centims. of

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* Röntgen and Schneider, 'Wied. Ann.,' vol. 29, 1886, p. 209.

† 'Journ. Phys. Chem.,' 1906, p. 290.

various strengths of solutions. He finds that there is no perceptible absorption with solutions of more than 0·1 to 1 gramme-equivalent per litre concentration. More dilute solutions of HCl, $CuSO_4$, NaCl, KCl, and sucrose are absorbed in relatively increasing amounts with increasing dilutions, but, as might be expected from the method of experimentation, the amount adsorbed first increases and then decreases with increasing dilution. Barium chloride is not adsorbed even in a dilution of 0·005 of a gramme-equivalent per litre. It follows from this that when a more concentrated solution is travelling up the wood vessels the solutes are not held back to the same relative extent as when the solution is more dilute, in which case the solutes line the interior of the vessels, and are continually carried outwards by the lateral diffusion of the watery contents of the vessels to the exterior.

When sugar begins to ascend in a vessel containing dilute sap, it is restricted to the periphery of the vessel at the front boundary of the ascending stream. When air-bubbles are present, each will have its surface tension temporarily raised somewhat by the higher concentration as the sugar reaches it, and in this way an upward wave of pressure or movement might be produced. Since, however, an upward wave of decreasing concentration would produce the reverse effect, and the concentration cannot be continually rising, only a slight tendency to upward and downward oscillations could be produced in this manner. A vessel filled with sugary sap and with more watery sap outside would steadily discharge sugar as its contents flowed upwards. This phenomenon of surface adsorption is of great importance in regard to the function of the vessels as conducting elements for sugar and other soluble nutrient materials. Hence details are given of a few observations made in this direction. In the first paper it was shown that in similar stems, under otherwise similar conditions, the amount, and hence also the rate of flow, were directly proportional to the head and inversely proportional to the length of the stem. Hence, if two similar stems are cut so that one is twice the length of the other, and the former has double the head applied to it, the rate of flow through each should be the same, but if a solution containing a solute capable of surface adsorption is used, we should expect to find the interval of time between the appearance of water and the solute at the free end of the longer stem greater than in the case of the shorter piece. This is easily shown by using $\frac{1}{2}$–1-per-cent. solutions of KCNS and NaCl, allowed to drip into Fe_2Cl_6 and $AgNO_3$ respectively after being driven through 25 and 50-centim. lengths of stems of Oleander, Eucalyptus, Salix, and Acacia by heads of 75 and 150 centims. of water, the time intervals depending upon the diameters of the vessels and the strengths of solutions used. The stronger the solution the less is the interval, and if a saturated watery solution of eosin is driven through 50 or even 100 centims. length of a dried stem, the very first portions to issue are distinctly coloured, and the intensity of coloration rapidly rises. This surface adsorption, according to Ostwald, decreases with rising temperature, and also with increasing concentration, *i.e.*, as saturation point is reached. Hence a strong solution of eosin travels up ordinary wood vessels as rapidly or nearly as rapidly as the transpiration current, whereas a dilute solution is considerably retarded.*

If equi-molecular solutions are used simultaneously of two solutes which can be recognised by colour or precipitation, the one which produces the greatest change of surface tension will tend to be held back more than the other, and in this way a rough relative comparison of the surface adsorption of two solutes can be made. Thus when an equi-molecular mixture of $Ba2NO_3$ and $AgNO_3$ of approximately $\frac{1}{2}$ per cent. total strength was driven through 50 centims. of a fresh Oleander stem (vessels average 0·033 millim. diameter) by a head of 150 centims. of water, pure water began to drip from the distal end in 1–3 minutes, and continued to be free from the salts for one hour, drops falling alternately into hydrochloric and sulphuric acid solutions. By cutting lengths from the stem and testing two drops at each cut, the silver nitrate was found to have reached 28 centims., and the $Ba2NO_3$ 22 centims. along the stem. In this time 4·2 cub. centims. entered the stem, whereas a similar stem saturated with water contained less than half this amount (1·9 cub. centims.) of water, which would be driven out by an air pressure of $1\frac{1}{2}$–2 atmospheres applied at one end.

This latter method can be used to show the retention of sugar. Thus on driving a 5-per-cent. solution of cane sugar through a similar Oleander stem (same diameter, age, and length), previously saturated with water, the drops did not become appreciably sweet until 9·4 cub. centims. of liquid had issued from it. The same applies to grape sugar, although here 12 or more cub. centims. issue before the sugar can be detected. This is possible, because the reduction of the Fehling's solution only takes place when a moderate amount of sugar has issued and been collected. In any case this factor would considerably delay the rise of sugar to the buds in spring if the vessels contained no sugar during winter. The retention is still more pronounced when large air-bubbles are present, but fortunately in spring the vessels are usually filled with sap, and hence are more efficient in the translocation of sugar.

Section 4.—PUMPING ACTIONS AND EXUDATION PRESSURE.

The pumping action theory usually ascribed to GODLEWSKI and WESTERMAIER was first put forward by GREW in 1682,† as can be seen from the following quotation: "As to the manner of the ascent of sap, I say, first, that considering to what height and plenty the sap sometimes ascends, it is not intelligible how it should thus ascend by virtue of any one part alone, that is, neither by virtue of the parenchyma nor by virtue of the vessels alone. Not by the parenchyma alone. For this, as it hath the nature of a sponge or filter to suck up the sap, so likewise to suck it up but to a certain height, as perhaps to about an inch or two and no more. Nor by the vessels alone for the same reason. For although we see that small glass pipes immersed in

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* 'Allgem. Chemie,' vol. 11, 3 T., 1906, p. 252.

† 'Anatomy of Plants,' p. 126.

water will give it an ascent of some inches, yet there is a certain period, according to the bore of the pipe, beyond which it will not rise. We must therefore join the vessels and the parenchyma both together in this service, which we may conceive performed by them in the manner following." GREW then details how the distended wood parenchyma cells exude water into the vessels, from level to level, and so raise the water upwards. In the absence of any valvular mechanism, such action would of course drive the water downwards as well as upwards, although, as we have seen, the menisci of the air-bubbles in the vessels do actually provide a valvular mechanism capable of adaptable adjustment. The existence of a power of pumping water upwards in plants is usually supposed to be indicated by the power of exuding water under pressure from cut stems, branches or roots, and from water-glands, and since the water exuded (vine, etc.) is often extremely dilute, even when a high pressure of exudation is shown, the latter apparently cannot be due to a continued osmotic indrawal of water from the soil.

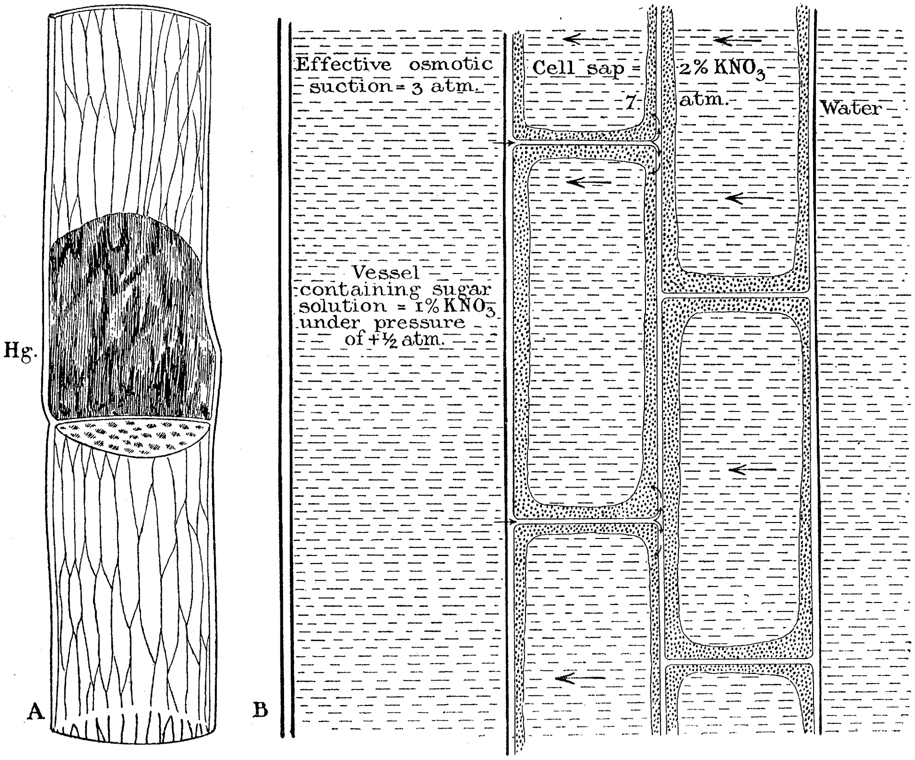

FIG. 2.—A, End of vessel of *Wistaria*, 5·64 metres in length; B, Diagram of osmotic system in root.

Since these actions are commonly misunderstood, a word of explanation may be given. Thus in fig. 2, B, suppose the living cells to have water on both sides of them and to be fully turgid and distended (*i.e.*, the osmotic pressure of the sap is balanced by the tension of the stretched cell-walls), and in equilibrium as regards the inflow and outflow of water on all sides. If the water level outside is raised, water will flow inwards through the cells into the vessel until the levels are the same. This water will be pure water if the protoplasm of the living cells is impermeable to the solids dissolved in the cell-sap, but if the vessel contains any dissolved salts, the water level in it will be raised above that outside according to the difference of osmotic pressure between the liquid outside the root and that in the wood vessel, when the flow has ceased. This flow takes place quite independently of the osmotic pressure in the living cells between, and no matter how concentrated their sap may be. In this way a difference of concentration between the sap in the vessels and the water outside the root, equivalent to 0·1 per cent. sodium chloride will be able to produce a pressure of exudation from the vessels of 0·6 of an atmosphere, or to support in them a column of water 6 metres high, in spite of the high concentration of the sap of the cortical cells across which this action takes place. The backward flow through the substance of the radial cell-wall is hindered by the relatively high resistance to flow in them and their small sectional area, and is further prevented by the abutment of these walls upon the median regions of cells, where the feeble stream is swept back by the more active inward one. So long as absorption is active and the outer living cells of the root fully distended, this tissue acts as a perfect osmotic membrane, and as an imperfect one like parchment when inward flow ceases.

In precisely the same way the feeblest osmotic solution will draw water from a nectary so long as its cells are kept fully turgid and distended by supplies of water from within. To withdraw water when the plant is insufficiently supplied with water so that the cells are no longer fully turgid, the external solution must have an osmotic concentration greater than the released portion of the osmotic pressure within the cell. This can be shown very well by removing the leaves from a beet-root growing in the soil, exposing a small portion of the cortex and placing on it a drop of ½ or 1-per-cent. sugar solution within a small ring of vaseline. If the whole is covered with a bell-jar to prevent evaporation, the drop slowly enlarges and trickles over, whereas a drop placed on a portion of the outer surface smeared with vaseline undergoes no appreciable increase in size. If, however, the leaves are left on the beet-root and the plant freely exposed, or if the plant is pulled up, only stronger and stronger syrup will draw water from the uninjured cortical cells as they become increasingly flaccid.

Further, the major part of the increase in the external concentration is required before the cells have undergone any pronounced contraction, *i.e.*, before the concentration of the cell-sap has appreciably increased. A fully turgid cell acts merely as an osmotic membrane, and transmits the osmotic pressure of an external solution unaltered, whereas a partially turgid cell either does not transmit the pressure or reduces or antagonises it in transmission. It is in virtue of this principle that cells of varying osmotic pressure can exist side by side in the same tissue, and it is only when the supply of water is insufficient that the cells with a higher osmotic pressure draw water from those with more dilute sap.

The osmotic withdrawal of water from fully turgid cells by the vessels, even when they contain very dilute sap, is therefore readily comprehensible, but in itself this can never produce a pressure of exudation greater than that corresponding to the osmotic concentration of the sap in the vessels. If, however, the sugar and other dissolved materials were removed from the sap in its upward passage by the medullary ray cells, converted into starch, and transferred by repeated mobilisation as sugar to the phloem, and then downwards from sieve tube to sieve tube, the escaping sap might be much more dilute than would be expected from its exudation pressure. Since the vessel contains no osmotic membranes, the dilution of the sap on its upward passage would not affect its pressure of exudation, so long as the neighbouring parenchyma cells were all fully turgid. It is worthy of note that an increase of osmotic concentration will not involve any increased absorption of water when the cell is already distended to its maximal size, so that there would be no tendency to absorb water from the vessels or to influence the pressure in them or in neighbouring cells. The energy expended in raising the water would be represented by that needed to produce the requisite concentration of the carbohydrate material.

In this connection an observation of BURNETT'S,* which has been confirmed by WIELER,† is of interest. BURNETT and WIELER found that herbaceous plants, whose roots are placed in 3–16-per-cent. solutions of cane sugar, droop at first but later recover, and as sugar appears in the root cells they may be accommodated to a 20-per-cent. solution of cane sugar, or to solutions of grape sugar and potassium nitrate of corresponding osmotic concentration. Recovery takes place when sufficient sugar has reached the vessels to make the sap in them slightly more concentrated, or when only the osmotic suction of the leaves is in play, at least as concentrated as that outside.

According to PRINGSHEIM,‡ when the apex of a cut shoot is withdrawing water from the older parts, it does so in virtue of the osmotic pressure being higher than in the older ones, and the same difference generally exists in the osmotic pressure of young and old parts of intact shoots, although in the case of *Phaseolus* and other plants also, the older cells have a higher osmotic pressure than those at the growing apex, which therefore shrivels first. The higher osmotic pressure at the apex will not in itself explain the continued withdrawal of water from the older parts of the cut shoot of a succulent, for as the older parts begin to dry up and the sap in their cells concentrates, they should draw water from the younger and still succulent parts. Further, a rise of osmotic pressure in the cells of one part will not necessarily drain water from neighbouring parts with a lower pressure, for if the cell-walls are inextensible the additional pressure merely acts against the wall without stretching it, and since water is practically an incompressible fluid, no inflow whatever occurs.

* 'Phil. Mag.,' vol. 5, 1829, p. 390.

† 'Ber. d. D. Bot. Ges.,' 1887, p. 375.

‡ E. PRINGSHEIM, 'Jahrb. f. Wiss. Bot.,' 1906, vol. 43, p. 111.

If the cells with a lower osmotic pressure lost water by evaporation and partially collapsed, while those with a higher osmotic pressure were kept fully distended, a steady flow of water towards the regions of lower concentration would take place across the tissue, so long as any portion of the osmotic pressure was free to draw water inwards, *i.e.*, so long as the transpiring cells were not fully distended.

If all the cells have the same osmotic pressure, and all begin to transpire equally, while some have stretched and contractile walls and others rigid walls, the latter will at once begin to draw water from the former, since the whole of their osmotic pressure comes into play as soon as they begin to lose water, whereas in the distended cells the contraction of the stretched cell-wall still antagonises a portion of the osmotic pressure. These cells, therefore, will contain more concentrated sap than the older ones, and this is a condition which will commonly be brought about when transpiration is active. The increased osmotic pressure in the thin distensible cells of the growing apex is the result and not the cause of the flow of sap in that direction.

As the sap concentrates in a cut shoot, the older cells are first killed. Their water and dissolved salts then escape, and being now free to move are at once drawn towards the apex, where, as the water evaporates, the sap concentrates, and the osmotic pressure rises. In this respect certain observations of my own on the osmotic pressure of leaves transpiring at different levels need further explanation. Thus comparing Elm leaves transpiring 1350 and 250 centims. above ground, the former appeared to have an osmotic pressure higher by 2–3 atmospheres, and the observed pressures were often extremely high, being equivalent to 6 per cent. or more of potassium nitrate. When testing small cells, however, the concentration of the plasmolysing solution does not give the real original osmotic concentration of the sap. At least three sources of error are involved. However little the cell may be plasmolysed its sap is more concentrated than when unplasmolysed, and in small cells this error becomes relatively considerable. Secondly, under the stimulating action of the plasmolysing solution the sap may become more concentrated by automatic adjustment. Such changes are often rapid, and can only be overcome by rapid observation, which again tends to become inaccurate. Thirdly, the influence of the adhesion of the protoplasm to the cell-wall in retarding plasmolysis is a factor hitherto neglected, but which becomes of considerable importance in small cells, and can even be shown in relatively large ones. Thus if the cells in leaf segments of *Hymenophyllum* are momentarily plasmolysed and then placed in water until expanded, they are plasmolysed more readily and rapidly than in halves of the same leaf segments left attached or kept in water. The first plasmolysis loosens the adherence of the protoplasmic membrane to the wall, the second readily raises it from the wall at the same point. If the cells remain for some time in the plasmolysing solution without being killed, their osmotic pressure may undergo a distinct regulatory increase, but the first action is almost constantly of the kind indicated, and produces an apparent temporary fall of osmotic pressure, though not a tangible and measurable one.

It is more correct therefore to use the term "plasmolysing concentration" for results obtained in this manner, and a series of observations on the plasmolytic concentrations for leaf cells of species of *Acacia*, *Eucalyptus*, and *Grevillea* taken from 1–12 metres height show that the concentration may vary from 2–6 per cent. KNO_3 in one and the same plant, that the variations between leaves at the same level is at first as great as between leaves at different levels, and that the size of the cell and the age of the leaf appear to influence the plasmolytic concentration more than any other factors apart from food storage and assimilation.[*] Hence this promising line of investigation into the problem of the ascent of sap must be abandoned as inaccurate and misleading.

In criticising the conclusions based upon the experimental results in my former paper, Professor LARMOR[†] suggests that the main part of the ascent of sap may be by a chain of osmotic actions from vessel to vessel, and that the weight of liquid in each vessel may rest on the base of the vessel, so that no summation to a high total pressure occurs. That no high total pressure or tension appears at any point in a tall tree is certain, but the explanation given by Professor LARMOR does not coincide with the facts. In involves three assumptions:—(1) That the sap increases in concentration upwards; (2) that the vessels contain semi-permeable membranes; (3) that the weight of the separate columns can be supported on the permeable bases of the vessels without being transmitted through them. The last-named could only be the case if the membranes were impermeable, when all upward flow would cease, and any decrease of their permeability simply increases the resistance to flow, and hence also the pressure required to produce a given rate of flow upwards or downwards. Further, the vessels, being dead elements, contain no semi-permeable membranes. Where imperforate transverse partitions of lignified cellulose do occur they are equally permeable to water and dissolved salts, so that within the vessels themselves no osmotic raising of water is possible, even if the required concentrations existed at the higher levels. In regard to the latter the following data may be given:—

Section 5.—CONCENTRATION OF THE SAP IN VESSELS.

The sap obtained from bleeding stems may contain as much as 1–3·5 per cent. of sugar, although usually very much more dilute. According to HARTIG,[‡] sugar is present in quantities approaching the above amounts in the sap obtained from wood in winter time, especially in the case of the Willow and Poplar, but also in that of Conifers.

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[*] See also PRINGSHEIM, *loc. cit.*

[†] 'Roy. Soc. Proc.,' 1905, p. 460.

[‡] 'Bot. Ztg.,' 1888, p. 405.

FISCHER* found that in summer also the sap in most vessels contains more or less glucose in trees, but not in herbs and small shrubs. None was present in the vessels of leaves, but sugar was abundant in the sheaths around the bundle endings, so that an osmotic pull could in this case be directly exercised on the sap in the vessels like that which the somewhat more distant mesophyll cells can also bring to bear when they are not fully saturated. The young shoots on trees resemble herbs in so far as the vessels contain no glucose, which appears as they grow older. In winter time the distribution of the sugar is the same, but at the end of February the amount of glucose in the vessels begins to increase. In the case of the Maple where cane sugar is present, the osmotic action for the same percentages is one-half the nominal one where glucose is present, but the whole phenomenon is undoubtedly one of translocation, and in so far as the presence of sugar increases the viscosity of the sap, the flow is retarded instead of accelerated. It is only natural that the duramen should be free from sugar, and that the wood of Conifer roots should usually be poorer in sugar than that of the stem† can be understood as the result of the upward flow of the dilute entering sap coupled with the greater storage of starch in the stem.

No sap could be obtained during active summer transpiration from the Maple or Poplar, even by applying suctions of 65–70 centims. for several hours, either at the base or top of the tree. Large branches were then cut, the leaves at once removed and placed under a head of 2 metres of water containing eosin. The sap escaping was protected from evaporation and collected in a weighed glass vessel until some time before the eosin had travelled two-thirds of the distance along the stem, as told by previous testing of a similar branch and subsequent examination of the same branch. The vessel was then weighed, the contents evaporated to dryness and weighed again. Sap obtained in this way contained from less than 0·1 per cent. of dissolved matter in branches at the base and 45–55 feet up, to a maximum of 0·4 at the top and 0·36 per cent. at the base. The residues were gummy in character, had a slightly bitter taste, and contained appreciable quantities of reducing sugar. Obviously, the sap does not concentrate to any pronounced extent in its upward flow, as Professor LARMOR's theory postulates.

An Oleander growing in the Melbourne University grounds was found to exude sap in appreciable quantity from the proximal distal ends of branches cut in September. The collected sap left behind 1·8–2·2 per cent. of a gummy residue having a bitter taste, but consisting largely of a reducing sugar. The fact that the sap oozes out of the vessels when the cut surface of a separated branch is kept uppermost shows the existence of a positive pressure at the moment of cutting, and on examination but few of the vessels were found to contain air-bubbles which could be driven out by pressure. After the escape from the wood has ceased, water

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* 'Jahrb. f. Wiss. Bot.,' vol. 22, p. 73.

† STRASBURGER, 'Leitungsbahnen,' p. 894.

continues to ooze out from the distended pith, cortex, and phloem of the upper and under cut surfaces, and since the flow continues after repeated washing with distilled water and drying, it cannot be due to plasmolytic excretion. Large cut branches with the leaves removed continued to well out water for $\frac{1}{2}$–1 hour after bringing into the laboratory, and the application of very dilute sugar solution to the cut ends temporarily renews the escape of water. The surplus water in the tissues must either have been forced into them by some kind of pumping action, or they must have undergone a fall of osmotic pressure as the immediate result of injury, just as when a motile pulvinus is stimulated. This phenomenon of exudation from saturated stems separated from the absorptive organs is one of very general occurrence, and it may even be shown by the cut petioles of the Maple (*Acer pseudoplatanus*). There is, indeed, some reason to suppose that it represents in a generalised form the special power of response by exudation possessed by highly irritable pulvini such as those of *Mimosa*. The peculiarity is that the cells in this case are normally kept in the overcharged condition even when transpiration is fairly active.

Section 6.—Capillarity and Capillary Suction.

Capillarity was first invoked by Grew as a partial explanation of the ascent of sap, was given predominant importance by Boehm, and even at the present day is unnecessarily called upon to partially explain this phenomenon. Thus Dixon and Joly, with whom Professor Larmor is in accord, consider that the capillary suction from the leaves aids their osmotic suction in drawing off the water from the vessels. This is, however, not correct unless, by including imbibition, we give the term "capillary" a wider range than it enjoys in physics. The phenomenon of capillarity can only be shown where two dissimilar media meet between narrow bounding walls or in a capillary tube. The ascent of the lower liquid involves an ascent of the contact surface where the capillary forces are acting, and when this membrane reaches its highest point it can support a column beneath it but can produce no further upward flow. To produce any further flow the same amount of work will have to be done in raising the water and overcoming the resistance to flow in the tube as if no capillary ascent at all had taken place. In addition, the presence of a meniscus below a water column neutralises the action of the one on its upper surface and, in a chain of columns, the upper meniscus of the topmost air-bubble will exert a downward pull on the water in the leaves.

Strasburger[*] states that narrow elements always tend to draw water from wider ones, and that the narrower they are the more energetic this action is. He considers that it is for this reason that the final terminations of the bundles are always composed of narrow cells, that the first formed elements in the primary wood of the root are narrower than the internal ones, because their function is to take up

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[*] 'Leitungsbahnen,' p. 873.

and convey water to the tissue of the developing apex in the opposite direction to normal flow. Further, the increase of diameter of the wood elements of a tree as it grows older, which may amount to a quarter or one-third of their original size, is supposed to aid in the transference of flow to the newer wood. STRASBURGER fails to see, however, that a higher retentivity at the ends of the bundles would operate against the transference of water to the mesophyll, whereas a ready transference is what the plant needs, and in fact the narrowing of the diameter of the wood elements merely enables the bundle endings to be finer and more numerous and gives a relatively greater surface to the elements themselves for the outward passage of water. Furthermore, under normal conditions the flow of water in the first formed wood elements of the root apex is towards the stem, just as in other parts of the root, since the absorption through the root-cap is greater than the amount used locally in growth. This is all that needs to be made good, since there is no loss by transpiration in ordinary moist soil.

STRASBURGER'S generalisation is based solely on the fact that the wider vessels are the first to empty, which is the natural result of the lesser resistance to flow, and to the readier formation and expansion of air-bubbles in them. In the narrower elements the surface tension pressure of the air-bubbles is higher, and hence a greater suction is required to cause them to expand and allow the vessel to empty. When the supply of water is renewed, any sap ascending in the larger vessels will tend to diffuse to the smaller ones, whose air-bubbles being smaller and under greater pressure, are the first to be dissolved away. When all are filled with water, the main flow will be through the larger elements and no capillary actions at all come into play.

According to VON HÖHNEL, a head of 30–40 centims. mercury is required to overcome the capillary depression and cause mercury to flow into vessels of *Æsculus Hippocastanum* of 25–30 μ bore. STRASBURGER* finds that the capillary depression in vessels of 0·063 millim. internal diameter is overcome by a head of 20 centims., and a head of 40 centims. drives mercury into vessels of 0·025 millim. diameter, but will not drive it through pores in a partition membrane or burst the latter. These values are, however, influenced by a variety of factors. Thus, if the stem is moist and transpiring, mercury may be drawn into quite narrow vessels by suction. Further, the capillary depression in dry vessels is much greater than in ones wetted with water, owing to the surface tension of the mercury being reduced from about 500–390 dynes per centim. and to the changed angle of contact due to the presence of a film of water between the mercury and the wall of the vessel. When a vessel in a vertical piece of stem is completely filled by attachment to a tube of mercury, the mercury continues to run through until only a small head is left above. Then the column usually breaks near the upper end, and the long column is driven downwards, the shorter one upwards. In the case of dry mercury escaping from

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* 'Leitungsbahnen,' 1891, p. 511.

vessels of the Oleander 0·0033 centim. diameter, the escaping droplets have to overcome a surface tension pressure of rather more than half an atmosphere, which is sufficient to prevent the escape of the mercury when the stem is placed horizontally or when a portion has escaped if the stem is vertical. When the stem contains a good deal of water, however, or even when the ends are placed under water, the mercury escapes much more readily owing to the lowering of its surface tension.

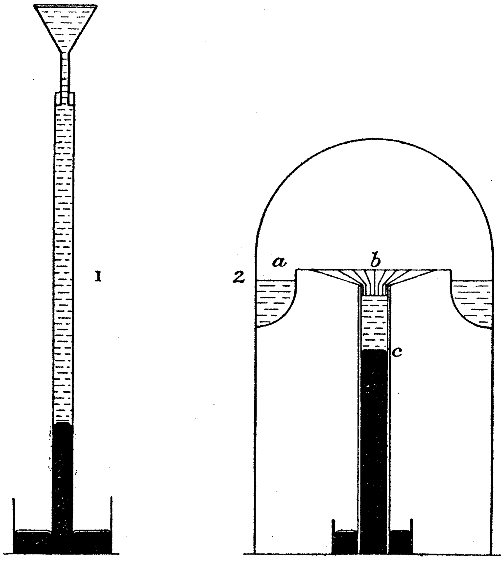

FIG. 3.

1. Suction by Evaporation, and
2. By Osmotic Action through Air.

Section 7.—SUCTION BY OSMOSIS AND EVAPORATION.

The mere evaporation of water from a membrane of plaster of paris at the head of a column of water was found by ASKENASY* to be able to support a column of 14 centims. of Hg, after which a bubble of air appeared below the plaster of paris, and the column slowly sank (fig. 3 (1)). This experiment was first described by MAGNUS in 1827, and a theoretical modification of it is figured by NERNST† (fig. 3 (2)). The height to which the mercury is raised depends upon the difference between the osmotic concentration of the water in the tube and of the saline solution in the ledge. In this case the suction is transmitted through air, so that when the stomata are closed the saline sap of the outer mesophyll cells might exercise a suction upon the water in the vessels across the air spaces in the leaf. Such action would, however, only come slowly into play, although in submerged plants with large air spaces it may be of greater importance. Within the vessels of plants more powerful suctions come

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* ASKENASY, 'Beiträge zur Erklärung des Saftsteigens; Verhdlg. des Naturh.-med. Vereins zu Heidelberg,' vol. 5, 1896.

† NERNST, 'Theoretische Chemie,' 4te Aufl., 1903, p. 161.

into play. BOEHM[*] even goes so far as to state that a twig of *Thuja* drew mercury 16 centims. above the level of the barometer, *i.e.*, 92 centims. in all, but this observation has never been repeated and great doubt attaches to it. In fact, VON HÖHNEL has shown that, when using a simple manometer, BOEHM was unable to correctly estimate the pressures from his own measurements.

Section 8.—THE BREAKING STRESS OF A WATER COLUMN.

Professor POYNTING considers that perfectly pure water in a tube with perfectly smooth and rigid walls to which it adhered with infinite tenacity would show an almost infinitely great breaking stress, and hence arises BERTHELOT'S measurements of over 100 atmospheres. In a personal communication, Professor WORTHINGTON expresses a similar opinion, and considers that in narrow tubes the apparent breaking strain of a water column would reach more nearly to its actual value than in a broad tube more subject to tremors. In the vessels, however, the walls are neither smooth nor rigid, dissolved gases are always present, and the walls are permeable to air under moderate pressure. Even then, according to DIXON and JOLY,[†] tensions of as much as 7 atmospheres may be supported. STEINBRINCK, using a mercury vacuum siphon, found maximal breaking stresses of 4 atmospheres for tubes of 2 millims. diameter, and of 5 atmospheres in tubes 0·5 millim. diameter. Since small columns of water were present at which the break occurred, these values apply to the water flowing at velocities approaching 2 millims. per second, and are unaffected by ordinary rises of temperature. When at rest, slightly higher values may be given, but these tensions, low as they are, are only shown when the tube is free from air. STEINBRINCK[‡] concludes that a tension of 5 atmospheres is sufficient to explain the ascent of water in a tree 50 metres high, making the common mistake of regarding the flow of sap as a statical instead of what it mainly is, a dynamical problem.

In common with other supporters of the water-tension theory of the ascent of sap, STEINBRINCK pays insufficient attention to the conditions actually existing in the wood vessels. All observations, including those of STRASBURGER, show that at least for some portion of the year the functioning wood vessels contain air, although from the nature of the observations the possibility remains that a limited and changeable number of vessels might at all times contain continuous water columns, especially in the last formed elements, and that these elements might carry the water to the topmost parts of the tree, while the lower regions were supplied by the less efficient air-containing vessels. Some observations made at Melbourne upon an Oleander are of interest here. A plant growing in the shade was found in September to have all its

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[*] 'Ber. d. D. Bot. Ges.,' 1893, p. 210.

[†] 'Phil. Trans.,' B, 1895, p. 570.

[‡] 'Jahrb. f. Wiss. Bot.,' 1906, vol. 42, p. 584; 'Physik Zeitschr.,' 6 Jahrgang, vol. 25, p. 911.

tissues so fully charged with water as to exude drops freely from the wood and to a less extent from the phloem on cutting the stem. A leafy stem was cut under water, eosin solution added, and the whole exposed to full wind and sun, the shade temperature being 22° C. The maximal rate of flow was 164 centims. per hour in one stem and 290 centims. per hour in the other (a more leafy one), as seen by cutting the stem from above downwards until a coloured spot was seen. On attaching a pressure-tube under the liquid and applying a pressure of 1–1½ atmospheres, it was seen by means of a lens that no air-bubbles issued from the two coloured vessels in the less leafy stem, or from the single coloured one in the more leafy stem. In a short time small air-bubbles issued from the other parts of the wood, though not in any abundance, but the three vessels mentioned apparently contained continuous water columns. Similar stems gave an average transpiration rate of flow of 40–50 centims. per hour in the whole of the outer wood. In this case, evidently the flow through the vessels forming a continuous water column was from three to seven times as rapid as the average flow in the outer wood.

The diameters of the vessels mentioned were 0·038, 0·035, and 0·033 millim. respectively, the longest vessel being 41 centims., 12 being 26 centims., and most less than this. At rates of 290 and 164 centims. per hour, 0·00034 cub. centim. pass through the larger and 0·00029 cub. centim. through the smaller vessels, amounts which formed considerably less than $\frac{1}{10}$ per cent. of the loss by transpiration from similar stems (0·4–0·7 cub. centim. per hour at 20°–22° C.). Nevertheless 10 per cent. of the vessels of the last year's wood at a rate of 50 centims. per hour would carry, when fully saturated, sufficient water upwards to satisfy maximal transpiration. Similar relationships hold good for trees in general, so that a considerable restriction of the conducting channels is possible without any injury to the leaves, although in such cases the conducting tissues may be working dangerously near their maximal efficiency.

Tests of the continuous water column theory were also made in 1905 at Birmingham upon plants of *Wistaria*, Maple, and Poplar. Branches 1½–2 metres long were cut under water and, after being attached under water to a column of water 1½–2 metres high, were placed horizontally, the leaves, if any, on the lateral branches removed, and the distal ends cut off and watched with a strong lens. In the case of *Wistaria*, the water begins to exude from the vessels in the superficial wood practically instantaneously, from June to September, but, nevertheless, on increasing the pressure to over an atmosphere, scattered air-bubbles escaped from the majority of the vessels. In September a slight delay could be observed, especially in certain tracts among the superficial vessels, and the quantity of air driven out from the vessels increases. Exact counting is impossible, but the general impression was received that the number of vessels which might contain continuous water columns never sank below 10 per cent. of those in the current year's wood during the whole four months. In the case of the Maple and Poplar during periods of June, July, and August, and in September at all times it took from 20–75 minutes before water began to exude from the vessels in the peripheral wood, and it occasionally appeared first in the vessels of the next inner annual ring. Here all the conducting vessels contained air under negative pressure, and hence on cutting the distal end, air was at first drawn in and then re-expelled, or if cut under mercury the latter was drawn into all the wider elements. Branches at the base of the tree gave similar results to those at the apex, except that the latter usually contained more air. In these cases, therefore, no continuous water columns existed in the peripheral branches at the time when they were most needed. Continuous columns might have been present in the wood of the main stem, but a break at any point is sufficient to prevent the transmission of any tension by cohering columns.

Similarly in the case of the Oleander at Melbourne, the vessels of the last two to four years' wood contained mostly continuous water columns in September, but air appeared in most in October, and nearly all functioning ones appeared to contain more or less air in November, while air bubbles were present in all the vessels in December.

Section 9.—Additional Data.

Length and Course of the Vessels.

The longest vessel found was in the stem of *Wistaria*, and was 5·64 metres in length from the cut end to the finely perforate transverse partition to which the mercury was traced (see fig. 2 (A)). Only the present year's wood was conducting in this stem, the previous three years' wood vessels being all blocked by tyloses, and the application of water under high pressure (1½–2 atmospheres) to a 34-foot length of stem only drove water and air-bubbles from the outermost ring.

Over 20 per cent. of the vessels in this ring were 2 metres 80 centims. in length, whereas STRASBURGER* gives the longest vessel as 3·6 metres, and most as less than 1 metre, while those of other climbers vary from 1 to 5 metres and the vessels of the Oak are supposed to be as long as the tree. Most of STRASBURGER's measurements were made on shoots killed by heat and then dried in air, a treatment likely to cause cracks and splitting. STRASBURGER also obtained similar results with living branches, but out of a large number of living oak branches tested with mercury after saturation with water, the greatest length found by the author was 1·82 metres, while but few of the vessels approached or exceeded a metre in length in *Quercus robur* and *Q. sessiliflora*, while in *Quercus ilex* the vessels are shorter by one-third to one-half on the average.

In the case of a seven-year-old basal branch of a sycamore, beyond 4 centims. the mercury was almost solely in the last three years' wood, and the average length of the vessels was 4–8 centims., the longest vessel (16·4 centims.) being in the spring wood of 1903 (three years back). In a 20-year-old branch from the top of the tree,

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* 'Leitungsbahnen,' p. 513.

the longest vessel was in the seventeenth ring (16·8 centims.), five vessels 11 centims. long were in the 8th–18th years' wood, and the average length of the vessels was 6–8 centims., so that the length of the vessels seems to increase slightly in the upper branches.

One source of error in all these experiments is that the course of the vessels is never exactly parallel to the length of the stem, and in the case of *Wistaria* the irregular course of the vessels is very readily demonstrable. The accompanying photograph, fig. 4, was obtained by injecting the longer vessels with a strong solution of ferric sulphocyanide (KCNS and Fe_2Cl_6) and photographing the wood cylinder after the cortex had been removed. The vessels not only diverge laterally but also inwards and outwards, even crossing one another. In many cases the actual length of the vessel is 10–20 per cent. greater than that of the stem in which it lies. The same applies to the narrower vessels of trees, and in the case of an elm with a trunk curved from a horizontal to a vertical position at its base, the wood elements crossed at angles of 30°–40° to the length of the stem in alternately interlacing layers, so as to form a very tough wood in which the length of the vessels was from 50 per cent. to nearly double that of the stem.

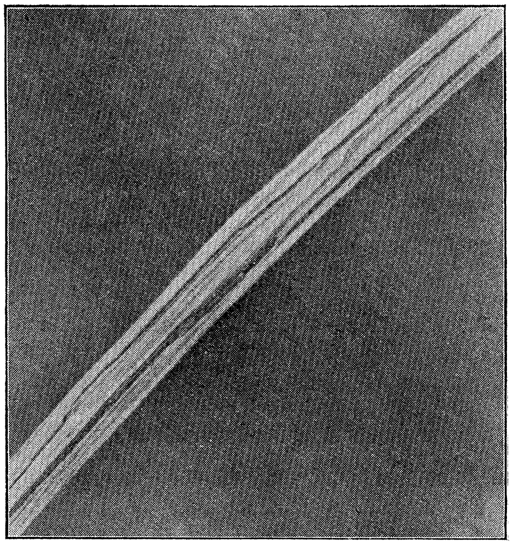

FIG. 4.—Injected Wood Cylinder of *Wistaria*.

Data on Rate of Flow and Resistance to Flow.

To obtain the true viscosity resistance, pure mercury was driven under a head equivalent to 516 centims. of water through 190 centims. of the stem of *Wistaria chinensis* placed horizontally at a temperature of 17° C. The mercury escaped at a rate of 0·31 cub. centim. per minute. The surface tension of the escaping mercury resists the flow, however, and when the free end was kept under mercury the amount escaping rose to 0·39 cub. centim. per minute. The mercury escaped from 12 vessels open at each end, and having diameters varying from 0·25 to 0·225 millim.

According to POISEUILLE'S formula, the volume escaping through 12 circular vessels of 0·024 centim. diameter and 190 centims. length at 17° C. under a head of 516 centims. of water would be, per minute:

$$\frac{60 \times 12 \pi r^4 gh}{8 \mathrm{L} \eta} = \frac{\pi \times 12 \times 60 \times 0{\cdot}000000020736 \times 981 \times 516}{8 \times 190 \times 0{\cdot}016} = 0{\cdot}99 \text{ cub. centim.}$$

Through 12 vessels of diameter 0·22 millim. the amount should be 0·68 cub. centim. per minute. The difference between the observed and calculated amount of flow is due to the fact that: (1) the vessels, as already seen, are longer than is indicated by the length of stem; (2) they are not perfectly circular in outline; (3) their internal walls are not perfectly smooth. In any case it is evident that the viscosity resistance in this especially favourable case is two to three times greater than would be expected from a viscosity calculation when the vessels are completely filled with liquid. Living wood was used for this experiment, but the viscosity of water and mercury are so nearly alike that the presence of a molecular film of water adhering to the inside of the moist wall could hardly affect the flow appreciably. In addition, the mercury escaping after the first few minutes was quite dry.

The maximum rate of flow through a 150-centims. length of a *Wistaria* stem in October, under a head of 150 centims. of water, was 840 centims. per hour at 18° C. The particular vessel through which this rapid flow took place was filled with sap when examined, and was 0·24 millim. diameter. The rate of flow on account of the viscosity resistance alone should equal $\frac{r^2 9}{81 \eta}$ = 1·4 centims. per hour. Hence only one-sixth of the resistance to flow in this vessel was due to pure viscosity, and this with a rate of flow but little greater than the maximal rate of the transpiration current.

There is, however, a distinct fall of conductivity in autumn, partly due to gummy growths on the walls of the vessels or to tyloses in their interior, and in midsummer (June 15, 1905) stems immediately examined after cutting under water showed a relatively smaller "viscosity" resistance.

Thus the maximum transpiration current observed at this time was 7·8 metres per hour, and the head of water required to produce the same rate of flow was only 20 centims. per metre of stem or one-fifth the length of the stem. The conducting vessels in the stem examined contained but little air. Thus a length of 1·9 metres, under a head of 1·6 metres of water, gave a rate of flow of 1 metre per 125 seconds and an amount of flow of 1 cub. centim. per 248 seconds, at 23° C. Water was then forced through under high pressure and a few air-bubbles seen escaping. On cutting fresh ends (decreasing the length of the stem by $\frac{1}{2}$ centim.) and applying a head of

1·6 metres, the maximum rate of flow was 1 minute 40 seconds, and the total amount of flow was 1 cub. centim. per 98 seconds. The slight increase in the maximal velocity of flow shows that a few air-bubbles were present in some at least of the most efficient vessels, and the relatively greater increase in the amount of flow showed that the removal of the air from several of the vessels of this and previous years' wood produced a levelling up of the general rate of flow.

Sycamore.—A leafy branch 16 years old and 2·5 centims. diameter, cut under water, and after half an hour placed in eosin and fully exposed at 22° C., gave a maximal rate of flow of 3·4 metres per hour, the wood being coloured throughout for a distance of 44 centims. by the strong eosin solution used. A similar branch placed in formalin solution gave a rate of ascent of 180 centims. per hour, as tested by heating slices of wood in a drop of water and then adding a drop of a solution of magenta decolourised by SO_2, to which formalin restores the pink colour. This test is very delicate if an excess of sulphur dioxide is avoided, but the slower ascent of the poisonous formalin is partly due to its retention by the wood, and partly to its higher viscosity, and cannot be taken as a proof of the existence of any vital pumping action.

Under a head of 150 centims. of water, 150 centims. of the horizontal stem gave a maximal rate of flow of 47 centims. per hour at 18° C., the branches being stripped of their leaves and the petioles sealed by burning and then smearing with vaseline. Under a suction pressure of 66–65·5 centims. of mercury applied at the distal end, a maximal rate of flow of 220 centims. per hour was observed, and the application of a head of 53 centims. of mercury was needed at the basal end of the stem to produce a rate of flow of 3·4 metres per hour. Hence, to produce the maximal transpiratory rate of flow, a pressure of 7·2 metres of water per metre of stem or a suction pressure of 8·9 metres would be required. In these experiments none of the vessels appeared to be entirely free from air, but some probably contained very little, and hence the small difference between the heads required under pressure and suction. In this case, therefore, the resistance to the transpiration current appears to be equivalent to a head of seven times the height of the tree under pressure, and nearly nine times its height under suction.

Populus Canadensis.—The longest vessels were from branches 26 to 30 centims. in diameter, the average length being 6–10 centims. and the average diameter 0·06 millim., with fluctuations of from 0·04 to 0·07 millim. The average rate of the transpiration current under favourable conditions (temperature 20°–22° C.) lay between 42 and 90 centims. per hour, the maximal rates observed being from 180 to 216 centims. per hour. A branch 140 centims. long gave a maximal rate of flow of 112 centims. per hour at 20° C. under a head of 150 centims. of water, and a branch 2 metres long gave a rate of flow of 140 centims. per hour under a head of 2 metres, so that to produce the transpiratory rate of flow, a head of water of from one to two times the length of the stem would be required. According to POISEUILLE's formula, water at 20° C. under a head of 2 metres should flow through a circular vessel 0·006 centim. diameter and 2 metres long at a rate of 400 centims. per hour approximately, so that in this case the viscosity resistance is about one-third of the total resistance to flow, and the total resistance to the upward ascent of sap during active transpiration is equivalent to a head of water from two to three times the height of the tree.

Section 10.—THE HEIGHT OF THE TALLEST TREES IN AUSTRALIA.

The tallest tree in Australia appears to be *Eucalyptus amygdalina*, but the values given in MUELLER'S 'Eucalyptographia' are much too high. The heights are given as observed by WALTER, Cape Otway; ROBINSON, Mount Baw Baw; HOWITT, Gippsland; and D. BOYLE, in the Dandenong Ranges, and are 415, 471, 410, and 420 feet respectively. None of the erect trees appear to have been properly measured, but BOYLE'S measurement was stated to be made on a fallen tree from which the top was wanting. The accuracy of the last-named observer is sufficiently indicated by the fact that the height of a tree was first given by him* as 525 feet, subsequently reduced to 466 feet, and proved on accurate measurement by Mr. FULLER, in May, 1889, to be 220 feet high and 48 feet girth 6 feet above ground. Various statements as to the existence of specially tall trees of over 350 feet in height have all proved on proper measurement to be considerably exaggerated when the supposed giant was found. Many fallen giants with heights given as from 450 to 500 feet evaporated into thin air on the approach of accurate instruments and unbiassed observers.

The tallest trees are usually found in thick groves or in valleys. The trees of greatest girth are found in the open but are of less height. The tallest tree, however, observed by Professor KERNOT (302 feet), was on the edge of a ridge. The tallest trees measured by PERRIN, DAVIDSON, and FULLER were all in thick groves, and were 271, 294, 296½, 297, and 303 feet respectively. The tallest Australian tree, therefore, hitherto accurately measured, barely exceeds 300 feet, and it is possible that some of the records from other countries, notably America, may suffer a similar diminution when accurately tested.

A common, though by no means universal, feature with these giants when aged appears to be that the top dies, while branches at a lower level remain living for a long time. Possibly this may be taken as an indication that the tree has approached the maximal height to which the sap can be raised with efficiency and economy.

In my first paper it was calculated that the maximal total resistance to the transpiration current might amount to 100 atmospheres in the tallest trees. As regards Australia, this value must now be reduced to between 30 and 50 atmospheres.

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* 'Argus,' 18/1/89.

Section 11.—The Suction and Exudation Pressures in Wood.

The exudation of drops of water in spring from the leaf traces or leaf scars of the Hornbeam[*] and other trees is evidence of the existence of a positive pressure in the vessels, but, unfortunately, the height above ground is not given in any of these scattered observations, and neither the poplar nor the maple examined by me showed any exudation of water or positive pressure at heights of from 45 to 50 feet. Clark observed that manometers inserted into the base of a birch in spring registered pressures of 1 atmosphere or more,[†] and when one manometer was removed the other fell to zero, although the open hole was 6 feet or more away. This is because continuous water columns were present, but this peculiarity is no longer shown when active transpiration begins and air appears in the vessels. Horvath[‡] observed that of two branches of a vine 70 centims. apart, one showed a pressure of $+46$ centims. of mercury, the other one of -20 centims. In this case the stem between the two branches must have been blocked, for a pressure of 20 centims. will drive water through 70 centims. of a freshly-cut vine stem at a sufficiently rapid rate to prevent the production and maintenance of any such differences of pressure as recorded by Horvath. In any case, as Hofmeister[§] was the first to show, the root-pressure alone yields less sap than is needed for active transpiration, and a positive pressure is in the latter case always absent.

Vesque[||] was the first to observe the waxing and waning of the air-bubbles in the vessels according to the relative gain or loss of water by the stem, and he concluded, in fact, that the main function of the vessels is to act as reservoirs for water, and that they conduct only under special conditions. He also erroneously concluded that the resistance to a given velocity of flow is proportional, *ceteris paribus*, to the fourth power of the radius, whereas it is proportional to the square of the radius and the volume passing to the fourth power. In any case, the bubbles in the vessels always appear under a pressure of less than an atmosphere, and hence arises the fact, as shown by Von Höhnel, that, when actively transpiring branches are cut under mercury, the latter is usually drawn up into the vessels in spite of its capillary depression. The latter is given by Von Höhnel[¶] as—

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[*] Hartig, 'Bot. Ztg.,' 1853, p. 478.

[†] Clark, 'Flora,' 1875, p. 511; Hartig, 'Bot. Ztg.,' 1863, p. 281.

[‡] 'Beitr. über die Wurzelkraft,' Strassburg, 1877, p. 51.

[§] 'Flora,' 1862, p. 107.

[||] 'Ann. Sci. Nat. Bot.,' vol. 15, 1883, p. 5.

[¶] Inaug. Diss., Strassburg.

Plant.	Age of wood.	Diameter of vessels.	Capillary depression.
		μ	cm.
Quercus pedunculata	1st year	37—42	13—15
	8th ,,	94—97	
Æsculus Hippocastanum	—	25—30	30—43
Syringa vulgaris	1st ,,	18—25	Averages 35
	4th ,,	38	
Juglans regia	1st ,,	45—54	
	3rd ,,	62—70	

Von Höhnel observed the mercury to be drawn up 60 centims. in some cases, and Strasburger[*] saw it rise 70 centims. in *Wistaria*. In winter, Von Höhnel observed little or no negative pressure, but, as shown by Strasburger, was incorrect in supposing that air spaces never come into direct contact with the vessels. Many of Von Höhnel's physical conclusions are, unfortunately, inaccurate, and this vitiates his measurements of the pressure in the vessels, but the latter suffice to show that while the pressure is never zero, it is often much less than an atmosphere.

The Permeability of the Wood to Air.

Von Höhnel greatly over-estimated the resistance to the flow of air along open narrow tubes, which plays little or no part in the maintenance of negative tensions in the vessels. The latter is, in fact, due solely to the relative impermeability of the moist walls and pit-membranes of the vessels. Strasburger[†] confirms Von Höhnel's observation that a stream of air-bubbles escapes through branches of the Maple and other trees closed at their outer cut surfaces and subjected at their inner ends under water to a pressure 60 centims. or more of Hg less than an atmosphere. The stream ceases when the difference of pressure is less pronounced and, according to Strasburger, dry wood allows air to pass more readily than wet wood. Lietzmann[‡] as well as Wiesner and Molisch,[§] state, however, that gases diffuse more rapidly through walls saturated with water than through dry walls. The latter statement is quite correct, for a uniform imperforate cellulose membrane is more permeable to a gas when saturated with a liquid in which that gas is soluble than when dry. Owing to the structure of wood, however, the reverse is the case with this tissue. Apart from the formation of cracks, and the presence of open intercellular spaces between the contracted medullary ray cells and other elements of dry wood, the gas in a dry vessel has only to pass through the thin middle lamellæ of the pores, whereas in one containing a living film of water it must also pass in solution through the water, filling the pore on each side.

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[*] *Loc. cit.*, p. 712.

[†] *Loc. cit.*, p. 719.

[‡] 'Flora,' 1887, pp. 339, 376.

[§] 'Ber. d. Wien Akad.,' 1887; 'Bot. Centralbl.,' 1889, vol. 39, p. 214.

Rods of dry sound wood or dry branches of Dicotyledons or Gymnosperms 6 inches or so in length allow air to pass readily under a suction of 65 centims., but if soaked in water for a few minutes become highly impermeable to air, and prolonged drying is required to restore the original permeability. When the length of the stem is greater than that of the longest vessel, the difference between the permeability when wet and when dry becomes still more pronounced. Thus, a 6-inch length of a fresh Maple stem under a suction of 65 centims. allowed 3·7 cub. centims. of air to pass per hour, whereas a 6-centim. length, in which many of the vessels were open at both ends, allowed 320 cub. centims. to pass per hour, and 24 cub. centims. per hour when the exposed cut surface was smeared with vaseline. In the latter case the air entered through the numerous lenticels on the surface, but, as in the case of water, much greater resistance is offered to the transverse transference than to the longitudinal.

Satisfactory experiments can only be made by using lengths of stem longer than the vessels. Thus, on connecting a 25-centim. branch of a poplar with a receiver containing air at 16 centims. mercury pressure, the latter rose to 33 centims. in one hour, showing the entry of 18 cub. centims. of air and water vapour. After smearing the peripheral surface with vaseline, the pressure rose from 16 to 30 centims. in two hours, and after smearing the cut end as well it rose from 16 to 25 centims. in two hours, the air evidently being taken in through the bark and cut surface in nearly equal proportions, and being able to pass slowly through a thin layer of vaseline. With a similar fresh stem the pressure rose from 16 to 36 centims. in four hours. After smearing thinly with vaseline the pressure rose three days afterwards from 16 to 36 centims. in four hours, and after smearing thickly with vaseline changed from 16 to 29 centims. in 16 hours.

On attaching the receiver to a branch of a poplar 50 feet above the ground, the pressure rose from 15 to 23 centims. in half an hour in one case, and from 13 to 24 centims. in another in the same time. This was on September 26, in England, and in spite of the fact that the stem contained much water. Thus, a branch 0·7 centim. diameter from the top of the tree contained 54 per cent. of water, and a similar one contained 55·9 per cent. after water had been passed through for one hour. Similar results were given by branches at the base of the tree, and differences of only 3–5 per cent. in the percentage of water existed between freshly cut basal branches, and ones through which water had been passed. Hence, a branch nearly saturated with water is freely permeable to air while attached to the parent plant.

The Influence of External Pressure on the Tension in the Vessels and on the Absorption of Water.

That herbaceous plants are able to absorb sufficient water to cover the loss by moderate transpiration when their roots are in water contained in a vessel from which the air has been pumped, was shown by DE SAUSSURE,[*] although cut stems absorbing from vessels in which the pressure has been reduced to + 2 or + 36 millims. have air drawn backwards from them, and their vessels become blocked so that the leaves shrivel.[†]

STRASBURGER[‡] found, however, that the shoots of such Conifers as *Taxus* and *Tsuga* drew water in abundance from vessels in which the pressure was equal only to 2 or 3 centims. of mercury, and that this water was drawn up the outer rings where the vessels contained very little air. STRASBURGER concludes that air-pressure plays no part in the ascent of water, which is hardly correct, since this cause must aid in driving water towards any region where a lower pressure exists. It is, however, a factor of minor importance, and is neither the exciting cause of the ascent of water, nor the sole force maintaining it.

The reverse experiment was performed on the poplar, in this case water intervening between the mercury in the manometer and the cut surface, so that the suction pressure is given. Considerable air pressure applied to the branches of a standing poplar seemed to exercise no effect upon the suction pressure of neighbouring transpiring branches as compared with the further removed ones.

Poplar.—September 11, few leaves fallen. Sunny, shade temperature 12°–15° C. Air pump applied to a basal branch, the pressure over which was reduced to 5–12 centims. of Hg, and manometer attached to a neighbouring one and to one 50 feet above ground.

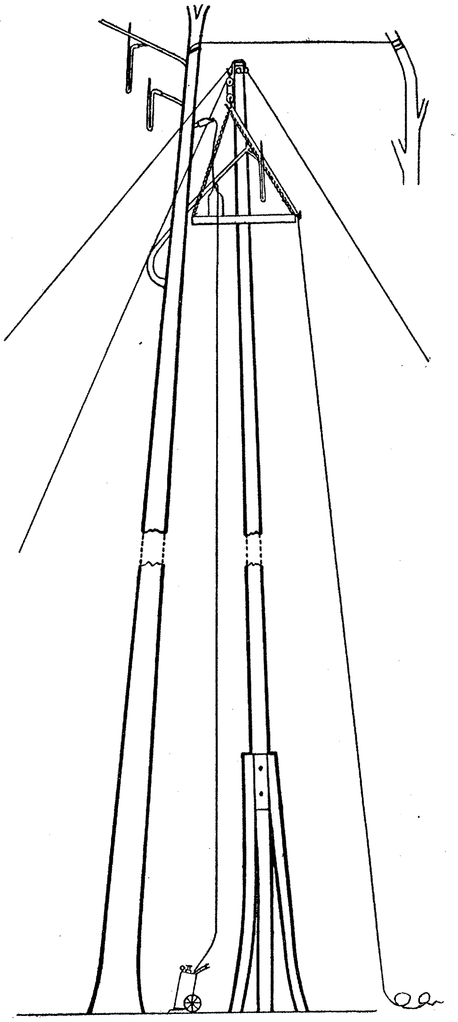

FIG. 5.—Experiment on Poplar.

Height of manometer above ground.	10.30 A.M.	12.30 P.M.	3.30.	4.30.	5.30.	6.30.	9.30 A.M.
10 feet	+1·4 cm. Hg*	−2·8	−1·1	−0·6	+0·2	+2·8	−0·1
50 „	0·0 „ *	−3·7	−4·7	−4·3	−2·7	−1·0	0·0

* Starting pressure.

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[*] "Rech. Chim. sur la Végétation," 1804, chap. 4.

[†] JANSE, 'Jahrb. f. Wiss. Bot.,' vol. 18, p. 3; SCHEIT, 'Jen. Zeitsch. f. Naturw.,' 1885, p. 694; STRASBURGER, 'Leitungsbahnen,' p. 794.

[‡] *Loc. cit.*

No air entered either manometer, but at the close of the experiments the vessels near the cut end of the branches were found to be blocked. A positive pressure is very rarely shown by the Poplar, and appeared in this case in spite of the action of the air pump, which, however, drew no water, but only air from the trunk. In other cases negative pressures were shown throughout, those at the base being usually a little lower than those at the top of the tree, whether the air pump was applied to branches at the top or bottom. Similarly, considerable quantities of air can be driven in under pressure without apparently affecting the pressures in neighbouring manometers.

Sycamore.—A fork 13 metres above ground was sawn through 80 centims. from its junction, and connected by means of glass and rubber adapters to pressure tubing joined to a powerful pump at the base of the tree. Manometers were attached to cut branches with air between the cut end and the mercury, 3 metres of stem intervening between (*a*), 4 metres between (*b*), and 8 metres between (*c*) and the large cut branch. After forcing air into the latter at a pressure of 25–30 lbs. per square inch, between 11 A.M. and 5.30 P.M., the following pressures were shown in millimetres of mercury :—

	11.30 A.M.	12.45 P.M.	4 P.M.	5.30 P.M.
	millims.	millims.	millims.	millims.
a . . .	+1	+3	+2	+2
b . . .	+1	+3	+4	+5
c . . .	+2	+3	+0	+0

Evidently, therefore, air passes only with difficulty across a transpiring Maple stem, but does pass slowly when the pressure is great. Hence, the presence of columns of water under high negative tension would cause air to be drawn in from any cut surface, and the channels to be blocked. If however, in this experiment, the cut surfaces were made the day before, no evidence could be obtained of any forcing of air through the stem, the vessels presumably having become blocked.

Even when water is used a large amount has to be driven in under high pressure to produce any effect, and this is only shown in manometers close to the branch used, and on the same side of the trunk. Thus, on driving water into a branch 5 centims. diameter and 55 feet above ground under a pressure of 30–35 lbs. per square inch (*cf.* fig. 7), a manometer attached to a branch 25 centims. below on the opposite side still showed a small negative pressure of − 1·6 centims. after water had been driven in at an approximate rate of ½ litre per hour for three hours (10 A.M. to 1 P.M.), while another manometer 25 centims. below on the same side showed a pressure rising from + 2 centims. to + 7·5 centims. in three hours, and falling to zero by next day. A manometer attached at the base of the tree showed a pressure of + 3·5 centims. at

10 P.M., at 1 P.M. + 0·2, at 3 P.M. — 9·6 centims., and at 7.30 P.M. had fallen to zero, air having entered. Manometers attached the previous day registered zero throughout this and the following experiment.

Next day 5 centims. of the stump 55 feet above ground were removed, and water under a pressure of 35 lbs. per square inch applied at 11.30 A.M. The water entered at a rate of 0·7 litre per hour in the first hour, 0·5 litre in the third hour, 0·3 litre in the night, and 0·2 litre in the morning, when the pressure in the air holder of the force pump had fallen to 12 lbs. per square inch.

Manometer Pressures on Branches.

	10 A.M.	11 A.M.	11.20 A.M.	11.25 A.M. (fresh manometer).	11.30 A.M. (pressure applied at top).	12.30 P.M.	1 P.M. (air entered).
10 feet up . .	+4·2	−7·8	Zero: air entered	+11·5 cm.	+8·7	−5·9	−1·5 to zero
52 feet up . .	—	+2·5	−5·1	—	−6·5	−1·4	

Fresh Manometer applied.

	2.35 P.M.	3.30 P.M.	4.30 P.M.	5.30 P.M.	6.30 P.M.
10 feet up . . .	+2·1	−7·4	−1·1	zero	zero
52 feet up . . .	+0·3	−1·0	−7·6	−2·2	zero

During this experiment the day was sunny and the temperature averaged 4°–5° C. higher than on the previous day. No positive pressure was shown by any branch, the positive pressures in the table being merely the starting pressures of the manometers.

These results conclusively show that no continuous network of water columns existed in this poplar tree at a time when transpiration was active, although different results might be obtained when all the vessels were completely filled with water and transpiration reduced to a minimum. In fact, CLARK* states that when manometers are attached to the Maple in spring the formation of each new boring causes the pressure to fall temporarily to zero in widely distant manometers. Such a condition is, however, of very rare occurrence, and probably never occurs in any plant when transpiration is active.

Section 12.—THE SUCTION OF TRANSPIRING BRANCHES.

BOEHM† stated that the transpiring branches of a variety of plants could raise mercury to the barometric height, but STRASBURGER has shown that BOEHM'S

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* 'Flora,' 1875, p. 509.

† BOEHM, 'Ber. d. Bot. Ges.,' 1889, p. 53; 'Bot. Centralbl.,' vol. 42, 1890, p. 234.

method was not free from error. The maximal rise obtained by STRASBURGER was 26 centims. of mercury with herbaceous plants, the plants usually drooping some time before this tension was reached. Woody Dicotyledons generated suctions of 45 (*Wistaria*) to 67 centims. The highest values were given when the lower end was boiled to drive out air,* but even then tender leaves soon droop, and the experiment always ends in the entry of air. By closing the cut surface and allowing the water to enter through the surface of the wood of a Conifer, a suction of as much as 70 centims. was shown, and since the branches were 2 metres long and erect, the total head was greater than the atmospheric pressure. VINES† has shown that dead branches may ultimately generate as high a suction as living ones, and in fact the higher suctions are more the result of imbibition forces than of leaf suction. Ordinary transpiring leaves should theoretically be able to transmit an osmotic suction of several atmospheres to the vessels, whereas as soon as the tension in the vessels reaches $\frac{1}{4}$–$\frac{1}{2}$ of an atmosphere, the transpiration current is either strongly retarded or entirely stopped, even when short lengths of stem are used. Long lengths of stem do not develop a higher but usually a lower suction than short ones. Thus, 31 feet of a leafy *Wistaria* stem developed a maximal suction of 32 centims. of mercury, and this in 15 minutes, instead of the 40 or more centims. suction which shorter stems may show. A similar stem was so arranged with a water valve that the mercury could not be raised above 25 centims., and in this case although no air was drawn back from the stem for over two hours, the leaves were drooping slightly at the end of the first hour (23° C. and sunny), and strongly at the end of the second hour.

When a water-filled manometer is attached to a cut branch so that continuity exists between the external water and that in the charged vessels, the latter draw in water until a sufficient tension is reached to draw air out of the air-containing vessels and the air spaces.

Hence, the manometric pressure does not necessarily measure the negative pressure in either set of vessels, but something between them. The fact that air is drawn back shows that in the stem it exists under a higher pressure than in the manometer, and still higher than in the actively absorbing vessels. A much smaller pressure will draw air readily from a cut surface than will drive it freely through the saturated walls of intact vessels. Hence, an attempt was made to demonstrate the actual pressures in the vessels of a transpiring stem when these are uninjured and functioning.

A lateral two-year-old branch near the base of a large *Wistaria* was cut under water, and a glass Y-tube filled with water attached. The clamped rubber ends were then attached to two glass receivers, one containing a strong almost black

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* 'Leitungsbahnen,' p. 783.

† 'Annals of Botany,' 1896, vol. 10, p. 292.

solution of ferric sulphocyanide* and joined to an air pump, the other containing air and joined to a suction pump (fig. 6).

Above and below the origin of the branch, small portions of the bark were removed at intervals over a short distance, so that the contents of the superficial vessels could be determined by the aid of a hand lens. The exposed portions were kept moist, the main stem was 8 feet long in the basal portion below, and 28 feet in the distal portion above the lateral branch. The coloured liquid was now driven into the stem under a head of 10 lbs. per square inch. It appeared in numerous superficial vessels below the branch and travelled down 20 centims. before it appeared in two superficial vessels 4 centims. above the branch. The tube was then clamped and suction applied. With a suction equal to 30 centims. of mercury, the liquid was drawn slowly down the vessels and also up to the branch, approximately 0·6 cub. centim. being drawn out of the vessels and tubes. Further flow then ceased, even when the suction was raised to 70 centims. of mercury. After keeping up this suction for three hours during an afternoon with a hot sun, the leaves on the shoot were not perceptibly drooping, although on a cut shoot in air they drooped strongly in half an hour, and very strongly in one hour.

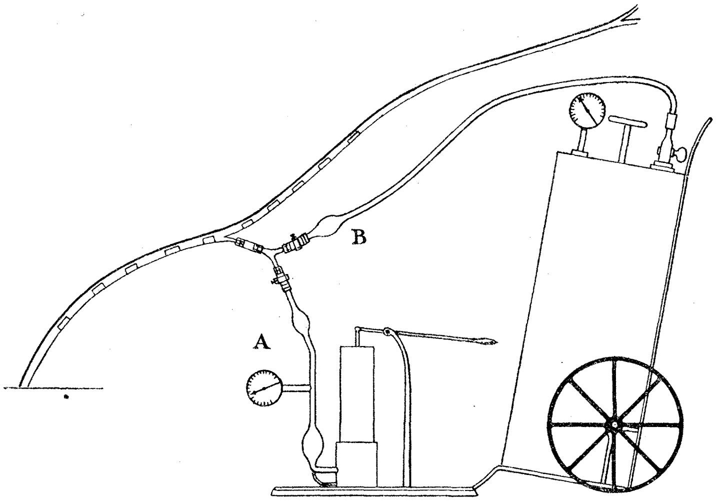

FIG. 6.—Measurement of Pressure in Vessels of *Wistaria*.

Two repetitions of this experiment gave similar results, except that on a dull damp day a suction of 12 centims. was sufficient to draw liquid slowly down from the upper vessels, and one of 20 centims. drew it down rapidly. A similar branch cut under water at the same time, and attached to a mercury manometer, developed a maximal suction of 15 centims. in rather more than half an hour. Apparently, therefore, in this plant the suction developed by a cut branch approximately corresponds to the average of that existing in the vessels of the intact stem prior to cutting, and when

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* The ferric sulphocyanide does not appreciably stain the walls of the vessels, but remains located in them, filtering only with great difficulty through lateral walls and more readily through end walls. When too much diluted, especially by the presence of alkali, ferric hydrate is thrown down.

the water is drawn out of one set of vesssls, leaving nearly complete vacuums in them, neighbouring ones filled with water may continue to function actively without any apparent disturbance, although the pressure of their contents is less than that of the atmosphere.

In other words, the difference of pressure acts on the bounding wall, and is only very slowly transmitted through the water saturating it. Nevertheless, so long as a film of water lines the pits in the wall, a vessel left to itself will slowly draw water in from its neighbours containing water at a higher pressure. Thus, suppose B in fig. 1 contains water at 40 centims. pressure, and that the contents were pumped out of A. The pressure in A can never be less than 1 or 2 centims. owing to the vapour pressure of the water evaporated from the moist walls. Even then so marked a difference of pressure will cause air to pass through the wet walls in solution, so that the pressure rapidly rises to 10 or 20 centims. The entry of air now takes place more slowly, so that 20–30 centims. are available to draw water inwards. The resistance to transverse flow in *Wistaria* may, however, be more than 100 times greater than the resistance to longitudinal flow, so that the latter may continue with an almost undiminished velocity even when the neighbouring empty vessel is slowly drawing water in as at *a*.

Attempts were made to determine the pressure in vessels of a transpiring branch of *Wistaria* filled with water by inserting fine capillary glass tubes into the cavity of the vessel. The tubes used were made by allowing water to rise in them, sealing the upper end a little above the meniscus, and then breaking away the greater part of the water-filled portion. On using the tubes, however, they either broke or made an incision in the vessel through which air entered before the movement of the meniscus in the tube enabled any sure estimate to be made of the pressure in the vessel.

Section 13.—The Influence of the Height above Ground and of the Seasons upon the Suction Tension.

These observations were all performed by attaching mercury manometers to cut branches so that no air, but only water, was included between the cut end and the mercury. In all the later experiments the manometers used were provided with a tap and funnel at the upper bend, and with a clamp between the tap and the manometer, so that air could be removed and water added without affecting the height of the manometer. With this form (fig. 7) continuous observations may be made on the same branch so long as the vessels remain unblocked.

Sycamore.—On June 24, 1905 (England), 18°–25° C. in shade. Half sunny. The manometers were attached to three-year-old branches 1 metre and 13 metres from the base of the tree, the starting pressures being in each case positive.

In this case the suction at the base took longer to develop, but attained a higher ultimate value than at the apex, possibly because the vessels at the base contained more water and less air than those at the top of the tree.

When the leaves have nearly all fallen smaller suctions are shown, and these are more slowly produced. Thus on testing leafless branches at the base of a 38-feet maple and a 50-feet poplar on October 6 (8°–11° C. shade temperature and sunny day), the following values were given :—

Time.	13 metres up.	1 metre up.
10.15 A.M. . . .	+ 8 centims. mercury.	+ 12 centims. mercury.
11.15 ,, . . .	− 16·0 ,, ,,	− 0·6 ,, ,,
12.15 P.M. . . .	− 17·35 ,, ,,	− 10·4 ,, ,,
3.15 ,, . . .	− 17·0 ,, ,,	− 21·3 ,, ,,
7.0 ,, . . .	− 14·2 ,, ,, (Air entered)	− 26·8 ,, ,,
8.45 A.M. . . .	zero	− 25·0 ,, ,,
10.0 ,, . . .	,,	− 12·4 ,, ,, (Air entered. Rapid fall.)

Time.	Maple.	Poplar.
	centims.	centims.
3.20 P.M. . . .	− 1	—
3.50 ,, . . .	− 3·8	− 8
5.0 ,, . . .	− 7·6	− 7·6

Air then entering and the pressure in the maple falling rapidly, and in the poplar slowly to zero.

On October 16, under closely similar conditions, a basal branch of the same diameter and age converted a positive pressure of 6·5 centims. into a negative one of 7·8 in five hours. The activity of absorption by the wood is here approximately one-half of what it was on the 6th of the same month.

The following results with the poplar, after all the leaves had fallen, are given in tabular form for convenience (p. 378).

The highest suctions were usually observed in the late afternoon or evening. No positive pressure appeared to be produced at any time except in one doubtful case, and the smallest suction is shown in winter. The highest suction is usually accompanied by an increased rate of absorption, but this is not always the case, and both the rate and amount of suction, as well as the relation between them, fluctuates during the seasons. In these experiments the value obtained is partly determined by the amount of air in the vessels; but in the experiments with the tap manometer this factor is largely eliminated, and higher suction values were obtained (fig. 7).

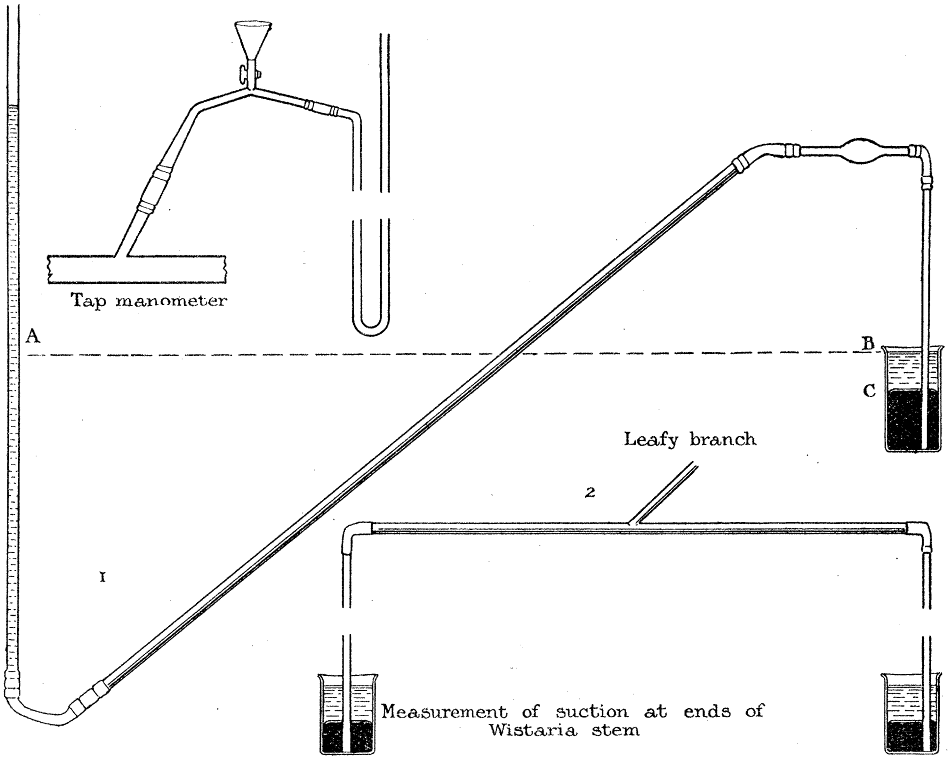

FIG. 7.

After a tap manometer had been attached for one to three days, no further amount of air was drawn back from the branches of the poplar used. Evidently all the

Date.	Conditions.	Elevation of manometer.	Maximal suction.	Rate of absorption as measured by change of pressure.
1905.		ft.		
October 18 . .	Fine rain,	4	−7·1 centims. Hg	5·7 centims. per hour
	7°–10° C.	48	−7·4 ,,	16·3 ,, ,,
November 8 .	Showery,	5	−8·1 ,,	2·4 ,, ,,
	7°–10° C.	6	−7·2 ,,	3·9 ,, ,,
		48	−6·3 ,,	2·6 ,, ,,
December 20 .	Clear,	5	Branch 0·6 centim. diameter	16·0 ,, ,,
	1°–4° C.			
		45	Branch 0·8 centim. diameter	2·4 ,, ,,
1906.*				
January 17 . .	Sunny,	6	−4·4 centims. Hg	6·0 ,, ,,
	3°–6° C.	48	−2·0 ,,	1·5 ,, ,,
February 24 .	Cloud and snow,	6	−3·3 ,,	3·6 ,, ,,
	0°–2° C.	48	−4·0 ,,	6·4 ,, ,,
March 28. . .	Snowy,	4	−3·8 ,,	1·3 ,, ,,
	2°–4° C.	46	−2·5 ,,	1·6 ,, ,,
April 27 . . .	Sunny,	5	−4·5 ,,	1·7 ,, ,,
	5° C.	47	−3·5 ,,	2·8 ,, ,,
May 30 . . .	Bright,	6	−7·1 ,,	2·0 ,, ,,
	15°–18° C.	48	−6·5 ,,	2·2 ,, ,,

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[*] The 1906 observations were made for me by CHARLES LOWE, Botanical Assistant at Birmingham, after my departure from England.

vessels for some distance from the cut surface became filled with water, and these columns prevented any backward passage of air. The following were the maximal suctions observed:—Beginning on March 7 at 3.30 P.M., the suction rose to −15 centims. (17° C.) at 2 P.M. on the 8th, fell to −14·5 centims. by 6 P.M., and remained at −14·5 until March 10 at 9 A.M. The suction then slowly decreased to −7 centims. by March 13 at 9 A.M., the average temperature having steadily fallen from the 8th to the 13th (17° C. to 3° C.).

During another set of observations in April the temperature remained very constant, averaging 13° to 17° C. during the day time. Started at 2.30 on April 4, the suction rose to −13 centims. by 6 P.M., and to −20 centims. by 2 P.M. on the 5th, remaining at that until 9.30 A.M. of the next day, and then falling at a rate of $1\frac{1}{2}$ centims. per day until the 10th, when it had fallen to −13 centims. As with the other manometers, the continuous fall in the suction of the manometer does not indicate any corresponding change in the tree, but is in this case due to the gradual blocking of the vessels near to the cut surface cutting off the manometer from the suction of the functioning wood vessels. The gradual entry of air into the blocked vessels then causes a progressive rise of pressure, and this air may appear in the vessels so far away from the cut surface that none is drawn into the manometer.

Section 14.—ATTEMPTS TO DEMONSTRATE THE EXISTENCE OF A PUMPING ACTION IN TRANSPIRING STEMS.

Stems of *Wistaria* are especially suitable, since long lengths of uniform and moderate diameter are readily procured bare of leaves, or with a single leafy branch only. They have, however, the disadvantage that the vessels are rather large, and block rapidly in living wood by gummy ingrowths formed after cutting.*

A 4-metre length of a bare stem placed horizontally under a suction of 2 metres of water at each end did not pump any water from the vessel attached to the basal end towards that joined to the distal one, and air was soon drawn out of the stem. A similar length of stem was then placed under a head of 68 centims. of water at each end. The water level fell more rapidly in the tube attached to the basal end, being 1·2 centims. below that in the tube attached to the distal end in 18 hours, and 1·4 below at the end of two days, the total fall being 7·4 centims. In a second experiment differences of 1·4 and 1·5 were shown at the ends of the first and second days respectively. On testing these stems, however, under a head of 1 atmosphere no appreciable flow took place through them, the terminal metre of each being blocked, but the median 2 metres being open and the vessels filled with rarefied air. Hence the difference of level was due to the blocking coupled with the slightly more rapid absorption at the basal end.

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* Knowing this, the Japanese dip the ends of cut flowering stems of *Wistaria* in boiling water, which keeps them longer fresh and unblocked, but this is inadmissible with experiments on living stems.

A third experiment was made with a stem 3½ metres long and 0·8 centim. diameter at each end, by arranging it as shown in fig. 7 (1), with the root end at the lower level, while another similar stem was arranged with the distal end downwards. After 24 hours the water had fallen 1·5 centims. below the level A, B, and the mercury risen 3 centims. above C, in the first case, while with the second stem the water was 6 centims. below A, B, and the mercury 3·1 centims. below B. Apparently an upward pumping action had taken place in the reversed stem.

Another stem arranged with the root pole downwards gave the following results :—

Time.	Temperature.	Level of mercury.	Level of water.
After 8 hours . . .	78° F.	3·2 centims. above C.	12·6 centims. above A.
„ 16 „ . . .	82° F.	3·2 centims. below C.	11·8 „ „
„ 24 „ . . .	76° F.	Level	10·8 „ „
„ 26 „ . . .	65° F.	3·3 centims. above C.	10·2 „ „
„ 38 „ . . .	80° F.	Level	9·0 „ „

On forcing in water under a head of 2 atmospheres, only a slight oozing with a barely measurable flow was shown, the stems being blocked for 80 centims. at the root end, but only for 30 centims. at the upper end. The results, which were at first very puzzling, are evidently due to the changes of temperature acting on the air in the vessels of the median portion of the partially blocked stem, which, when opened under mercury, showed no rise of the latter in the vessels. A rise in temperature caused the air to expand and, acting through the less blocked upper end, depressed the mercury, while a fall caused it to rise again, absorption continuing all the time at the lower root end.

The same experiment was again repeated with a stem from the lower two-thirds of which the cork had been scraped, and this part kept submerged in water :—

Time.	Temperature.	Mercury.	Water.
Start	78° F.	Level	4·0 centims. above A.
After 24 hours . . .	80° F.	„	0·5 „ below A.
„ 48 „	65° F.	3·2 centims. below C.	10·5 „ „
„ 72 „ . . .	84° F.	4·8 „ „	25·5 „ „
„ 96 „ . . .	80° F.	7·2 „ „	38·2 „ „

In this case water was steadily absorbed at the lower end, and the pushing down of the mercury at the upper end is evidence of a feeble but distinct pumping action. Almost exactly similar results were, however, given by a stem arranged with its root pole upwards, so that this action, whatever its origin may be, is not correlated with any fixed polarity in the stem.

In the case of the first stem, 30 centims. of the lower end and 20 centims. of the upper end were found to be blocked at the end of the fourth day, and showed only a slight oozing flow under a head of 2 atmospheres. The vessels in the median portion were open, contained air and a little water, and when opened under mercury showed a pressure not perceptibly less or greater than that of the atmosphere.

The apparent pumping action is merely due to the stem acting as an osmometer. Water is drawn in by the osmotic suction of the sap in the vessels through the cut end and scraped surface more rapidly than it diffuses backwards through the nearly completely blocked vessels at the lower end, so that ultimately a small positive pressure is produced. The experiment in fact differs from Pitra's on the exudation pressure of cut branches simply in the fact that the blocking at the cut surface is natural instead of artificial, and all the exudations observed by Pitra can be explained as being the direct result of an osmotic absorption of water by the stem or branch. In any case the action is a slow and feeble one, and none is shown so long as the vessels are fully open, or when the stem is immersed in a 5-per-cent. solution of potassium nitrate. The point to determine is whether any differential pumping action can be detected in an actively functioning stem when intact or immediately after its removal from the plant. Accordingly stems were cut under water at points equidistant by 40 or 50 centims. from a single leafy branch, and arranged horizontally under a suction of 50 centims. of water so as to draw up mercury (fig. 7 (2)), or placed under equal heads of water at each end. The following gives the typical results of such experiments:—

Under Suction.

	Start.	After 15 min.	After 30 min.	After 45 min.
Pressure at basal end, in centims.	– 50 centims. H_2O	– (46·8 H_2O + 3·2 Hg)	– (45·6 H_2O + 4·4 Hg)	– (41·5 H_2O + 8·5 Hg) (air then entered)
At apical end	– 50 centims. H_2O	– (48·6 H_2O + 1·4 Hg)	– (47·6 H_2O + 2·4 Hg)	– (44·4 H_2O + 5·6 Hg)
Difference, in centims. mercury	0	1·7	1·85	2·8

Under Pressure.

	A.			B.		
	Start.	After 15 min.	After 1$\frac{3}{4}$ hours.	Start.	After 2 hours.	After 4 hours.
Pressure at basal ends, in centims. of water	45	40	0	49	31	24
At apical end	45	43	11	49	38·5	32
Difference, in centims. water .	0	3	11	0	6·5	8

Under both pressure and suction water is drawn in more rapidly at the basal than at the apical end. This is possibly merely owing to the more direct continuity of the vessels in the leafy branch with those opening on the cut surface of the basal end, the difference of pressure being the result and not the cause of the unequally distributed suction exercised by the transpiring branch. In any case a maximal difference of pressure of 8–40 centims. of water per metre of stem would not be able to keep a continuous column of water supported when the stem was erect, and would be still less able to give it the required upward velocity of movement.

No experiments have been able to show the existence of any pumping actions sufficient to explain the upward ascent in a tall tree, or indeed to show the existence of any pressure of exudation which could not be explained by direct or indirect reference to osmotic action. Nevertheless, the ascent of water is still a vital problem in so far as the conditions for the continued transference of water are only maintained in living wood.

Section 15.—The Influence of Injury, Age, and Death upon the Power of Conduction.

Quite apart from the blocking at the cut surface of a stem, the cavity of an opened vessel in living wood always becomes closed at one or more points by tyloses or plugs of gum or mucilage. Weber* states that this begins 10–20 hours after the vessel has been opened, but Wieler† observed a commencement of blocking in *Acer platanoides* and other trees, one to three hours after branches had been cut off. My own observations have given values within these limits in summer time, but in winter the blocking appears to take place more slowly, and also when sterilised and filtered normal saline or hard tap water are used in place of distilled water.

Apparently a lower osmotic concentration in the vessels hastens their blocking.

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* 'Ber. d. Bot. Ges.,' 1884, p. 367.

† 'Jahrb. f. Wiss. Bot.,' vol. 19, 1888, p. 106.

When the vessels are fully blocked pressures of 1–3 atmospheres are unable to drive air or liquid through them.[*]

In intact wood the vessels become blocked after the second to ninth year in most trees, and after the first to fourth year in the case of *Robinia* and *Æsculus*. According to Wieler,[†] only from two to five of the outermost rings of wood conduct in the case of *Acer platanoides*, but this is certainly an error, since I have found the wood in large stems of this plant to retain a moderate power of conduction in some cases for as long as 20 years. In the case of a branch 22 years old, propped up and then cut through to the 15th year and the injury covered up with wet clay, sufficient water still passed to keep the leaves fresh and turgid for 15 days in hot, dry weather, when the branch was snapped by the wind. HARTIG[‡] indeed states that in all sap-wood trees (Beech, Birch, Willow, Poplar, Lime, Horse Chestnut, Hornbeam), all the wood conducts down to the pith, and that the alburnum may remain living and capable of conducting water 18 years after such a tree has been ringed. In any case all authors agree that wood which contains no living cells loses the power of functioning as a conducting channel, except in the most trifling degree, and this applies to the duramen, even when it is only distinguished from the alburnum by the absence of living cells. STRASBURGER'S statement that the conductivity may be restored to dead wood, if the vessels are not blocked, by injection with water is quite correct, but the restoration is temporary only, the conductivity being rapidly lost again when a stem of two or more metres length is subjected to moderate suction, and this without any blocking of the vessels except by the entry of air.

The Influence of Death on Conductivity.

HANSEN[§] found that dipping the basal ends of branches in boiling water favoured the subsequent absorption, but JANSE[||] showed that this was due to the driving out of the air which partially blocked the vessels. The same author and also VESQUE have shown that stems killed by boiling continue to transfer water in sufficient amount to keep the leaves fresh for from 1 to 20 days, *i.e.*, until the vessels become blocked. In these experiments only short lengths of stem were used as well as in those of E. F. SMITH, who found[¶] that cucumber stems, of which 18–20 centims. had been killed by hot water, lost their conductivity in three to four days.

STRASBURGER'S well known experiments with poisons were carried out on a larger scale and gave similar results, the stems retaining their conductivity some time after

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[*] BOEHM, 'Sitzungsb. d. Wien Akad. d. Wiss.,' vol. 4, II Abth., 1867, p. 852; MOLISCH, *ibid.*, vol. 97, I Abth., 1888, p. 285.

[†] *Loc. cit.*

[‡] 'Bot. Ztg.,' 1865, p. 238; 'Ber. d. D. Bot. Ges.,' 1888, p. 222.

[§] 'Arb. d. Bot. Inst. in Würzburg,' vol. 3, p. 305.

[||] 'Jahrb. f. Wiss. Bot.,' vol. 18, 1887.

[¶] 'American Naturalist,' 1896, p. 557.

they had been killed. These experiments of STRASBURGER's are usually credited with far more decisive value than they actually possess. All that they show is that the conditions required for the ascent of water in a tree and which are only set up in the living wood, persist for a short time after the wood has been killed.

Evidence to show that the conductivity of the wood is connected with its vital activity is not wanting. Thus KOSAROFF[*] found that when lengths of ½–2 metres of the stems of *Phaseolus multiflorus*, *Humulus lupulus*, *Lonicera sempervirens*, and *Passiflora cærulea* were cooled to 0°–2° C., the leaves beyond began to droop in two to four hours. The first two plants died subsequently, however, whereas no drooping was produced in plants of *Ampelopsis*, *Aristolochia*, and *Vitis* after cooling the stems to −4° or −5° C. for two to three hours. In capillaries of 0·7 millim. diameter no ice formation occurs, even at −7° C., so that a lower temperature would be required to freeze the water in the vessels. Young shoots of *Ampelopsis* and *Wistaria* drooped and died after cooling to −1°·5 C. At 0° C. the viscosity of water is nearly double what it is at 20° C., so that the resistance to flow in the cooled stems might be doubled, and with active transpiration this might suffice to limit the flow and produce drooping. It is also possible that the vessels became blocked in the case of the plants which died subsequently, but no investigations in this direction were made. URSPRUNG[†] has repeated the same experiment on the Beech by cooling with ice 14-centim. lengths of branches 60–80 centims. long and found that the leaves shrivelled in two to seven days, and that the same result followed when a similar length of the branch was killed by induction currents, heat or ether. URSPRUNG argues that since the blocks are formed in the vessels only at the boundaries of the living portions, the fact that the leaves droop sooner when a long length is killed than when a short one is treated, shows that the loss of conductivity is not due to blocking of the vessels. In some cases URSPRUNG could find no blocks in the vessels at all, but this is always difficult to demonstrate when the blocks are few and far apart. In any case the first premise is not always correct, for blocks appear at various points in the peripheral wood vessels along the whole length of a stem of *Wistaria* killed by heat, provided that the transpiration current is resumed for a time after treatment. I have also found thread-like irregular or globular gummy ingrowths in the walls of the peripheral vessels of a stem of *Wistaria* which had been cooled in ice for several hours and examined a day afterwards, and in some cases the vessels were completely blocked.

The loss of conductivity of dead wood is, however, certainly not due solely to the blocking of the vessels or even to changes in the character of the walls of the wood vessels, for in many cases the mere injection of the dead portion with water may temporarily restore the conductivity so long as continuous water columns capable of transmitting tension are maintained in the vessels. Such a condition, however, or

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[*] 'Einfluss Versch. Faktoren auf die Wasseraufnahme,' Inaug. Diss., Leipzig, 1897.

[†] 'Jahrb. f. Wiss. Bot.,' 1906, vol. 42, p. 503.

an analogous one produced by vital activity when air is present in the vessels, cannot be maintained for any length of time in the wood in the absence of living cells, and in this sense the ascent of sap must be regarded as a vital problem.

STRASBURGER cut a living oak 22 metres high and lowered the base into picric acid. He found that the amount absorbed fluctuated between 4 and 6½ litres in the first five days, then falling to 0·3 litre on the ninth day. The picric acid had risen 15 metres in two and a half days, when fuchsin was added. On cutting down the tree, six to eight of the outer rings were found coloured (4–7 millims. deep) 5–15 metres up, whereas tyloses appeared first 20 rings in. At the top of the tree all the rings were coloured to the pith and the presence of fuchsin immediately evident. It is, however, quite possible that in this experiment the picric acid had not reached and killed all the living cells in the wood before the fuchsin had ascended, and accordingly this experiment was repeated at the Birmingham Botanical Gardens in 1905 and 1906.* The tree first used was a sycamore 38 years old and 15 metres high. Preliminary testing soon showed that picric acid is not a satisfactory substance to use, owing to its pronounced retention by the walls of the wood vessels. As regards lateral diffusion, it is intermediate between such substances as lithium chloride and eosin, which diffuse readily laterally, and such substances as sodium sulphindigotate,† indigo carmine, iron chloride, sulphocyanide, which diffuse little or not at all laterally and so remain restricted to confined paths.

Ultimately formic aldehyde was selected for use in place of picric acid. Its presence was readily recognised by boiling a chip of the wood in a few drops of water and adding a few drops of a solution of magenta decolorised by sulphur dioxide, when a pink colour is formed in the presence of formic aldehyde with or without warming. If an excess of sulphur dioxide is avoided, the test is an extremely delicate one. On July 25 at 10.30 A.M., after attaching the top of the tree to the scaffolding by ropes and pulley blocks, the base of the tree was cut two-thirds through with sharp axes, and after the central portion was sawn through, the trunk was lowered into a tub containing 60 litres of water and 20 lbs. of formalin. The whole operation took less than 15 minutes, and the cut surfaces were kept wet while exposed, by sprays of water. In 10 hours (up to 8.30 P.M.) the formalin had travelled 8 metres up in the superficial wood of the main stem and had also appeared in the leaves of a branch 4 metres long and 3 metres up the stem. In the first five hours the formalin ascended at a rate of 1·2 metres per hour. In 34 hours traces of formalin were detected in the wood and leaf petioles at the top of the tree. After two days, sufficient solid eosin was added to make a dilute solution

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* I have to thank Mr. HERBERT STONE, F.L.S., for the erection of the required scaffolding and for the loan of a skilled mechanic, as well as for the provision of a movable platform, by means of which the experiments at different heights previously quoted were made. Permission to destroy two trees at the gardens was obtained for me by the Secretary, Professor HILLHOUSE. (See Plate 30.)

† TSCHERMAK, 'Sitzungsb. der K. Akad. der Wiss. in Wien,' vol. 105, I Abth., January, 1896.

strong enough to tinge the wood distinctly, but not to give rise to pronounced lateral diffusion. After four days 2 lbs. of potassium sulphocyanide were added.

Portions of the superficial wood examined on the fifth day, from 1 to 6 metres up, were dry and uncoloured, the vessels filled with air and no potassium sulphocyanide could be detected with ferric chloride, although this test is not influenced by the presence of formalin or of wood, or the formalin test by the presence of the other reagents. Formalin was abundant in this wood on the sixth day. Streaks of eosin were detected in the wood two years in and 3 metres up the stem, but no sulphocyanide could be detected. After dipping a living freshly cut 2-metre branch from another tree in sulphocyanide solution, the latter could be detected 150 centims. up in six hours, the leaves rapidly dying, and the test was still given, except in the basal 8 centims., after the branch had been kept for two days with its base in water.

The absorption of water from day to day by the tree is given in the following table :—

Date.	Time.	Litres absorbed per hour.	Evaporation control.*	Temperature and condition.	State of leaves.
July 25 . .	10.30 A.M. to 3.30 P.M.	1·2	0·012	Half sunny.	All living.
	3.30 P.M. to 5 P.M.	1·4	—	Averaged 76° F.	
	5 P.M. to 8.30 P.M.	0·9			
July 25–6 .	8.30 P.M. to 10.30 A.M.	0·43			
	10.30 A.M. to 12.30 P.M.	0·45	—	55°—68° F. Showers to 3 P.M., then half sunny.	All the lower leaves drooping, but still fresh and green.
	12.30 P.M. to 5 P.M.	0·24	0·01		
July 27 . .	10.30 A.M. to 12.30 P.M.	0·25	—	65°—72° F. Overcast.	Lower leaves beginning to curl and shrivel.
	12.30 P.M. to 5 P.M.	0·38	0·01	72°—76° F. Showery.	
	5 P.M. to 6 P.M.	0·5	—	72°—68° F. Half sunny.	
July 27–8 .	6 P.M. to 12.30 A.M.	0·25	0·01	64°—70° F. Overcast.	Lower leaves mostly shrivelled.
	12.30 A.M. to 7.30 P.M.	0·2	—		
July 28–9 .	7.30 P.M. to 10.30 A.M.	0·11	—	60°—66° F. Showery.	Few younger leaves living at base, young and many old ones living at top.
	10.30 A.M. to 3.30 P.M.	0·08	0·004		
July 29–30 .	3.30 P.M. to 3.30 P.M.	0·075	0·02	60°—72° F. Sunny.	Few of younger leaves at top living.
July 30–1 .	3.30 P.M. to 12.30 A.M.	0·11	0·028	64°—76° F. Sunny.	Few of youngest leaves at top living.

At the end of the first day nearly half the formalin had been absorbed and from the second day onwards distilled water was added to bring the liquid up to the original mark in the tub after each reading.

The tree was then lowered, and sections sawn out at intervals of a metre from top

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* A stump of equal size projecting 2 feet above the water in a tub of the same size.

to bottom. Potassium sulphocyanide was present 1 metre up throughout the wood, but none above this in the outer wood, and doubtful traces in the central wood up to 3 metres. Formalin was abundant in the three outer rings of wood, and diminished towards the centre at the base of the tree, none being present in the central three or four rings between 4 and 10 metres, traces in the centre above 10 metres, and more in the peripheral wood. A few young leaves at the extreme apices were still living, although they contained traces of formalin, which was abundant in all the old dead leaves below 12 metres. The leaves above 12 metres came off when touched (abscission), whereas below 10 metres, all the leaves having been rapidly killed, they shrivelled firmly on the branches. Living cells were found at various points in the wood above 5 metres, three layers or more in, especially in the parts faintly tinged by eosin. The distribution of the eosin was so remarkable that a detailed description with figures is appended (Plate 30, fig. 8).

The base of a branch 3 metres up and 6 centims. diameter showed a nearly complete eosin ring, beginning 4 millims. from the surface of the wood and extending 4 millims. in, the outer three rings and the central wood being uncoloured. The colour extended 3 metres along the branch, coming gradually nearer to the surface. From 3 to 10 metres, none of the large branches contained any eosin, which reappeared in all the branches above 11 metres, and was traced to the topmost point on the tree, $14\frac{1}{2}$ metres above ground.

The distribution of the eosin in the trunk can be seen from the appended figure. Even at 1 metre some of the peripheral wood was unstained, although the deepest coloration was $\frac{1}{2}$–5 centims. in (diameter 25 centims.). At 3 metres the coloured portion hardly touched the last annual ring, and thence up to 9 metres the eosin became more centrally distributed, leaving an outer zone of the younger wood little or not at all coloured. Up to 7 metres the borders of the coloured patches were sharply defined and enclosed by a faint brownish halo, but above this the edges of the coloured zones were slightly diffuse and a clear red. The coloured zones were all moister than the uncoloured ones. From 11 metres upward the colour was distributed more and more through the whole of the wood and comes more to the surface again.

In this experiment, therefore, the sap had ascended after the treatment with formalin, but left the path which the latter had travelled, and as far as possible made its way upwards in wood to which the formalin had either not penetrated or only in very dilute form. This ascent was a temporary phenomenon only, and by the close of the experiment the conductivity of the wood was almost entirely lost.

Apparently the foregoing results show that the water and eosin, instead of ascending in the young wood killed by formalin, travelled through the still living portions of wood, although a considerable amount of lateral transference was required and a highly increased resistance encountered, owing to an increasing number of vessels being blocked in the older wood. Living cells were found at various points in the wood above 5 metres, three layers or more in, especially in the parts faintly coloured by eosin, which the coloured formalin-containing liquid had reached last and in very dilute form.

A few experiments were also performed on cut branches from 2½ to 3 metres long, which had been kept with the cut end under water for a week. By this time all the leaves had shrivelled except the youngest, and on cutting a fresh surface, placing in eosin, and exposing to the sun with a shade temperature of 60°–80° F., the eosin ascended 200–224 centims. in 24 hours (8·5–9 centims. per hour). The eosin travelled furthest in the oldest central wood, the last three years' wood being uncoloured 35–40 centims. below the topmost coloured zone, and 85–95 centims. below it in the present year's wood. The vessels of the last three years showed on examination numerous blocks, but plugs of yellow gum were also to be seen in the vessels of the wood older than three years, even when examined fresh from the plant.

Similar results were given with picric acid, except that the rate of flow was much slower (2–3 centims. per hour); the dye was localised above, mainly in the older wood, and lower down it extended nearer to the periphery, but with intervening uncoloured rings of wood.

The leaves of the Maple are closely dependent upon the most recent wood for an adequate supply of water. Thus the removal of a ring of the present and last year's wood from 6 and 10-year-old leafy branches in the morning caused the leaves to show signs of shrivelling by the end of the same day, and to be completely shrivelled by the following mid-day. The same effect follows the disturbance due to injury, even when a branch is cut and kept under water. Thus 9 and 10-year-old branches exposed to the air had all except the youngest leaves shrivelled by the end of the day, and even when the cork and cortex were removed from the basal 2 feet, which was kept immersed, the shrivelling of the great majority of the leaves was only delayed until the next day.

At first sight these observations seem to indicate that in the experiment with the tree the ascent of the liquid in the median older layers of wood is merely due to the blocking of the youngest layers as the result of injury. It must, however, be remembered that the older layers are already more or less completely blocked, that on examination the outer layers did not show more blocks than the inner ones, but less, and that in the upper levels above 7 metres the vessels of the outer three rings appeared to be open almost without exception. Further, stems cut and at once killed with boiling water, or by passing formalin solution through them, show a ready passage of liquid through the outer layers of wood for some time if filtered sterilised water is used, and in intact stems the rate of transference through the inner layers rapidly decreases as the age of the wood increases. Maple wood 20 or more years old practically ceases to be capable of conduction so far as the requirements of the tree are concerned, while the whole of the wood from the 3rd to the 20th year cannot convey sufficient water upwards to satisfy the maximal loss by transpiration. Nevertheless, this is the path followed when the younger wood is killed by formalin, and the ascent of fuchsin in STRASBURGER'S oak may also have taken place in still living wood.

Decisive proof that water can ascend a tall tree at a moderate rate in entirely dead wood, even for a few days, is still wanting, and nothing is more certain than that the conditions for continuous upward flow can only be maintained in living wood.

From this point of view at least, the ascent of sap in trees must be regarded as a vital problem in which vital actions, directly or indirectly, take part. By the term vital action we merely indicate a complex of contemporarily unresolveable physical and chemical factors. In this sense no one can deny that the problem is a vital one, in that it involves hitherto unknown properties of matter regularly utilised by living trees.

Section 16.—THE ENERGY REQUIRED FOR THE ELEVATION OF SAP IN TALL TREES.

In criticising the statement that this must involve in the tallest trees a pumping action of some kind or other, Professor LARMOR enquires whether there is a sufficient fund of energy latent in the stem to provide permanently the motive power for the elevation of the sap, and in what form could this energy be transported there. In answer to this it is only necessary to state that the surplus carbohydrate manufactured by the leaves is stored by the plant in the living cells of the wood along the path of the transpiration current, and that the energy stored in this way is sufficient to supply all the work done in raising the water evaporated by the tree a hundred times over.

A tree such as *Eucalyptus amygdalina*, 100 metres high, would have a total assimilating surface represented by at least 500 kilogrammes of material, and would have an estimated average rate of transpiration of 100 litres per day. This water would be raised on the average 50 metres, and hence 5000 kilogramme-metres of work would be done per day in merely raising it. This is equivalent to 10,000 gramme-calories or a theoretical consumption of 2–3 grammes of starch per day. If the motor mechanism is assumed to be about as wasteful as a steam engine, this would mean a consumption of 20–30 grammes of starch per day.

A fairly active leaf can manufacture its own weight of carbohydrate in 10–20 days, so that the total production of carbohydrate per day on the given tree could hardly be less than 25 kilogrammes per day, of which $\frac{1}{8}$–$\frac{1}{12}$ per cent. would be sufficient to cover the work done in merely raising the water transpired by the tree. The total work done in overcoming resistance may, however, be in tall trees as much as six times the actual head.[*] Hence the maximal total consumption of carbohydrate for this purpose in a tree 100 metres high might be $\frac{1}{2}$–1 per cent. of that manufactured

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[*] 'Phil. Trans.,' B, 1905, p. 57.

daily by the tree. The amount required decreases with increasing rapidity as the tree decreases in height, until a height is reached (10–60 feet) according to the rate of flow and character of conducting elements, at which the suction of the transpiring leaves is able to extend to the ground.

The consumption of energy in pumping water upwards must ultimately set a limit to the possible height of a tree, although this limit would be many times beyond the height of the tallest tree known. Even in a tree 100 metres high the pumping action represents a comparatively feeble vital activity, bearing in mind the fact that a seedling may expend so much energy as to produce 1 per cent. and a fungus 6 per cent. of its weight of carbon dioxide per day. A single human heart doing 30,000 kilogramme-metres of work per day would be able to pump up all the water required by six trees 100 metres high, the relative weights of the man and the trees being approximately 1 : 5000. It is, in fact, the feeble intensity and diffuse character of the pumping action in the stem of a tall tree, coupled with the immediate disturbance of the conditions in the vessels when they are opened, which renders its direct demonstration so exceedingly difficult.

Summary.

The physical conditions in the vessels interpose no obstacle to the exertion of a pumping action on their contents controlled by the medullary ray cells. There are many theoretical ways in which surface tension action could be brought into play in this manner, but no practical proof of the existence of any such action in the wood vessels has as yet been obtained. Similarly, the bleeding of roots and stems affords no absolute proof of the existence of a vital pumping action in them, since all the observed cases can be explained as the result of osmotic action coupled with a reabsorption of the osmotic materials from the ascending stream and their surface adsorption by the walls of the vessels. Instances are given in which an apparent pumping action proved to be of this character.

Nevertheless, the experiments detailed or quoted in the above paper all tend to show that the continuous ascent of water is only possible in living wood, and that the power of conduction is rapidly lost on death, without any mechanical blocking of the vessels being necessarily responsible for the change. Hence we are forced to conclude that the living cells in tall trees continually restore the conditions for the ascent of water wherever these are affected by the excessive emptying of the vessels, and decrease the resistance to flow as far as possible by maintaining continuous water columns in parts at least of the wood. So long as these are present *ab initio*, a pumping action only becomes necessary in trees over 20 to 50 metres in height, but suspended columns cannot be maintained for any length of time in the vessels of tall trees without the aid of the living cells of the wood.

The energy required to pump water upwards in the tallest trees represents only a small fraction of that produced by the daily photosynthetic assimilation, and it is the feeble character and diffuseness of the pumping action which renders it so difficult to demonstrate practically.

Contrary to STRASBURGER'S statement, no vessels appear to run as open channels from end to end of any tree, the longest vessel observed being 564 centims., as measured by the length of stem in which it ran (*Wistaria*). In this plant, however, and others also, owing to the irregular course followed by the vessels, these are always longer, and sometimes considerably longer, than the piece of stem in which they occur.

Experiments on the suction and exudation of trees at different levels, and upon the influence of the entry of air and water under pressure, showed that no continuous suspended water columns or high internal tensions existed in the conducting elements of the trees experimented on (Maple and Poplar) during active transpiration, or, indeed, at any period of the year. The same was shown by direct measurements of the pressure in intact vessels of *Wistaria* during active transpiration. This fact, coupled with the high total resistance to flow, shows that this resistance is overcome locally from point to point, and not by any enormous tension from above or pressure from below, neither of which exists nor could be maintained to a sufficient extent to carry on the elevation of water in a tall tree. A high tension from above leads to rapid blocking with air; a high pressure from below leads to great loss by lateral exudation from the vessels.

The apparent differences of osmotic pressure previously observed between leaves at the base and apex of a tall tree are not evidence of the existence of any greater osmotic suction at the higher level, but are the result of the different ages and sizes of the cells, and of the different conditions to which they have been exposed. Equally great differences may exist between leaf cells at the same level.

The surface adsorption of dissolved solids in the vessels plays a very important part in their function as translocatory channels, causing a delay in the ascent of dissolved solids such as sugar and salts, and an accumulation of them along the outer walls of the vessels. The latter facilitates their outward diffusion, but at the same time renders the transference of small quantities of material between widely removed organs difficult or impossible.

The tallest trees in Australia do not appreciably exceed 300 feet in height, so that the values previously given for the maximal total resistance to the upward flow of sap in actively transpiring trees must be reduced to between 30 and 50 atmospheres.

In a maple tree, whose younger wood had been killed by formalin, the transpiration current turned to the older partially blocked but still living wood, and none of STRASBURGER'S experiments show definitely that efficient conduction is possible in the dead wood of tall trees. The ascent of water is, therefore, a vital problem in so far as it depends upon conditions which hitherto can only be maintained in living wood.

Note Received August 7, 1907.

Professor DIXON* has repeated a few of the experiments detailed in the 'Transactions of the Royal Society'† in a different manner, and has obtained considerably lower values for the resistance to the flow of sap in the vessels. He suggests that as I make no mention of any precautions, the stems may have contained air and the water may have contained suspended solids. To this I can only reply by reference to p. 386, and the concluding sentence, "Hence . . . water free from suspended solid particles must be used." As to the presence of air, most of the stems used by me did contain air, but not more than when attached to the plant and functioning, and they usually contained less at the close of the experiment. Professor DIXON has measured the minimal value for the resistance in a particular case; my own results give for the most part maximal values, such as occur only when transpiration is very active. If the cohesion theory is unable to explain how these maximal resistances are overcome, it becomes of very subordinate value. No mechanism can work permanently under a strain which tests every part nearly to breaking point, and the cohesion theory, to be accepted as a full explanation, must give a considerable margin to overcome resistances beyond the minimum. At present the cohesion theory does not do this, nor does it explain all the facts. No one will deny that cohesion may aid in the ascent of sap, but it appears to be of subordinate and mainly temporary value, the columns in the vessels breaking under moderate strain, and only being restored again when living cells are present in the wood.

* 'Roy. Soc. Proc.,' B, vol. 79, 1907, p. 41.

† 'Phil. Trans.,' B, vol. 198, 1905, pp. 41—85.

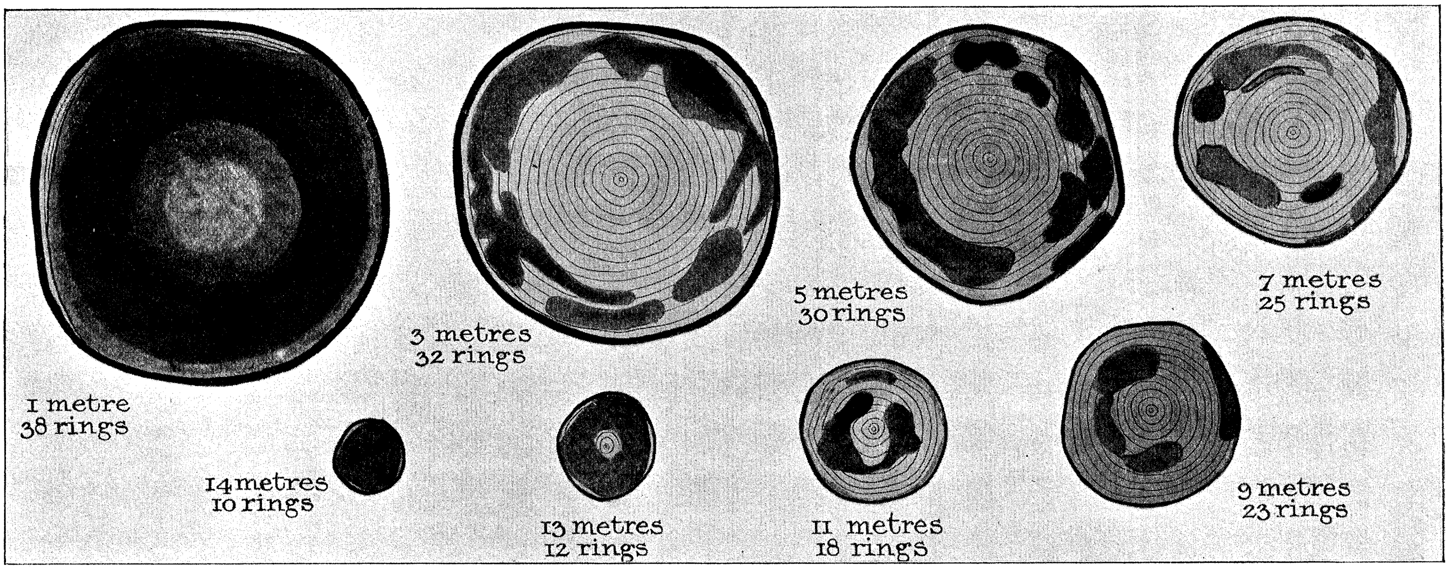

FIG. 8.

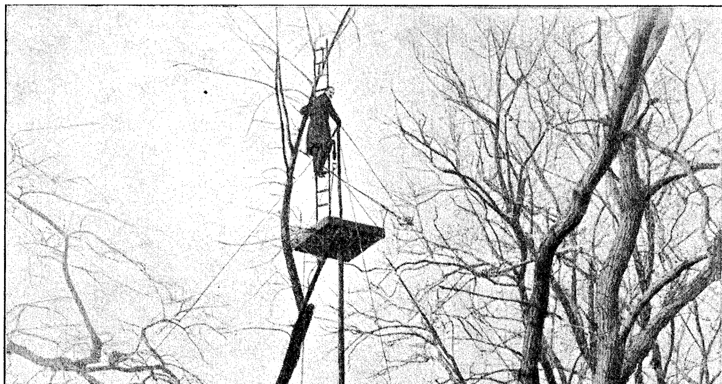

FIG. 9.

FIG. 10.

Showing mode of ascent and of attaching apparatus.

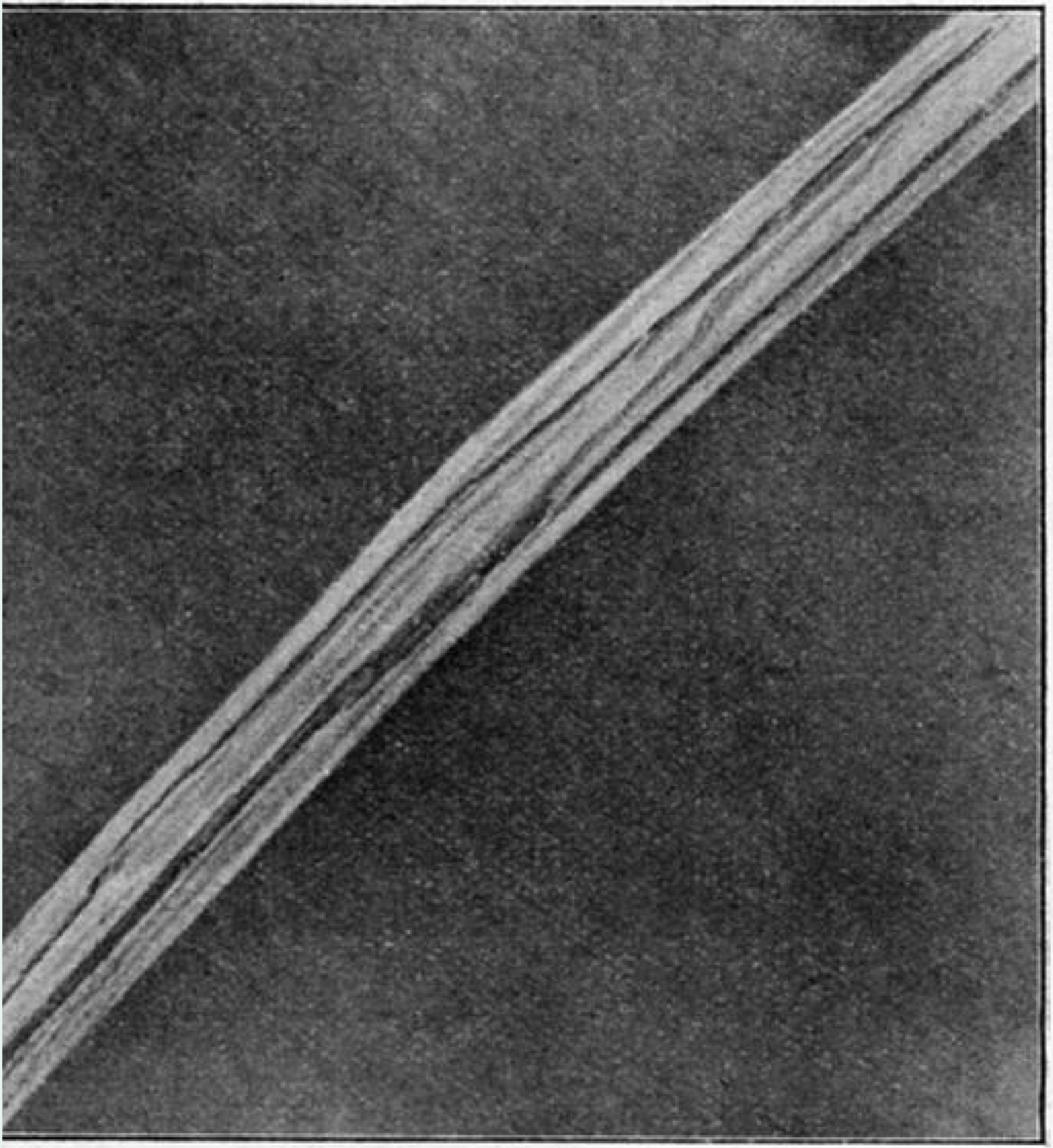

FIG. 4.—Injected Wood Cylinder of *Wistaria*.

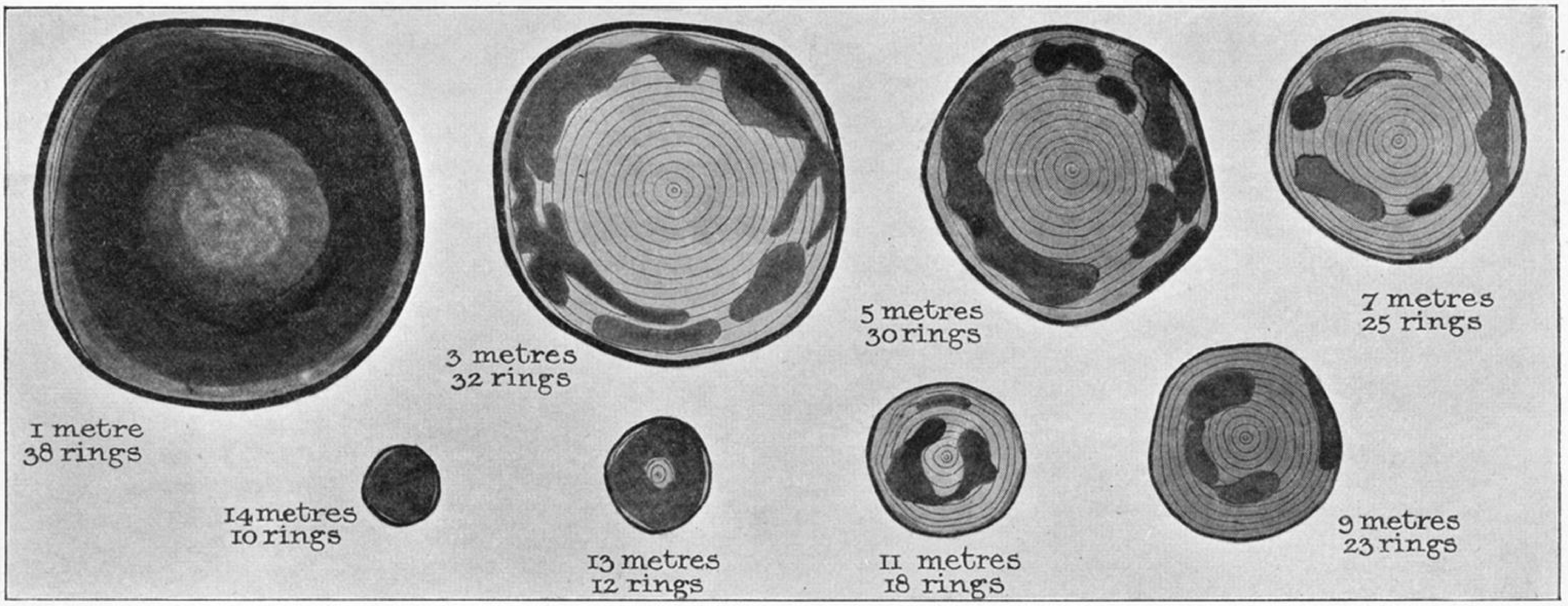

Fig. 8.

Fig. 9.

Fig. 10.

Showing mode of ascent and of attaching apparatus.