

### III. *The Ascent of Water in Trees.*

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*Section 1.—Introduction.*

IN the earlier discussions of this problem, it has been tacitly assumed that it was only necessary to find forces sufficient to balance a head of water equal to the height of the loftiest tree to explain the ascent of sap in it. The problem is, however, rather one of dynamics than of statics, for we have to find forces sufficient not only to balance the head of water, but also to keep this water moving upwards in narrow tubes with a velocity varying from a few centimetres to as much as 6 metres per hour. JANSE has in fact shown empirically, and his results have been confirmed by STRASBURGER, that to drive water through the stem of a Conifer at the transpiration rate requires a head of water several times the length of the stem.\*

Water is a liquid of definite viscosity, and the resistance offered even to its slow flow through tubes of small diameter and considerable length is a factor of great importance. The purpose of the following research has been to find the amount of this resistance in definite cases, the forces required to overcome it, and hence the total force required to raise the water with sufficient rapidity to the summit of an actively transpiring tall tree. Furthermore, an attempt has been made to determine the possible means by which this force could be generated, and propagated in the conducting wood.

A series of preliminary investigations were made with a climbing plant 20 feet high (Virginian creeper), and with a tree 65 feet high (common elm). After estimating the maximum daily transpiration, the number of conducting vessels in the young wood and their average diameters were found. Hence the rate of flow and amount passing per second in each vessel were estimated, on the assumption that each vessel was an open tube filled with water, and that all the water passed through the cavities of the vessels. From these data and from the known viscosity of water at the average daily temperature the resistance to flow per metre of stem was found. In the case of the climbing plant it appeared that when horizontal, only one-tenth the head of water required when vertical would be necessary to produce the same rate of flow through it, whereas in the case of the tree a pressure of water equal to one-half its own height would still be required.

The theory put forward by DIXON and JOLY,† as well as by ASKENASY‡ to explain the ascent of water in trees assumes that the water in the vessels is subject to a longitudinal stress set up by the transpiration in the leaves, and that it is thus pulled up the stem and drawn in at the roots. This can only occur to any extent in vessels completely filled with water, for the appearance of a single air-bubble of appreciable

\* JANSE, 'Pringsheim's Jahrb.,' vol. 18, 1887, p. 1; STRASBURGER, 'Leitungsbahnen,' p. 779. These results apply only to the wood of Conifers, where the resistance, owing to the short length of the conducting elements, is largely a question of filtration under pressure through the dividing walls.

† DIXON and JOLY, 'Ann. of Botany,' 1895, vol. 9, p. 419; 'Phil. Trans.,' B, 1895, vol. 186, p. 564.

‡ ASKENASY, 'Ueber das Saftsteigen,' 1895, p. 17 (reprinted from 'Verhand. d. Naturf.-Vereins in Heidelberg').

size in a vessel will cause a rapid fall of the longitudinal stress to some fraction of an atmosphere.

DIXON and JOLY found that the presence of dissolved air does not affect the longitudinal stress that water can withstand, but, as will be shown later, this only applies when there are no nuclei around which air-bubbles can form. The maximal stress observed by them was 7 atmospheres, but it is usually considerably lower, and indeed the maximal stress observed by OSBORNE REYNOLDS in air-free and dust-free water was 5 atmospheres. Now trees may attain a height of from 400–500 feet, which corresponds to a head of water of from 10–14 atmospheres. Any increase of resistance due to the viscosity of the sap and the narrowness of the channels through which it passes becomes of considerable importance, and without knowing the relation between the frictional and gravitational resistances, it is impossible to predict the action of external factors, or to propound any satisfactory theory as to the ascent of sap. For instance a rise of temperature decreases the viscosity, but at the same time accelerates transpiration, and diminishes the solubility of the dissolved air. The first factor decreases the resistance to flow, the second will increase the stress to which the water-columns are subjected, the third, by producing the appearance of air-bubbles, will cause them to block with air and become incapable of transmitting downwards any stress greater than a fraction of an atmosphere.\*

### *Section 2.—Mode of Investigation.*

Water was in the first instance driven under definite pressures through a variety of young stems in which the whole of the wood was capable of conducting. The volume passing in definite intervals of time was measured and the number of vessels and their average cross-section estimated.

In order to calculate the resistance due to viscosity, the rate of flow was needed, so that the volume passing in unit time through a single vessel could be found. At first, dilute solutions of sodium carbonate were used, and the issuing fluid tested with phenolphthalëin until found to be alkaline, or the reverse method was employed, a few drops of phenolphthalëin solution being added to the water used, and the latter being received in a solution of sodium carbonate. Neither method is, however, altogether satisfactory. Thus if the solution of sodium carbonate is strong it raises the viscosity and also acts as a poison, while if too dilute the carbon dioxide produced in the living wood neutralizes the first portions passing and retards the appearance of any alkalinity in the escaping sap. Further, if a watery solution of phenolphthalëin is passed through, it is in many cases largely retained by the wood.

A more satisfactory method is to use extremely dilute solutions of potassium

\* An excellent and most stimulating summary of the subject up to 1896 is given by FRANCIS DARWIN, F.R.S. ("On the Ascent of Water in Trees"), in the 'Proc. of the Brit. Assoc.,' Section K, Liverpool, 1896. See also PFEFFER'S 'Physiology,' 1900, vol. 1, p. 220.

sulpho-cyanide or ferro-cyanide, allowing the issuing fluid to drip into a solution of ferric chloride. The solutions may be used so dilute as to avoid any increase of viscosity and all poisonous action, while the water and dissolved substance, especially in the case of the sulpho-cyanide, appear to travel at practically the same rate even when the flow is slow.

The water issuing from the cut ends of the wood vessels might exert, owing to their small diameters, a considerable back pressure due to the surface-tension of the drops formed at their ends when the water dripped from them into air. Actual experiments showed, however, that the rate of flow was the same under moderate pressures whether the cut end was just under water or in air. The reason is that a continuous surface-tension film forms across the entire end of the cut stem, and the water escapes from the vessels beneath this film. If potassium sulphocyanide is used as the indicator, the free end of the stem may be kept just beneath a dilute solution of ferric chloride, without any danger of blocking.

This method gives the maximal rate of flow, and in calculating the volume passing, the assumption is made that the vessels in question are filled with fluid throughout, as is actually the case if they have been opened at both ends. The effect of the presence of *stationary* air-bubbles in a vessel is to retard the flow of water through them, the amount of flow decreasing owing to the lessened area of cross-section, and the rate of flow decreasing possibly owing to the increased frictional surface (the surface-tension film around each air-bubble). There is in addition a special resistance due to the unequal convexities of the ends of each air-bubble, which are always of such character as to produce a progressive diminution of any pressure or strain acting on a chain of air-bubbles and water columns in a capillary tube. This action is shown whether the air-bubbles move or are stationary.

### *Section 3.—Theoretical Calculation of the Resistance Due to the Viscosity of Water.*

The following theoretical calculations made with *Cucurbita* and *Ulmus*, using POISEUILLE'S formula for the flow of viscous liquids in rigid tubes, will make matters clearer.

#### *Pumpkin.*

*Data.*—Rate of flow of sap = 6 metres per hour or  $\frac{1}{6}$  centim. per second ; length of stem and root = 6 metres.

Viscosity of water at  $20^{\circ}$  C. = 0.01016 C.G.S. units ; diameter of largest vessels = 0.04 cub. centim.

Area of cross-section of vessel = 0.001256 sq. centim.

Hence volume escaping per second =  $\frac{0.001256}{6}$  cub. centim.

Now  $h = \frac{8vl\eta}{\pi r^4 g}$ , where

$v$  = volume passing in cubic centimetres per second ;  $r$  = internal radius of tube.

$l$  = length of tube ;  $\eta$  = viscosity of water ;  $h$  = pressure in centimetres of water.

$g$  = acceleration due to gravity ; *i.e.*,

$$h = \frac{8 \times 0.001256 \times 600 \times 0.01016}{3.1416 \times 0.00000016 \times 981 \times 6} = 20.4 \text{ centims. of water.}$$

or 20.4 grammes per square centimetre, *i.e.*, nearly 1/50 of an atmosphere.

### *Wych Elm.*

*Data.*—Amount of water evaporated per day = 20 kilogrammes ; average height water is raised = 10 metres ; average temperature = 20° C. ; average diameter of wood-cylinder = 30 centims. ; average breadth of water conducting layers = 5 centims.

Hence, water conducting area =  $(15^2 - 10^2) \pi$  sq. centims. = 393 sq. centims. Suppose this to be made up of tubes 10 metres long and 0.01 centim. diameter, then if the internal area of cross-section of these represents a quarter of the total area, the number of tubes will be 130,000. Each tube carries  $\frac{20}{130,000}$  kilogramme per day, giving a rate of flow of  $\frac{1}{57 \times 10^4}$  cub. centim. per second.

Hence, pressure required in centimetres of water to overcome the resistance due to viscosity

$$= \frac{\eta 8vl}{\pi r^4 g} = \frac{0.010164 \times 8 \times 1000}{\pi \times (0.005)^4 \times 57 \times 10^4 \times 981} = 62.6 \text{ centims., or } 1/16 \text{ of an atmosphere.}$$

Apparently, therefore, the raising of the water forms the main bulk of the work done in conveying it upwards, and only a small fraction of this work would still have to be done when the stem was horizontal. Several of the data are, however, only approximations, and, further, the vessels are not filled with water, nor is any account taken of the nature of their walls or of the transverse partitions across them. There is in addition always considerable danger in attempting to argue from purely physical grounds that certain conclusions must apply to living organisms. Not because plants and animals are in any way exempt from the operation of physical and chemical laws, but rather because unexpected factors may enter into play, or even because living organisms may regularly utilise physical and chemical properties which have yet to be discovered. In the present case it is necessary to determine by experiment whether the flow of water through the vessels of the wood

takes place in accordance with POISEUILLE'S formula for the flow through rigid circular tubes with smooth walls, or whether any peculiarities are shown.\*

The tracheæ are relatively rigid, and the fact that their internal walls are not smooth should be expected to increase the resistance to flow. Arteries on the other hand are distensible, but elastic, factors which tend to decrease the resistance to flow through them. The sap contains few or no suspended particles, and can be regarded as a very dilute saline solution with a viscosity approximately equal in most cases to that of water. Contrary to the statement generally accepted in animal physiology, the presence of an abundance of suspended particles in a liquid (diatom ooze and *Pleurococcus* in water, blood corpuscles in serum) does considerably increase the resistance to flow through narrow tubes, and the effect is pronounced even when the diameter of the capillary is from three to four times that of the suspended particles. Hence, in the smallest blood capillaries the corpuscles must considerably increase the resistance to flow, and the same effect will be produced by the passage of solid particles through an open vessel. Hence, also, when testing cut stems, water free from suspended solid particles must be used.

#### *Section 4.—Experimental Data.*

Living actively transpiring stems were cut under water, and water forced under definite pressures through selected lengths, the rates and amounts of flow being determined. When the wood is saturated, it is immaterial whether the water is driven through under pressure or is drawn through by the suction of a suspended column. If large quantities of air are present in the vessels a difference is shown, for, under suction, the bubbles in the vessels expand and retard the flow, whereas, under pressure, they are compressed, and more rapidly dissolved away. When the head of water used is not greater than 2 or 3 metres, the difference is small, however, and is usually below 5 per cent. at first, although it becomes greater subsequently.

*Wych Elm.*—Temp. averaged 18–20° C.

*Data.*—Head of water = 3 metres; length of stem = 25 centims.; diameter of wood-cylinder averages 1 centim.; of pith = 0.16 centim.; average number of vessels = 3400; average internal diameter = 0.005 centim.

*Observations.*—Rate of flow = 50 centims. per hour; amount of flow first two hours = 1.36 cub. centims. per hour; next 24 hours = 0.4 cub. centim. (cut surfaces covered with mucilage). End trimmed: rate of flow = 46 centims. per hour; amount of flow = 1.28 cub. centims. per hour.

3400 vessels, having a diameter of 0.0056 centim., have a total area of cross-

\* Cylindrical tubes give the greatest flow, the maximal rate being twice the average rate of flow. Any divergences from the circular form will lessen the rate of flow, and any local irregularities or thickenings on the internal wall will have the same effect.

section of 0.068 sq. centim.; hence, with a rate of flow of 50 centims. per hour, 3.4 cub. centims. per hour should escape. This discrepancy is partly due to the fact that the rate of flow observed is the maximal and not the average one, partly to the fact that all the vessels are not equally active, and partly owing to the presence of air in them. The result indicates, however, that the part played by the tracheides and wood fibres in water transport is small.

From POISEUILLE'S formula it was found that at 20° C., under a head of 3 metres of water, 384 cub. centims. per hour should escape from 3400 vessels 25 centims. long and of 0.0056 centim. diameter. Hence, very much less water appears to pass through the stem than would be expected from a viscosity calculation.

### *Raspberry Cane.*

*Data.*—Head of water = 250 centims.; length of stem = 18 centims.; external diameter of wood-cylinder averaged 1 centim.; number of vessels in cross-section averaged 2200; diameter of vessels averaged 0.005 centim.; diameter of tracheides averaged 0.008–0.0004 centim.

*Observations.*—Amount of flow averaged 2.4 cub. centims. per hour; rate of flow was 54 centims. per hour.

At this rate from 2200 vessels, having each a diameter of 0.005 centim., 2.376 cub. centims. per hour would escape.

By POISEUILLE'S formula, however, 196 cub. centims. per hour would escape at 20° C. from 2200 open tubes of diameter 0.005 centim., and 18 centims. long under a head of 250 centims. of water.

This is over 80 times the amount actually passing. Yet the calculation made from the velocity of flow shows that practically the whole of the water was actually passing through the vessels.

### *Black Currant.*

*Data.*—Head of water = 300 centims.; length of stem = 15.5 centims.; diameter of stem = 1.2 centims.; average number of vessels = 21,000; average internal diameter of vessels = 0.0044 centim.

*Observations.*—Rate of flow = 33 centims. per hour; amount of flow = 4.5 cub. centims. per hour.

At a rate of 33 centims. per hour, 21,000 tubes of diameter 0.0044 would discharge 10.5 cub. centims. per hour, but as calculated from POISEUILLE'S formula, 1373 cub. centims. per hour should escape, *i.e.*, 305 times the observed flow.

### *Elder.*—Temp. = 15–18° C.

*Data.*—Head of water = 250 centims.; length of stem = 45 centims.; diameter of stem = 1.8 centims.; diameter of pith = 0.9 centim.; average thickness of wood-

cylinder = 0.4 centim. ; average number of vessels = 5500 ; average internal diameter = 0.0048 centim. (largest = 0.007).

*Observations.*—Maximal rate of flow = 90 centims. per hour ; maximal amount of flow = 14 cub. centims. per hour.

At a rate of 90 centims. per hour, 5500 vessels of 0.0000181 sq. centim. internal cross-section would discharge per hour 8.96 cub. centims.

As will be shown subsequently, this discrepancy is due to the fact that in elder stems water passes through the pith when driven through under pressure.

By POISEUILLE'S formula, from 5500 vessels of length 45 centims. and diameter 0.0088 centim. under a pressure of 250 centims. of water at 18° C., 147 cub. centims. per hour of water would pass through, which is about 10 times the amount actually escaping.

*Apple.*—Temp. 20° C.

*Data.*—Head of water = 3 metres ; length of stem = 25 centims. ; diameter = 1.5 centims. (eight years old) ; wood = 1.35 centims. ; pith = 0.12 centim. ; diameter (internal) of largest vessels in cross-section = 0.005 centim. ; number = 28,000.

*Observations.*—Maximal rate of flow = 375 centims. per hour ; maximal amount passing = 155 cub. centims. per hour.

28,000 vessels, having a diameter of 0.005 centim., have a total internal area of cross-section of 0.5502 sq. centim.

Hence, at a rate of 375 centims. per hour, 206 cub. centims. per hour should escape instead of the 155 cub. centims. actually observed.

From the viscosity calculation, however, 1776 cub. centims. per hour should escape, which is 11 times greater than the actual amount of flow.

The same is shown by calculating the theoretical pressure required to produce the given rate of flow through the largest vessel (0.0066 centim. diameter), assuming the length to be the same as that of the piece of stem used (25 centims.).

Thus, a vessel of 0.0033 centim. radius has an area of cross-section of 0.043412 sq. centim. ∴ per hour at a rate of 375 centims. per hour, 0.01279 cub. centim. escapes.

$$h \text{ (Head of water in centimetres)} = \frac{8vl\eta}{981\pi r^4} = \frac{8 \times 0.01279 \times 25 \times 0.010164}{981 \times 3600 \times 3.14159 \times (0.0033)^4}$$
 = 18 centims. per 25 centims. of stem. Whereas the actual head of water was 3 metres.

*Pear.*

*Data.*—Head of water = 3 metres ; length of stem = 25 centims. ; diameter of stem (four years old) = 1.3 centims. ; diameter of larger vessels averages 0.0044 centim. ; average diameter of all vessels = 0.0036 centim. ; average number of vessels in cross-section = 25,000.

*Observations.*—Rate of flow = 115 centims. per hour ; amount of flow = 18.3 cub. centims. per hour.



At a rate of 115 centims. per hour, 20·9 cub. centims. per hour would escape from 25,000 vessels, having an internal area of cross-section of 0·00001015 sq. centim. (radius 0·0018 centim.).

From POISEUILLE'S formula, however, under a head of water of 300 centims. and at a temperature of 20° C., 844 cub. centims. of water should escape from the vessels, that is, 46 times the actual amount escaping.

#### *Yew.*

*Data.*—Head of water = 3 metres; length of stem = 35 centims.; diameter of wood = 1·5 centims.; diameter of duramen averages 1 centim.; hence, area of alburnum = 1 sq. centim. Total number of tracheides = 420,000.

Tracheides in cross-section of alburnum = 230,000; average internal diameter of tracheides = 0·0012 (area of cross-section = 0·00000113 sq. centim.).

*Observations.*—Rate of flow = 11·7 centims. per hour; amount of flow = 4·6 cub. centims per hour.

The volume passing through 230,000 tracheides (assuming all to be filled with water) at a rate of 11·7 centims. per hour, would be 30·42 cub. centims. per hour, nearly seven times as much as that actually observed.

According to the viscosity calculation, however, 35 cub. centims. per hour or seven and a-half times the actual amount should escape under the conditions given from the tracheides of the alburnum when completely filled with water.

#### *Section 5.—Discussion of Foregoing Results and Test Experiments.*

Two facts stand out prominently in the foregoing calculations. Firstly, the fact that the amount of flow calculated from the rate of flow is, except in the case of the elder, always greater than the actual amount, and, secondly, the fact that the amount of flow as calculated from POISEUILLE'S formula is from 7–300 times the actual flow, the difference becoming greater as the diameter of the conducting vessels increases.

The explanation of the first point is simple. The method used gives the maximal rate of flow, and not the average rate, and, further, the calculation is based on the assumption that all the vessels are equally active in the conveyance of water, and that all of them are completely filled with water. Using two- to three-year old stems of the apple and pear in which the whole of the wood was in the alburnum condition, it was found that the rate of ascent of sap, as measured by placing the cut ends of transpiring leafy branches in eosin solution, was very uniform. The distance between the highest point at which the eosin was perceptible and that at which the whole of the wood was tinged lay between  $\frac{1}{6}$  and  $\frac{1}{10}$  of the total rise. Similar stems were then attached to a pressure apparatus, and water which had been previously boiled was driven through for some hours to remove air from the vessels.

On cutting fresh surfaces it was found that the actual amount escaping and the amount calculated from the rate of flow were nearly identical.

Thus in a particular case (pear) the amount escaping was 14.4 cub. centims. per hour, with a rate of flow of 128 centims. per hour. The total internal area of cross-section of the vessels being 0.106 sq. centim.; this gave a calculated amount of flow through them of 13.6 cub. centims. per hour. In another case (apple) the observed and calculated rates were 11.2 and 10.3 cub. centims.; the difference being probably due to the fact that a little of the water passes through the tracheides and walls of the wood vessels. Full proof that in the absence of air the flow takes place in accordance with definite physical laws was obtained by selecting straight young stems bare of lateral branches for lengths of 10–25 centims., and saturating the stems fully with water under pressure. The stems used remained living for some weeks afterwards. Clean surfaces were then cut, water driven through, and the theoretical and actual amounts of flow compared. The first experiment with a crab apple is given in full.

*Crab Apple.*

*Data.*—Five-year-old stem; 13.5 centims. segment; diameter of wood = 0.7 centim.; of pith = 0.1 centim.

Number of vessels = 17,500; average diameter = 0.0022 centim.

Head of water = 210 centims.; temperature = 19° C.

*Observations.*—Maximal flow = 38.6 cub. centims. per hour.

By POISEUILLE'S formula, volume passing per second

$$\frac{\pi r^4 gh}{8l\eta} = \frac{3.1416 \times 0.014641 \times 981 \times 210}{8 \times 13.5 \times 0.010414} = 53.0 \text{ cub. centims. per hour.}$$

Similar results were obtained with other plants under the same conditions.

Name of plant.	Length of stem.	Age of stem.	Actual flow.	Estimated flow from viscosity calculation.
	centims.	years.	cub. centims. per hour.	cub. centims. per hour.
Pear . . . .	10	3	15.5	28.2
	25	5	38.4	82.2
Elm . . . .	20	3	9.8	25.1
Yew . . . .	15	3	4.2	9.8

The greater theoretical flow is readily explained by the fact that the vessels are irregularly thickened internally, which has the effect of decreasing the effective radius. Furthermore, transverse partitions occur at long intervals, and slight constrictions at much shorter ones, and these will also retard the flow.

The presence of imbibed water in the walls of the wood vessels is a factor worthy of consideration. When saturated, the lignified walls contain about 50 per cent. of

water,\* and if this water was flowing rapidly in the same direction as that in the vessels, the internal friction of the latter would be considerably diminished. The rate of flow of the imbibed water is, however, extremely slow, the maximal observed rate being 5 centims. per 10 hours, so that this action hardly comes into consideration. The estimations were made by noting the maximal rate of flow in a transpiring branch, and finding the head of water required to produce this rate of flow. A third branch was then injected with green wax, a clean surface cut, after cooling, and then eosin solution driven in under the same head of water. Subsequent sectionising revealed the distance traversed in the walls of the vessels. The stems of the pear and oak formed suitable material, but the amount of transference observed in the tracheal walls was not more than 0·5 centim. per hour, except in a couple of doubtful cases in which the vessels were apparently not completely blocked.

No appreciable change in the viscosity of the water passed through the vessels of living wood is noticeable if the liquid is examined immediately. If, however, the water is passed slowly through a long length of stem, the viscosity of the liquid which first issues may be from 4–6 per cent. higher than that of water. This is however, a natural result of the solution in it of soluble materials gained from the wood.

The fact that slow lateral diffusion into or out of the surrounding more slowly conducting tracheides is possible from the vessels, must have some effect upon the rate of flow, but probably not a very great one. In any case, it is of interest to find the relationship between the radii of the conducting vessels and the amount or rapidity of flow.

*Section 6.—The Ratio between the Radii of the Vessels and the Rates of Flow.*

The amount of flow through a capillary tube is, other things being equal, proportional to the fourth power of the radius, and hence the velocity of flow is proportional to the square of the radius. In the following table the relative values are given in parallel columns.

*Data.*—Head of water = 3 metres; length of stems = 25 centims. Temperature, averaged 18° C.

On studying the first two columns of ratios (columns 3 and 5) it can be seen that in both cases extremely great divergence is shown, and if we except the apple, the rate of flow is, if anything, more nearly proportional to the radius than to its square. This is possibly owing to the fact that the rate of flow in the larger vessels is not so much more active than in the smaller ones, as might be expected from purely physical considerations, there being a certain tendency to level up the flow by lateral diffusion, the slower streams being accelerated and the rapid ones retarded. However this may be, the ratios between the squares of the *average* radii of the vessels and

\* SACHS, 'Arb. d. Bot. Inst. in Wurzburg,' 1879, vol. 2, p. 312.

Name of plant.	1. Rates of flow in centimetres per hour.	2. Internal radius of larger conducting elements in centimetres.	3. Ratio of radius $\times 10^4$ to rate of flow.	4. Squares of internal radius $\times 10^8$ .	5. Ratio of squares of radius to rate of flow.	6. Relative volumes passing through each vessel. Total flow $\times 10^7 \div$ number of vessels.	7. Ratio of volume to radius $\times 10^4$ .	8. Average internal radius of vessels in centimetres $\times 10^4$ .	9. 4th power of radius $\times 10^{16}$ .	10. Ratio of volume to 4th power of radius.
Yew . .	26	0·0006	4·3 : 1	36	0·7 : 1	28	4·7 : 1	6	13	2·1 : 1
Pear . .	120	0·0022	5·5 : 1	484	0·3 : 1	730	40·6 : 1	18	1,050	0·7 : 1
B. currant	58	0·0025	2·3 : 1	625	0·09 : 1	210	9·5 : 1	22	2,340	0·9 : 1
Raspberry	41	0·0025	1·7 : 1	625	0·07 : 1	1,600	66·6 : 1	24	3,320	0·5 : 1
Elm . .	50	0·0033	1·5 : 1	1,099	0·05 : 1	400	16·0 : 1	25	3,900	0·1 : 1
Apple . .	375	0·0033	11·4 : 1	1,099	0·3 : 1	2,700	108·0 : 1	25	3,900	0·7 : 1
Elder . .	155	0·0034	4·6 : 1	1,156	0·1 : 1	1,200	50·0 : 1	24	3,320	0·4 : 1
Marrow .	1180	0·0200	5·9 : 1	40,000	0·03 : 1	90,000	900·0 : 1	100	100,000	0·9 : 1

the rates of flow correspond more closely than do those between the average radii themselves and the rates of flow. Considerable divergences are still shown, however, although these may fairly be assumed to be due in part, at least, to the dissimilar structure of the wood, and the unequal length of the vessels. Possibly also, many of the vessels still contained air.

The second two columns of ratios (columns 7 and 10) show a striking difference, the proportionality between the fourth power of the average radius and the volume passed being very much greater than that between the volume passed and the radius itself. The ratio given in the last column for the elm is unduly low, owing to the rapid blocking which occurs in cut stems of this plant. In the yew, owing to the small size of the tracheides and their relatively thick walls, an appreciable amount of water must pass through the permeable walls, and hence the ratio is high. Apart from these two the ratios lie between 0·4 : 1 and 0·9 : 1, a sufficiently close correspondence to justify the conclusion that in wood of similar structure and under similar conditions the volume passing through a vessel filled with water corresponds to the fourth power of its radius.

*Section 7.—The Ratio between the Average Radius of the Vessels and the Maximal Rate of the Transpiration Current.*

Another series of estimations were made by comparing the velocity of the transpiration current with the average radius of the vessels and its square. Branches were selected resembling one another as closely as possible in length (5 feet) and in the ratio between the area of cross-section of the conducting wood and the amount of leaf surface. After being kept in darkness for over half an hour with their stems cut under water, the ends were trimmed under water, placed in eosin solution\* at once exposed to bright sunlight in the open.

\* The lithium method employed by SACHS has no advantages over the eosin method for cut stems, and, indeed, using mixed solutions, frequently no lithium can be detected in parts of the stem in which the eosin is clearly visible.

Name of plant.	Rate of flow of transpiration current in centimetres per hour.	Average radius of vessels in centimetres $\times 10^4$ .	Ratio of flow to radius.	Square of average radius in centimetres $\times 10^8$ .	Ratio of flow to square of radius.
Yew . . . .	16	6	2.7 : 1	36	0.44 : 1
Apple . . . .	92	18	5.0 : 1	324	0.28 : 1
Black currant .	121	22	5.5 : 1	484	0.25 : 1
Raspberry. . .	129	24	5.3 : 1	536	0.24 : 1
Elder . . . .	130	24	5.4 : 1	536	0.24 : 1
Elm. . . . .	148	25	5.9 : 1	625	0.24 : 1
Pear . . . . .	158	25	6.3 : 1	625	0.25 : 1

In this case the ratios are such as to show that the rate of flow is more nearly proportional to the square of the radius than to the radius itself. The fact that in the first column of ratios an increase is shown from above downwards, but in the second a decrease indicates that the rate of flow varies as a power of the radius lying between one and two, and nearer to the latter than the former. Since, however, the force impelling the water in each case cannot be estimated, and was not always necessarily the same, some such divergence is to be expected.

*Section 8.—The Relation between the Length of the Stem and the Rate of Flow.*

The amount of flow through a capillary tube is inversely proportional to the length of the tube, and directly proportional to the pressure applied, if the rate of flow is not too rapid. The same applies to the flow through wood vessels. Thus, in an experiment with 26 centims. of the stem of the crab apple, water was forced under different pressures through the horizontally placed stem. The liquid escaping during a series of successive periods of 15 minutes under each pressure was collected, and the total measured in each case at the end of three hours.

*Crab Apple.—Temp. 16° C.*

Head of water.	Amount escaping.	Theoretical amount.
centims.	cub. centims. per hour.	
262	42.8	—
176	28.5	$\frac{42.8 \times 176}{262} = 28.7$ cub. centims.
96	15.2	$\frac{42.8 \times 96}{262} = 15.0$ „

Similarly, other things being equal, the rate and amount of flow vary inversely as the length of the piece of stem through which the liquid is passing. To show this the amount of flow through a measured length of uniform stem was noted, the

ends then trimmed, the stem shortened, and the amount of flow again noted, the head of water being kept constant.

*Wych Elm.*

Amount of flow during first hour = 1.28 cub. centims. per hour (26 centims. of stem); amount of flow during next 24 hours averaged 0.98 cub. centim. per hour; stem then cut to 10 centims. length and ends trimmed; amount of flow during next 16 hours averaged 2.8 cub. centims. per hour, *i.e.*, per 25 centims. of stem, 1.1 cub. centims. per hour if inversely proportional to length of stem.

Still better results were given by the apple and pear, each of the numbers being the average of three experiments performed simultaneously.

Name of plant.	Length of stem.	Amount of flow.	Length of stem.	Amount of flow.	Expected amount.
	centims.	cub. centims. per hr.	centims.	cub. centims. per hr.	cub. centims. per hr.
Apple . .	30	142	15	270	282
Pear . . .	30	156	15	295	312

If the pieces of stem are cut down to 3 or 5 centims. length, the amount of liquid escaping is somewhat greater instead of slightly less than the expected amount, probably because there are relatively fewer transverse partitions hindering the flow through the vessels, most of the latter being open at both ends.

*Section 9.—The Pressure Required to Produce the Maximal Rate of Flow in a Transpiring Branch.*

Although the resistance offered to the flow of water through wood is much greater than would be expected from a viscosity calculation, a fairly accurate estimate of it can be obtained in the following manner by direct observation:—Leafy branches 4–8 feet in length were cut under water and kept in darkness for half an hour. Clean ends were then cut under water, placed in freshly filtered eosin solution, and at once exposed in the open on bright cloudless breezy June days between 10 and 1 P.M., with a shade temperature averaging 18–22° C. The conditions for transpiration were, therefore, optimal.

The periods of observation lasted only from half to one hour, since with longer periods the leaves begin to droop, which is an infallible sign that the rate of ascent of sap is decreasing owing to blocking at the cut surface. Even then the leaves of the elder, and to a less extent those of the elm, begin to droop within an hour. After a timed period the stem was removed and rapidly sectionised from the apex downwards until the eosin solution was visible in the wood, the length of the

remaining portion of the stem giving the rate of flow during the period of observation.

Portions of the same stems and also similar ones from the same plants were then subjected to varying water pressures until closely corresponding rates of flow were reached. Since the maximal rate of flow was measured both here and under transpiration, and since the maximal flow takes place in those vessels of the terminal branches which are most completely filled with water, it is immaterial whether the water is drawn through by the suction exercised by the leaves, or driven through by pressure. The two sets of results are, therefore, fairly comparable, the only possibility being that the pressures required in a transpiring branch would be a little higher than those required to produce the same rate of flow in a cut stem.

Name of plant.	Maximal rate of flow of transpiration current.	Maximal rate of flow of—	Under head of water of—	Through length of stem of—	Approximate pressure required in metres of water per metre of stem to produce maximal transpiratory rate of flow.
	centims. per hour.	centims. per hour.	metres.	centims.	metres.
Raspberry . .	129	88	4.5	20	33
Elder . . .	130	108	4.0	50	9½
Apple . . .	121	125	3.0	50	6
Elm . . . .	205	160	4.5	20	29
Black currant.	121	116	4.5	25	19
Pear . . . .	148	134	4.0	30	15
Yew . . . .	23	19	4.0	25	19

*Section 10.—The Pressures Required in the Trunks of Trees for the Ascent of Water.*

If the rates of flow shown in the terminal branches were maintained throughout the stem, then the required pressures would be from 6–33 times that of a column of water the same height as the plant. In the case of the raspberry and black currant, the full length of the stem was used for the transpiration experiments, so that in these plants pressures equivalent to 50 and 29 metres of water (5 and 3 atmospheres) respectively were required to produce the maximal rate of flow during active transpiration.

A transpiring elder stem 4 metres high gave a rate of flow of 98 centims. per hour. The average rate of flow through three 50 centims. lengths of the same stem was 114 centims. per hour under a head of 3 metres of water. Hence, the head of water required in the stem would be 5.3 metres, or if the columns of water in the tracheæ were continuous, 6.3 metres per metre of stem, or 25 metres (2½ atmospheres) for the entire tree 4 metres high.

In the case of tall trees, however, the rate of flow in the main trunk appears to

be slower than in the terminal branches, or in other words, the area of cross-section of the effective conducting tissue decreases outwardly and upwardly in and from the main trunk. SCHWENDENER,\* for instance, calculated that in the stem of a beech, water must travel at a mean rate of 2 metres per day up the stem to make good the loss by transpiration from the leaves in summer. Since, however, the major part of the transpiration occurs during eight hours of the day, we may assume that the maximal rate of flow lies between 20 and 30 centims. per hour.

In the case of an elm, I observed a maximal rate of transpiration of 0·1 gramme per hour per 200 sq. centims. of the transpiring surfaces (upper and under surfaces of leaves). The total transpiring surface was estimated at 14,500,000 sq. centims. Hence, the maximal amount transpired per hour would be 7250 cub. centims. The total area of wood at the base was 1960 sq. centims., of conducting alburnum 640 sq. centims., and the area of cross-section of the water contained in the vessels, tracheides was approximately 160 sq. centims. Hence, the rate of flow would average 45 centims. per hour. To maintain this rate of flow would require, according to the preceding table, a head of 6·3 metres of water per metre of stem, so that an elm 12 metres high would require a head of 75·6 metres of water merely to overcome the resistance due to the viscosity of the water flowing through the vessels, to the limited length of the latter and to the presence of air-bubbles in them. A similar calculation with an apple gave a value of 5·5 metres per metre of stem, and with a pear of 6·8 metres per metre of stem. The trees being respectively 6 and 8 metres, the pressures required to maintain the flow, even when the stem was horizontal, would be 33 and 54·4 metres respectively (3–5 atmospheres).

In the case of the yew an estimation was made from the following data :—

Diameter of main trunk = 56 centims. ; height of tree = 11 metres.

Total number of leaves = 9,000,000 ; average total surface of leaf = 1·2 sq. centims.

A branch bearing 500 leaves was led through a split rubber cork into an air-tight glass chamber containing a weighed quantity of calcium chloride, and exposed to light and an average temperature of 21° C. for 8 hours. The average transpiration was 0·05 cub. centim. per hour. Hence, per hour, the whole tree exhaled about 900 cub. centims. during the daytime.

Only the extreme periphery of the trunk conducted water (rarely more than 0·4 centim.), the conducting area on the main trunk being 520 sq. centims., of this approximately 130 sq. centims. represent the actual area of water. Hence, for the passage of 900 cub. centims. per hour the rate of flow must be 7 centims. per hour. To produce a rate of flow of 19 centims. per hour through 25 centims. of stem required a head of 4 metres of water.

\* SCHWENDENER, 'Sitzungsb. d. Berl. Akad.,' 1892, p. 925.



Hence to produce a rate of flow of 7 centims. per hour through 11 metres of stem would require a head of 65 metres of water.

In all four of the foregoing cases the head of water required during active transpiration to overcome the resistance due to the viscosity of the water flowing through the vessels and to other factors appears to be approximately six times the height of the tree. If a similar calculation holds good for the tallest known trees (100–150 metres), then, for such trees, heads of water of as much as 1000 metres might be necessary, that is, pressures approaching 100 atmospheres. It is difficult to see how any such pressures could be generated and maintained in the leaves, or how they could be propagated downwards through the air-containing vessels of the wood.

*Section 11.—The Influence of the Length, Shape, and Structure of the Wood-Elements.*

The amount of flow in unit time under constant pressure through a capillary tube is inversely proportional to its length. POISEUILLE found, however, that in tubes less than 1 centim. in length the amount of flow was less than would be expected by calculation. Thus the time of flow of a certain volume through a tube 9 millims. long was 71 mins. 5 secs. instead of the expected 52 mins. 63 secs.\* The tracheides and wood fibres are rarely more than 1 or 2 millims. long, and frequently not more than  $\frac{1}{5}$  millim. in length. Even in the wood of *Pinus* the pitted tracheides are not more than 4 millims. long, and although in a few cases (stems of *Musa*, *Canna*, etc.) they may be over a centimetre long, and 0.008–0.01 centim. diameter, this is comparatively rare. In any case, if the resistance to flow becomes disproportionately great in very short tubes, we have a very striking reason for the development of vessels as conducting tubes, quite apart from the avoidance of repeated transverse partitions.

From POISEUILLE's observation it is not, however, clear whether the effect became progressively greater as the length of the tube decreased. Hence, experiments were tried with calibrated thermometer tubing of circular bore.

Temp. 19° C.

Head of water.	Length of tube.	Amount of flow.	Estimated amount.
metres.	centims.	cub. centims. per hour.	cub. centims. per hour.
3	9.25	12.4	$\frac{12.4 \times 9.25}{0.6} = 191.1$
3	0.6	123.0	

The velocity of flow in the short tube is, however, so high that it may have passed

\* Cf. WÜLLNER's 'Physics,' vol. 1, p. 385.

the critical velocity beyond which the friction increases as a power of the speed rising to two, and also the correction for the kinetic energy of the escaping liquid becomes considerable. Hence, similar experiments were tried with a smaller head of water.

Temp. 19° C.

Head of water.	Length of tube.	Amount of flow.	Amount estimated.
centims.	centims.	cub. centims. per hour.	cub. centims. per hour.
80	9·25	3·46	—
80	1·0	26·3	32·0
80	0·6	45·17	53·2

To reproduce more closely the conditions existing in the plant, a tube 8 centims. long was used, and the rate of flow through it observed and estimated. The tube was then cut up into 16 pieces, each approximately 0·5 centim. long, and the pieces sealed inside glass tubes of 4 millims. internal diameter and 5 centims. long (fig. 1). The tubes were first tested separately, and the whole system filled with water (a matter of some difficulty). They were then joined up in series and subjected to the same head of water as before. The difference in radius between the capillary tubes (0·0075 centim.) and the junction tubes (0·2 centim.) is so great as to render the influence of the junction tubes in the system negligible.

Head of water = 80 centims. ; internal diameter of tube = 0·015 centim.

Temp. = 18–20° C. (water and air temperatures).

1. Length of tube = 8 centims. Estimated flow = 4·1–4·3 cub. centims. per hour.

Observed flow = 4·0–4·2 cub. centims. per hour.

Tube in 16 0·5 cub. centim. lengths in series. Observed flow = 3·8–3·9 cub. centims. per hour.

2. Length of tube = 4 centims. Average flow = 8·6 cub. centims. per hour.

When in 10 0·4 millim. lengths. Average flow = 8·3 cub. centims. per hour.

Evidently, therefore, POISEUILLE'S formula applies to tubes of only 4- or 5-millim. lengths, as well as to longer ones, provided that the rate of flow is not too rapid.\* The slightly slower rate of flow is probably the result of the manipulation and of the unavoidable entry of dust particles.

We are therefore justified in assuming that the only advantage a long conducting vessel possesses over a short one of equal diameter is due to the fact that filtration

\* The apparent failure of POISEUILLE'S formula for short tubes is not real, but is due to an over estimation of the head, some of which is used in bringing the water up to the entrance and giving it kinetic energy. If we could measure the pressures at inflow and outflow, the formula would, without doubt, still hold almost exactly.

under pressure through the end partition walls with its resultant increased resistance to flow are largely avoided.

*Section 12.—The Influence of the Direction of Flow upon the Amount of Flow.*

As regards the longitudinal flow of water under pressure, it may be driven either upwards or downwards through the stem, and the latter may either be placed with the root pole downwards or upwards. In all four cases the amount of flow is approximately the same under otherwise similar conditions, the variations being inconstant and within the limit of experimental error when short lengths of the terminal branches are used.

Similarly, in the cases of stems fully saturated with water it is immaterial whether the water is driven through under pressure or drawn through by the suction of a suspended column of water. In the second case the upper end of the stem was attached to a small vessel containing a measured quantity of water, the lower end to a long tube filled with water and with its lower end under water. The amount of flow was found by measuring the amount remaining in the upper vessel.

If, however, the vessels of the stem contain much air, and a considerable head of water is used, a distinct difference is shown. Thus, with a portion of an actively transpiring 5-year-old stem of a pear, the amount of flow was 38.5 cub. centims. per hour under a head of 4 metres, but only 21.2 cub. centims. under the suction of the same column. The explanation is undoubtedly due to the fact that under pressure the air in the vessels is compressed, whereas under the action of a suspended column the pressure is less than that of the atmosphere, so that the air-bubbles expand and block the vessels more completely, besides tending to increase in size instead of diminishing, as when under pressure. This last effect can be avoided by using water containing no dissolved air. The oxygen contained in the water absorbed from the soil is converted into carbon dioxide, a more soluble gas, in its upward passage, but when the dissolved nitrogen reaches those parts where water is being drawn up by suction it will tend to appear as gas, and accumulate together with the superfluous oxygen. Further than this, the negative pressure in an actively transpiring stem will tend to draw gas inwards and downwards from the leaves. This action will be strongest when transpiration, and therefore, also, photosynthesis, are most active. So that a stream of air rich in oxygen will be drawn down the intercellular spaces, and thence diffusing into the vessels, will produce the excess of oxygen often found in them.

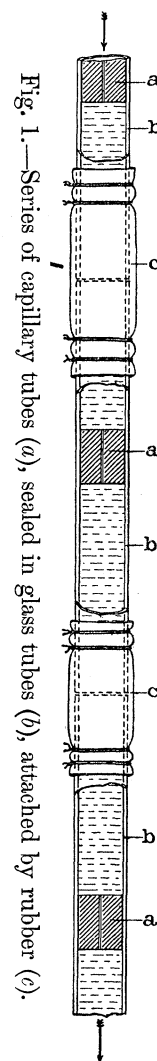


Fig. 1.—Series of capillary tubes (a), sealed in glass tubes (b), attached by rubber (c).

*Section 13.—The Influence of Death on Flow.*

The fact that the water flows equally well up or down cut stems appears to indicate the absence of any vital pumping action, for this would naturally tend to favour flow in the customary direction. Furthermore, STRASBURGER killed stems for considerable distances (as much as 10 metres) and observed that the parts above remained fresh for some time. The proof is not perfectly satisfactory, since in the case of a large tree, the trunk and branches may contain sufficient available water when fully saturated for from 1–3 weeks' transpiration. In addition to this stems killed by heating to 80° C. appear to have their conductivity permanently reduced, possibly owing to the swelling of the walls of the wood-vessels, or to the partial occlusion of their lumina. This is well shown by the following experiment with 25 centims. of an apple, using a head of 3 metres of water.

Time . .	1st 4 hrs.	—	1st $\frac{1}{4}$ hr.	2nd and 3rd $\frac{1}{4}$ hr.	1 hr.	1 $\frac{1}{4}$ hrs.	1 $\frac{1}{2}$ hrs.	1 $\frac{3}{4}$ hrs.	8th $\frac{1}{4}$ hr.
Amount of flow per hour	cub. centims. 82	Stem killed in water at 80° C.	cub. centims. 36	cub. centims. 38·4	cub. centims. 43	cub. centims. 48	cub. centims. 49	cub. centims. 51	cub. centims. 49·5
Rate of flow per hour	centims. 250		centims. 132	—	—	—	—	—	centims. 172

On the other hand if solutions of metallic poisons are used ( $\text{HgCl}_2$ ) the conductivity of the dead stem may be for a time greater than it was before. In the following experiment with a pear stem the ends were trimmed before each observation :—

Time . .	1st hour.	16th hour.	—	17–18 hour.
Amount of flow per hour	cub. centims. 18·3	cub. centims. 12	Stem then killed by poison	cub. centims. 16·8
Rate of flow per hour	centims. 115	—		centims. 120

Apparently the flow was accelerated more in some vessels than in others. On the other hand, if a fresh piece of stem is used, the effect of treatment with metallic poison is always to decrease the amount of flow by amounts varying from 5–50 per cent. of the original flow. These fluctuations are such as to readily mask

the existence of a feeble pumping action in the living wood, and render it incapable of detection by direct experiments on living and dead pieces of stem.

*Section 14.—The Changes of Conductivity in Cut Stems.*

The gradual blocking of cut stems placed in water is well known, as is also the fact that the conductivity can be restored by removing a slice from the cut surface under water. When water is forced through a cut stem which has been actively transpiring, the conductivity usually rises at first, if the blocking is not too rapid. In the following instances the rates and amounts of flow per hour are given, the head of water being 3 metres in all cases :—

*Yew.*—35 centims. of an actively Transpiring Branch.

Time . . . .	1st hour.	6th hour.	Ends trimmed.	12th hour.	Ends trimmed.
Rate of flow . . . .	centims. 11·7	—	—	—	centims. 19
Amount passing . . . .	cub. centims. 4·6	cub. centims. 4·2	cub. centims. 4·8	cub. centims. 2·9	cub. centims. 6·5

*Wych Elm.*—25 centims. of Stem.

Time . . . .	1st hour.	Next 24 hours averaged—	Slimy ends trimmed.	After 4 hours.	Stem then cut to 10 centims.
Rate of flow . . . .	centims. 50	—	centims. 46	—	—
Amount passing . . . .	cub. centims. 1·36	cub. centim. 0·4	cub. centims. 1·28	cub. centim. 0·98	cub. centims. 2·8*

*Black Currant.*—25 centims. of Stem.

Time . .	1st hour.	After 16 hours.	Ends trimmed.	Next hour.	Next hour.	Next hour.	After 16 hours.
Rate of flow . .	—	—	—	—	centims. 33	—	—
Amount passing .	cub. centims. 3·27	cub. centim. 1	cub. centims. 5·4	cub. centims. 4·8	cub. centims. 4·5	cub. centims. 3·8	cub. centims. 1·9

\* Per 25 centims. length this equals 1·1 cub. centims. per hour.

*Apple*.—25 centims. of a Stem Saturated with Water.

Time . . . . .	1st hour.	After 4 hours, ends trimmed.
Rate of flow . . . . .	375 centims.	250 centims.
Amount passing . . . . .	155 cub. centims.	82 cub. centims.

In the case of stems containing a large quantity of young pith such as those of the raspberry and elder, a marked rise of conductivity is shown after water has been flowing through under pressure for some time.

*Raspberry*.—25 centims. of an actively Transpiring Stem.

Time . . .	1st hour.	4th hour.	20th hour.	34th hour.	3rd day.
Amount . . . . .	cub. centims. 2·35	cub. centims. 2·4	cub. centims. 4·74	cub. centims. 11	cub. centims. 1·3
Rate . . . . .	centims. 54	—	—	centims. 120	—
Amount . . . . .	—	Clean ends cut. cub. centims. 6	4th day. cub. centims. 2·2	Ends cut. cub. centims. 3·5	5th day. cub. centims. 1·8

Elder stems give similar results, but if the branches were stripped of leaves and kept with their cut ends under water for some hours previously to testing, the rise was much less pronounced.

*Elder*.—45 centims. of Stem, partially Saturated with Water.

Time . . .	1st hour.	3rd hour.	Ends trimmed.	6th hour.	10th hour.
Amount . . . . .	cub. centims. 10·8	cub. centims. 7·2	cub. centims. 14	cub. centims. 13·4	cub. centims. 13·1
Rate . . . . .	centims. 67·5	—	centims. 90·8	—	—
Amount . . . . .	—	—	—	22nd hour. cub. centims. 10·4	—

In both these cases the water under pressure slowly drives out a portion of the air from the pith, and then percolates slowly through the intercellular spaces of the latter. This can readily be shown by using coloured solutions, and further proof was obtained in the case of the elder by noting the effects of the removal of the pith.

*Elder* 1.—26 centims. of 2nd Year Stem, 1·4 centims. diam. ; Pith, 0·9 centim. diam. ;  
Stem Saturated with Water. Pressure = 3 metres of Water.

Time . . . . .	1st hour.	2nd hour.
Amount of flow per hour . .	37 cub. centims.	29 cub. centims.

The stem was then pithed, the cavity filled with soft wax, and the ends trimmed.

Time . . . . .	1st hour.	4th hour.	Trimmed.	6th hour.	14th hour.	26th hour.
	cub. centims.	cub. centims.		cub. centims.	cub. centims.	cub. centims.
Amount of flow per hour	13	5·6	—	11	3·7	2·3

*Elder* 2.—21 centims. of 1·5 centims. diam., previously Saturated with Water.

Time . . . . .	1st hour.	After pithing and filling with wax.	After 10 hours.	After 20 hours.
	cub. centims	cub. centims.	cub. centims.	cub. centims.
Amount of flow per hour	28	10·5	5·5	3

Direct observations upon transpiring branches by means of eosin solutions showed that the amount of flow through the pith is negligible as compared with that through the wood, but, nevertheless, early in the year before the leaves are out, the root pressure, by saturating the pith, will render it more efficient as a temporary channel for the conduction of water. This is very probably a factor of some importance in avoiding the desiccating action of dry winds on sunny days upon the uncuticularised young foliage in spring.

Apart from all such changes as described above, a permanent fall of conductivity always ultimately occurs along the entire length of a piece of stem through which water is forced under pressure.\* This is well shown by the following experiments, with the stem of a crab apple, which was trimmed at the ends before each reading so as to avoid any effect due to blocking at the cut surfaces :—

*Crab Apple*.—25 centims. ; Head of Water = 250 centims. ; Temp. = 18–19° C.

Time . . . . .	1st hour.	2nd hour.	3rd hour.	8th hour.	28th hour.	34th hour.
	cub. centims.	cub. centims.	cub. centims.	cub. centims.	cub. centims.	cub. centims.
Amount of flow . .	32·4	34·6	38·2	36·1	19·2	13·5

The same effect is produced somewhat more slowly when filtered dust-free distilled water is used, though not quite so rapidly as with filtered tap-water. It seemed possible that the pure water might produce a swelling of the walls of the

\* A similar observation is recorded by ANDERSON (Brit. Assoc., 1902, Sect. K), but no attempt to determine its causes was made.

wood vessels, and hence a diminution of their internal bores, an effect which would be absent when sap, or a dilute saline solution, was passing through them. The same slow blocking is, however, shown when a dilute saline solution is passed through stems for prolonged periods, as is shown by the following experiment with 42 centims. of a 10-year old crab apple stem under a head of 2 metres of water :—

Average amount of flow per 22 hours in cub. centims. per hour—

Time . .	1st day.	2nd day.	3rd day.	4th day.	5th day.
	2·8	2·4	2·2	2·5	2·0

Flow in cub. centims. per hour after trimming ends—

6·86	—	5·6	5·2	4·7
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Incidentally, it was noticed that after the second or third day the liquid issuing from cut stems through which water was passing became rich in bacteria after standing, and on examination both motile and non-motile forms were found to be present in the vessels at the upper end of the stem, in some cases in considerable numbers. When tap-water is passed slowly through a capillary tube for some days, gradual blocking also occurs, but if filtered distilled water is used to which 1 gramme of  $\text{HgCl}_2$  has been added per 10 litres of water, this effect is very much delayed. In the case of stems, however, the treatment is less effective, possibly because the chloride of mercury acts on the walls of the wood vessels and affects their permeability.

#### *Section 15.—The Influence of the Presence of Air.*

It has already been mentioned that stems saturated with water allow much more water to pass than stems in which the vessels contain numerous air-bubbles, the presence of the latter considerably increasing the resistance to flow. This forms an interesting commentary upon the value of the JAMIN's chain hypothesis as an explanation of the ascent of sap in trees.\* If the bubbles of air are stationary as in the vessels, they simply increase the head of water needed to produce a given rate of flow. Even if the vessels were continuous tubes running from end to end of the plant, and if the air-bubbles and water columns moved bodily upwards towards the transpiring cells, the resistance to flow would be much greater than when the tubes were filled with water, while the result of an hour's flow would be the accumulation of many centimetres of air at the upper end of the vessel. This would rapidly retard further flow, since air only passes slowly by solution and diosmosis through the moist permeable walls at the upper end of the vessel.

The actual physical effect of the presence of air was found by using the chain of 16 capillary tubes of 5 millims. length as figured on p. 59. Small air-bubbles

\* SCHWENDENER's discussions, for instance ('Königl. Preuss. Akad.,' 1886, p. 561; 1893, p. 842; 'Ueber das Saftsteigen,' 1893, p. 50), are founded upon a complete misapprehension of the properties of a JAMIN's chain.



were left between each capillary, the chain was placed vertically, open end upwards, and the water also driven upwards, so that the bubbles of air would be forced into the capillaries. It was found that if the bubbles were all under the holes in the capillary tubes, no appreciable flow took place with a head of water of 80 centims. With 3 metres of water a slow irregular flow took place, which rapidly increased as the air-bubbles passed through the tubes. This is not surprising when we consider that the pressure inside an air-bubble, due to its surface-tension when under water, corresponds approximately to 40 centims. of water when the radius of the bubble is 0·0075 centim., and that this pressure has to be overcome before an air-bubble can be forced into the capillary tube.

When the chain was placed with the open end downwards and the water also driven downwards, the rate of flow was slightly greater or slightly less than when the tube was horizontal, according to the size of the air-bubbles. Here the surface-tension effect is practically avoided if the bubbles are small, for the descending stream pushes the bubbles away from the capillaries when the tube is erect, and when horizontal gravity produces the same effect. The difficulty of exactly adjusting the head of water so as to be the same in both cases probably largely explains the slight divergences shown in the amount of flow. The effect of the gradual removal of air by water under pressure is well shown by the following experiment. A similar chain of capillaries was placed under a head of a metre of water, but the chain was placed horizontally, and large air-bubbles were left between each pair of capillaries. The temperature varied from 18–21° C.

Time . . .	1–3rd	3–18th	18–22nd	22–26th	26–30th	30–45th	45–50th	50–65th	65–67th
	hour.	hour.	hour.	hour.	hour.	hour.	hour.	hour.	hour.
Amount of flow in cubic centi- metres per hr.	1·1	2·12	3	3·37	4·3	3·1	2·8	2·04	1·7

The air-bubbles were all removed by the 26th hour, beyond which time the effect of the gradual blocking of the tube became noticeable. It is curious how closely the changes in the rate of flow resemble those occurring when water is forced under pressure through a branch whose vessels contain more or less air.

#### *Section 16.—The Length of the Vessels.*

Water was forced under heads of 3–5 metres through stems until they were fully saturated with water. Fresh ends were then cut and placed under pressures of 30–40 centims. of mercury for a day or more. The free apical end was then cut away until the mercury could be seen exuding from a vessel. The length of stem remaining was then taken as the length of the longest vessel. The remainder of the stem was now cut away until mercury was exuding from approximately half the larger vessels in the spring wood. Twice the remaining length of stem was taken

as giving the average length of the larger vessels. A point which is especially noticeable in the elder is that the terminations of the vessels appear usually to be at nodes and not at internodes.

	Crab apple.	Apple.	Wych elm.	Rasp- berry.	Elder.	Pear.	Yew.	Black currant.
Greatest length observed in centimetres.	22	34	48	15	24	25	0·5	10·5
Average length of larger ves- sels in centi- metres.	15	24	36	12	21	18	0·25	7·0

To make sure that no breaking down of the partitions took place, less and greater pressures were applied to short and long pieces of apple branches of varying ages. The following instances will serve to show the close correspondence between the results :—

	Longest vessels.	Average length of larger vessels.
(a) 10-year-old branch, 100 centims. long	28	36
(b) 20-year-old branch, 50 centims. long	27	35
(c) 20-year-old branch, 50 centims. long, but mercury forced from apex to base	26	35

As soon as the pressure is removed, the mercury begins to exude from the vessels owing to the capillary depression exercised by the latter. If, however, the pressure is maintained, the threads of mercury in the vessels of the wood can, without difficulty, be traced to their termination by careful dissection from the surface and with the aid of an adjustable magnifying lens. It was, however, very difficult to satisfactorily demonstrate the terminations of the vessels under a compound microscope, since, as soon as a longitudinal section was made, the mercury rapidly escaped and was never found occupying a vessel up to its termination. Accordingly, mercury was used in which a small quantity of sodium had been dissolved; this was forced into the vessels, and in the course of a few hours causes a marked brownish discoloration of the walls. A thread of mercury was now traced to its termination as before, and this part of the wood cut out and sectionised. Only two satisfactory terminations were obtained, and curiously enough, instead of being transverse plates like the incomplete partitions commonly occurring across vessels, both endings were pointed and tapering, being more like the end of a wood fibre or tracheide than a wood vessel.\*

\* Values previously obtained by ADLER by a different method were: *Alnus*, 6 centims.; *Corylus*, 11 centims.; *Betula*, 12 centims.; *Quercus*, 57 centims.; *Robinia*, 69 centims.; *Aristolochia*, 300 centims.

*Section 17.—Transverse Rate of Flow.*

That transverse flow through wood must be possible is self-evident, but the actual rate appears to be slower than has usually been supposed.\* Thus the longitudinal rate of flow through 42 centims. of a 10-year old crab apple stem, having an area of cross-section of 1.2 sq. centims. of wood, was 6.8 cub. centims. per hour. The transverse flow through thin slices, arranged so that the flow was tangential to the surface, was so slow as only to be measurable with difficulty, and only with prolonged observations. Thus a slice 0.5 centim. thick and 1.2 centims. area under a head of 2 metres gave a flow of 0.01 cub. centim. per hour and one 0.3 centim. thick a flow of 0.02 cub. centim. per hour. In this last case the relative rates of longitudinal and transverse flow were, per centimetre of stem, as 1 : 45,000. Taking the average length of the vessels as 15 centims. and their diameters as 0.005 centim., 3000 partition walls would be interposed in the transverse direction to one in the longitudinal. Apparently, therefore, the resistance to filtration under pressure through a single partition wall is more than 10 times greater than that due to the flow through the entire length of a vessel. From this it is easy to see why water can be forced under considerable pressure through a stem without any appreciable lateral exudation taking place.

If the section is taken from the surface layers of the wood and arranged so that the flow is radial, the rate of flow appears to be from four to six times as rapid as above, namely, 0.08 to 0.12 cub. centim. per hour per square centimetre of area per 0.3 centim. thickness (head = 2 metres). This is probably because the arrangement of the medullary rays is such as to favour flow in this direction. Even in this case a single partition wall interposes at least two or three times as much resistance as the length of a vessel.

The wood of the pear and elm gave very similar results, but in that of the yew the difference between the radial and tangential rates of flow was not nearly so pronounced, the ratios being :—

Longitudinal.	Transverse tangential.	Radial transverse.
1050	1	$1\frac{1}{4}$

*Section 18.—The Influence of Temperature on Flow.*

Since the viscosity of water is a factor in the flow of water, temperature which affects the former must also affect the latter, and to a considerable degree, as is shown by the following values.

(STRASBURGER, 'Leitungsbahnen,' 1891). The values given above for the apple, elm, pear, and yew apply to the lateral branches only; in the older wood of the main trunk the vessels (or tracheides) may be longer, and possibly very much longer.

\* For literature, see STRASBURGER, 'Leitungsbahnen,' 1891, p. 595; 'Saftsteigen,' 1893, p. 34.

## Viscosity of Water in C.G.S. Units.

Temp. . .	0° C.	3° C.	10° C.	15° C.	20° C.	25° C.	30° C.
Viscosity	0·018086	0·016214	0·013257	0·011503	0·010164	0·009025	0·008121

Hence the viscosity of water at 30° C. is one-half that at 3° C., and that at 25° C. is one-half that at 0° C. So that at the two lower temperatures, twice the force is required to overcome the resistance to flow due to the viscosity of water that is required at the higher ones. Since an appreciable amount of the total resistance is due to this cause, temperature will form a factor of some importance in the regulation of the flow of sap. This action of temperature might, in fact, in some degree be responsible for the xerophytic character of winter evergreens, and for the gradual disappearance or dwarfing of trees towards the extreme north and south.

Physical deductions cannot, however, be applied to living organisms if unsupported by direct experiment. As a matter of fact experiment showed that using 50-centim.

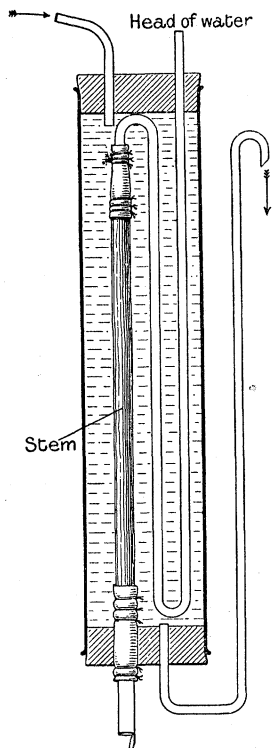


Fig. 2.

lengths cut from transpiring branches, the amount of flow though influenced by the temperature, altered to a less extent than would be expected from the changes of viscosity. This is probably owing to the presence of air in the vessels, which, apart from the expansion and contraction caused by the changes of temperature, and from the more rapid solution at the lower temperature, would exercise a resistance to flow slightly increased by a fall of temperature owing to the increased surface-tension of the air-bubbles in the vessels. In fact, after passing water through for some time under pressure it was found that the amount of flow became much more nearly proportional to the viscosity.

Accordingly test experiments were made upon short lengths of stems which had been previously fully saturated with water. The stems (crab apple) were fixed as shown in the figure, and surrounded by water led from a large vessel containing water at a known temperature. The current was regulated so that the temperatures of the issuing and entering streams did not differ by more than a degree, when the temperature of the entering stream was taken as that of the stem. At 0° C. the stem was simply packed round with ice. The readings were taken in pairs, the lower temperature first in one case, the higher in the other, and averages taken of the two readings. Each reading occupied half an hour, and a thin shaving was taken from the ends of the stem with a sharp razor after each observation. The stems were all five years old, 25 centims. length and with a wood cylinder 8 centims. diameter.

Temp.	Amount of flow in cubic centimetres per hour.	Calculated amount from viscosity of water at the given temperature in cubic centimetres.
Expt. 1— 15° C. . . .	27·4	
10 . . . .	25·3	$\frac{27·4 \times 0·011503}{0·013257} = 24·7$
Expt. 2— 21° C. . . .	38·4	
16 . . . .	35·7	$\frac{38·4 \times 0·009922}{0·011216} = 34·9$
14 . . . .	32·6	$\frac{38·4 \times 0·009922}{0·011803} = 33·2$
10 . . . .	29·2	$\frac{38·4 \times 0·009922}{0·013257} = 29·6$
Expt. 3— 19° C. . . .	36·0	
0 . . . .	19·5	$\frac{36·0 \times 0·010414}{0·018086} = 20·17$
3rd hour— 0° C. . . .	19·1	
5th hour— 4° C. . . .	21·22	19·1 at 0° C. = at 4° C., 21·9

Evidently, therefore, the flow through a wood vessel filled with water is strictly proportional to the viscosity of the latter, the differences between the observed and calculated amounts being within the limits of experimental error. None of the vessels were open at both ends, and hence the viscosity factor affects the filtration under pressure through the partition walls in the same way that it does the flow through the length of the vessels.

*Section 19.—The Relation between Water-Transport, Wood-Production, and the Rigidity of a Stem.*

The fact that the water is mainly or entirely transferred by the young wood is well known, but it is not known whether the continued production of new wood is solely to increase the rigidity of the stem, or whether it takes place because wood is only capable of transporting water for a limited time. In the first case the water would simply flow through the younger wood because this formed the easier path, but in the second case a continued production of new wood, far beyond the mechanical requirements of the tree, would become a necessity. For if a pumping action is exercised by the wood-parenchyma cells, it will cease as the vital activity of these cells diminishes with age, and hence the older wood, though still capable of transmitting water forced in by pressure, will be unable to aid in driving it upwards.

In POYNTING and THOMSON'S "Properties of Matter" a formula is given to determine the maximal possible height ( $l$ ) of a tree.

Thus if  $q$  = YOUNG'S Modulus for the wood,  $ak^2$  = moment of inertia of stem, and  $w$  = weight of stem, then  $l = 2.18 \sqrt{qak^2/w}$ .

In the case of a pine tree 15 centims. diameter with wood of sp. gr. 0.6 and where  $q = 10^{11}$  C.G.S. units,

$$w = 0.6gla \text{ and } k^2 = 15^2/16.$$

Hence

$$l^3 = \frac{7.84 \times 10^{11} \times 15^2}{0.6 \times 981 \times 16}, \text{ so that } l = 2.7 \times 10^3 \text{ centims.}$$

Hence the tree could not be more than 27 metres high. This value is absurdly high, since no allowance is made for the leaves or branches, or of the necessity of withstanding wind pressure and the impact of falling rain.

In the case of a vertical pillar loaded at the upper end with a weight,  $W$ , for stability,  $W < \pi^2 qak^2/4l^2$ . If the cross-section of the pillar is a circle of radius  $r$ , then  $W < \pi^3 qr^4/16l^2$ . Hence the maximal weight that can be supported without instability varies directly as the *fourth power of the radius* and inversely as the *square of the length*. Thus, suppose a tree to be 10 metres high and 20 centims. radius. Then, if it increased to 20 metres, its radius should increase to  $20 \times \sqrt{2} = 28.2$  centims. A cylindrical rod of pine-wood, for instance, 20 centims. long and 2 millims. diameter, should support 42 grammes at its upper end without instability ( $q = 10^{11}$ ).

The following data from young and old trees were then obtained by actual measurement and calculation :—

	Radius of main trunk (wood and half- bark) in inches.	Total height of tree from ground in feet.	Height of centre of gravity from ground in feet.	Weight* of tree above ground in lbs.	4th power of radius in inches.	Square of height of C.G. in feet.
Pear (a) . . .	4.7	$26\frac{2}{3}$	14	600	482	196
(b) . . .	0.44	$9\frac{1}{4}$	5	2	0.037	25
Apple (a) . . .	6.03	$22\frac{2}{3}$	$14\frac{1}{2}$	700	1625	210
(b) . . .	0.55	$9\frac{1}{3}$	$5\frac{1}{3}$	3	0.092	28
Plum (a) . . .	1.75	$12\frac{1}{2}$	$6\frac{1}{2}$	22	9.5	42
(b) . . .	0.5	$8\frac{1}{4}$	4	$2\frac{1}{4}$	0.0625	16

Since in each case the stem of the younger tree was strong enough for all ordinary requirements, it was calculated from its weight, and from the radii and heights of the

\* Stem and leaves in the dry summer of 1904. The weights, 600, 700 were estimated; the others obtained by direct weighing, and taken in round numbers, the pear being 2 lbs.  $1\frac{1}{2}$  ozs. and the apple 3 lbs. 1 oz.

centres of gravity of the larger and smaller trees, what weight of foliage, stem, and branches the taller stem could support with safety under natural conditions. Thus :—

$$\text{Estimated weight of larger pear tree} = 2 \times \frac{25}{196} \times \frac{482}{0.037} = 3000 \text{ lbs. (appr.)}$$

$$\text{Estimated weight of larger apple tree} = 3 \times \frac{28}{210} \times \frac{0.1625}{0.092} = 7000 \text{ lbs. (appr.)}$$

$$\text{Estimated weight of larger plum tree} = 2\frac{1}{4} \times \frac{16}{42} \times \frac{9.5}{0.0625} = 130 \text{ lbs. (appr.)}$$

The stems of the older trees are therefore from five to ten times stronger than is necessary.\* This is also shown by the fact that the sound main trunk of an ordinary tree never snaps under wind pressure, and that stems completely hollowed out at their bases, but not above, may remain erect for 100 years or more. Hence the continued formation of new wood is not so much for mechanical requirements, as in order to maintain good channels for the conveyance of water, that is, channels which contain active living elements. The general rule may, in fact, be formulated, that the more rapid the growth of an erect tree, the more slender will be its stem in regard to its height, and that slowly-growing trees will have relatively bulky stems. This is strikingly shown in the Tropics by palms, by such trees as *Albizzia*, etc., and by bamboos. The stem of the giant bamboo may attain a height of 60 metres, while not more than 40 centims. diameter near its base, which dimensions are not far short of the theoretical limits. All these facts afford strong indirect evidence towards the necessity of the presence of active living elements in the conducting wood of tall trees, but, of course, leaves it an open question as to whether these living elements exercise a direct pumping action.

#### *Section 20.—Critical Velocity for Stream-line Flow in Wood Vessels.*

POISEUILLE'S formula for the flow of liquid through tubes only applies when the motion takes place in straight lines. If the speed is high the motion becomes turbulent, and the resistance increases as a power of the speed, rising to 1.8 or 2.

\* A point of some interest in this connection lies in the fact that the modulus of elasticity varies much less than the breaking strain in different woods, and even in the wood of the poplar, the same is shown, though to a less degree. Thus :—

	Pine.	Beech.	Maple.	Poplar.	Birch.	Oak.
E in kilogrammes per square millimetre . . . . .	1113	980	1021	517	917	921
Breaking strain in grammes . . . . .	4180	3570	2710	1480	4300	5660

The modulus of elasticity depends mainly upon the properties of the walls of the wood-fibres, which are relatively constant, whereas the breaking strain depends largely upon the structure of the wood as a whole, which varies to a much greater extent.

OSBORNE REYNOLDS has shown that steady motion cannot exist if the mean velocity is greater than

$$\frac{1000\eta}{\rho a}, \text{ where } \eta = \text{coefficient of viscosity of liquid,}$$

$\rho$  = its density, and  $a$  radius of tube.

Hence, in a vessel of 1 millim. diameter, the critical velocity would be

$$\frac{1000 \times 0.01}{0.05} = 200 \text{ centims. per second.}$$

In tubes of less diameter the critical velocity would be still higher, whereas, in plants under normal conditions, it is rarely more than 0.2 centim. per hour, and is always slower in narrow vessels than in broad ones. Hence the rate of flow in plants is always considerably below the critical velocity, so that the resistance is directly proportional to the speed.

#### Section 21.—The JAMIN'S Chain Hypothesis.

A JAMIN'S tube is a fine tube containing alternately air-bubbles and water columns, as in the vessels of a transpiring stem. In such a tube, when no flow exists, a small pressure would support a considerable height of water, the height depending on the narrowness of the tube. This has no direct bearing whatever on the ascent of water in trees, since, as soon as any flow begins, the conditions change. Suppose the tube contains water columns, AB, CD, EF, with air-bubbles, BC, DE, etc., between. Then, if pressure is applied at A sufficient to produce flow, the surface-tension film at A will be more convex than that at B, that at C than that at D, and so on. Hence, the pressure applied at A is partly antagonised by the difference of pressure between A and B, so that each water column transmits successively less pressure to the next air-bubble, and so on along the tube. The difference of pressure depends upon the difference in convexity between successive pairs of films, which again depends upon the rate of flow through the tube, and upon the diameter of the tube. Hence, if the tube is narrow and long, and the air-bubbles numerous, it may require pressure of several atmospheres to produce an appreciable flow along the tube.

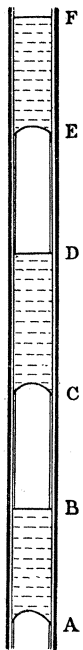


Fig. 3.

Suppose that a vessel ran from end to end of a tree 10 metres high, and that the radius of the vessel was 0.0025 centim., while it was occupied alternately by a millimetre of air and a millimetre of water along its length. Then there would be 5000 bubbles along the vessel. Suppose the lower side of each bubble to be hemispherical with the concavity downwards, the upper side flat. Then the pressure exercised by each bubble against an upward flow would be  $152/0.0025$  dynes, which, in the case of 5000 bubbles, amounts to a total pressure of



approximately 300 atmospheres. In a vertical tube the bubbles would tend to ascend, and hence maintain an upward movement, but this applies more to the air than to the water, and the effect is relatively small in a narrow tube. In the vessels, however, the bubbles are approximately stationary, and are unable to pass through the transverse partitions. The work done in this case in merely raising a definite amount of water against the action of gravity is the same, whether it passes through a JAMIN'S tube or through one of the same height filled with water. The total work done, and also the pressure required to maintain the same rate of flow, are both greater in the JAMIN'S tube than in a similar capillary tube completely filled with water.

*Section 22.—The Influence of Changes of Surface-tension in a JAMIN'S Chain.*

Any agency which will appropriately modify the difference of pressure between the surface-tension films at A and B, or which will reverse it, will favour or produce an upward flow in the tube. A rise of temperature lowers the surface-tension. Suppose the ascending stream is gradually warmed from 0° C. to 20° C., then the difference of surface-tension between the points A and B will be slightly lowered along the tube, and the flow will be accelerated. If the temperature falls in the ascending stream, the resistance to flow will be increased. The total effect is, however, very small within moderate ranges of temperature. Thus, suppose the temperature rose from 0° C. to 20° C. during the ascent, then, if  $T_t$  is the surface-tension at  $T^\circ$  C., and  $T_0$  the surface-tension at 0° C.,

$$\begin{aligned} T_t &= T_0 - \beta t, \text{ where } \beta \text{ is a constant (0.152 for water)} \\ &= 75.8 - 0.152 \times 20 = 72.8 \text{ dynes.} \end{aligned}$$

Suppose the full change of temperature is completed in passing a single air-bubble of 0.004 centim. diameter. Then the excess of pressure in the air-bubble over the hydrostatic pressure outside  $= \frac{2T}{r} = \frac{2 \times 72.8}{0.002} = 72,800$  dynes. Hence the pressure would correspond to 74 centims. of water at 20° C., and 77 centims. of water at 0° C.

A difference of pressure of 3 centims. of water is a negligible factor in a tall tree.

*The presence of substances in solution* influences the surface-tension. Thus DORSEY\* has shown that the surface-tension of solutions containing per litre the molecular equivalents in grammes are higher at the same temperature than that of water by 1.53 (NaCl), 1.71 (KCl), 2.0 ( $\frac{1}{2}\text{Na}_2\text{CO}_3$ ), 1.77 ( $\frac{1}{2}\text{K}_2\text{CO}_3$ ). An increasing concentration in the upward stream would therefore have the effect of retarding the flow through vessels containing air-bubbles. The concentration of the sap occurs, however, mainly in the leaves, and not in the wood vessels, and, furthermore, the total effect could never amount to more than a few centimetres pressure of water.

\* DORSEY, 'Phil. Mag.,' 44, 1897, p. 369.

If, however, the plant had any means of maintaining differences of surface-tension at intervals along the current, a very powerful propulsive mechanism could be generated. Suppose the cells *e* and *d* in fig. 4 were exuding soluble materials, and that these were being absorbed by *c*, slightly transformed and re-exuded at 3 and 10, the cell *b* carrying on the same process at 11 and 12. The net result would be that the surface-tensions at 1, 3, 6, 8, 10, and 12, would be greater than those at 2, 4, 7, 9, 11, and 13 respectively.

In narrow vessels with frequent air-bubbles arranged appropriately in regard to the medullary rays, pressures of a few centimetres of water per centimetre length of

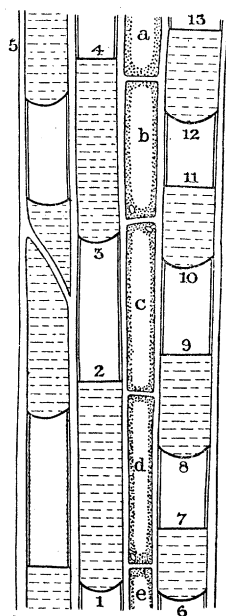


Fig. 4.—Diagram of wood-vessels with air and water columns and a medullary ray.

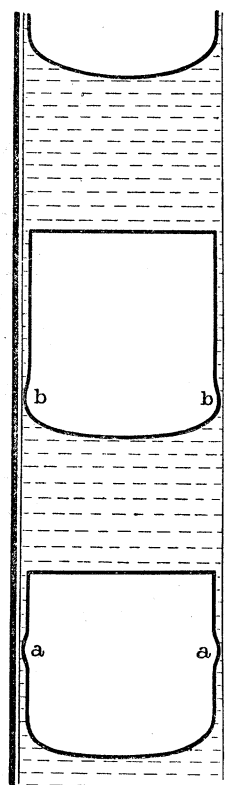


Fig. 5.—Diagram of air-bubbles in a vessel.

the vessel could easily be generated in this way. In an open tube this would produce a flow of the entire contents along the tube, but even in the closed vessels of the wood where the water flows past the bubbles, lateral exudation might aid in the transference of water. Thus, suppose the surface-tension film 3 rose, pushing water out from 4 into 5. Then when the film 3 came opposite the cell *b*, its surface-tension would be lowered, and the water column would fall only to be refilled from columns below, which were in the first phase of action. As soon as the film 3 is opposite *c*, its surface-tension will be again raised and the column once more lifted.

Furthermore, water might be driven past the air-bubbles while these remain

stationary. Thus, suppose that waves of decreased surface-tension passed upwards along the sides of the air-bubbles (fig. 5), while the surface-tension on the underside increased sufficiently to keep the bubbles stationary. Then bulgings would be produced, as at *bb* and *aa*,\* and these travelling upwards would push water in front of them and raise it from column to column in the chain. Yet another possible action is this, that if the surface-tension at 3 increases, the film stretching from 3 to 2 on the inside of the vessel, will be drawn upwards and with it water, which can be held up permanently at the higher level by a slight increase in the convexity of the film 3.

Attempts to demonstrate actions of this character in the wood were not particularly successful. Thus, strips of living wood containing a few vessels, were laid on a slide crossed by transverse bars of vaseline. Between these were placed alternating water and saline solutions, increasing in strength towards one end. Slight movements of the air-bubbles do occur when the fibre is moved, so that one end of an air-bubble is brought alternately nearer to a saline solution than to water, and then further away. In addition, a flow of (coloured) water takes place along the vessel towards the region of increasing concentration, but it is apparently independent of any action of the air-bubbles, and is probably the direct result of the unavoidable osmotic action. The water is able to pass the air-bubbles when these are stationary, a fact which has already been observed by STRASBURGER in the tracheides of Conifers.†

In addition, observations were made upon living wood *in situ* by the following means. A block of wood was chiselled out from a tree (pear, apple and elm), leaving intact a strip of the superficial wood on one side. The inner side of this was smoothed, a glass slide applied to it and sealed round the edges with wax. The moistened outer side was now shaved down with a sharp razor until transparent, and from one to two vessels thick. A cover slip was at once attached by a rim of soft wax, and the rest of the wood covered with wet cotton-wool. The preparation was illuminated by a mirror placed on the inner side, and viewed through a knee-bend microscope, the base of which was fixed against the trunk of the tree. I was not, however, able to satisfy myself of the existence of any definite relationship between the size and relative positions of the air-bubbles in the vessels and the medullary rays. In all cases, however, the vessels even of the youngest wood contain air-bubbles, at least in summer time, and when the tree is actively transpiring, these bubbles are often 2 or 3 millims. in length, while the water columns are usually from a little over

\* Professor POYNTING doubts the existence of the bulges at *aa* and *bb* for more than an instant, and considers that a weaker part of the surface film would be drawn over the whole surface almost instantly. If the movement took place towards the upper side of the bubble, the water would in this case also tend to be drawn upwards. A periodic lowering of surface-tension at the lower side of the bubble would in this case need to alternate with a periodic raising of surface-tension to the original level, over the general surface of the bubble. The author hopes, in a subsequent paper, to return to the discussion of what is at present merely a tentative hypothesis.

† 'Leitungsbahnen,' pp. 704, 709. SCHWENDENER ("Zur Kritik."—'sitz. K. Preuss. Akad.,' 1892, p. 935) denies the physical possibility of this phenomenon, but on what grounds it is difficult to say.

a millimetre to a small fraction of a millimetre in length. These values correspond fairly well with those obtained by SCHWENDENER,\* namely, water columns 0.1–0.5 millim. long, air-bubbles up to 1 millim. long.†

In spite of the lack of direct proof, it is difficult to avoid the conclusion, that if any vital pumping action is actually exercised in the wood, it can only be of the above character. Furthermore, it is difficult to see how the ascent of water could be produced in any other way in a tree 150 metres high, in which the total pressure required to produce an average rate of flow might amount to 100 atmospheres. The leaf-cells are unable to produce any osmotic suction at all approaching this, nor are suspended water columns able to transmit it. Thus, OSBORNE REYNOLDS gives the breaking strain of a water column free from air as 72.5 lbs. per square inch, or nearly 5 atmospheres, and although DIXON and JOLY‡ have shown that the presence of dissolved air does not lower the breaking strain, the moment even a small air-bubble appears it will expand either until it fills the vessel, or until its pressure is some small fraction of an atmosphere, and the tension transmitted beyond it will fall correspondingly.

The maximum negative pressure observed in the trunk of a transpiring tree is usually stated to be one atmosphere, and in transpiring branches to be less than half an atmosphere.§ By this is simply meant however, that in the first case, the pressure is zero and in the second half an atmosphere less than that of the atmosphere. In fact no negative tension can exist in the vessels, so long as large bubbles of air are present.

*Section 23.—The Influence of Surface-tension upon the Pressure of Air in the Vessels.*

A stationary bubble of air will have approximately the same pressure inside it, whether spherical or cylindrical with hemispherical ends. If the bubble is 0.005 centim. diameter, the excess of pressure in it over the hydrostatic pressure outside will be  $\frac{2T}{r} = \frac{2 \times 73}{0.025}$  dynes or 59 centims. of water at 20° C. ( $\frac{1}{18}$ th of an atmosphere).

This surface-tension pressure will aid in preventing the expansion of the bubbles.

\* SCHWENDENER, 'Sitzungsb. d. Berl. Akad.,' 1886, vol. 34, p. 567; 1893, vol. 40, p. 842.

† STRASBURGER, 'Leitungsbahnen,' p. 683, finds that the first year's wood of Conifers is usually almost entirely free from air in the tracheides, whereas even in the youngest vessels of the wood of Dicotyledons a certain amount of air is present, and that this rapidly increases in vessels which have been functioning for some time. The shortness of the tracheides of Conifers, and the slowness of the flow of water through them, are probably responsible for the delay in the appearance of air in them. Data in regard to the condition of the wood of *Sequoia gigantea* would be of the utmost interest in this connection.

‡ 'Phil. Trans.,' B, 1895, p. 568.

§ For literature, see PFEFFER'S 'Physiology,' Eng. trans., vol. 1, p. 211.

If the diameter of the air-bubble were 0·001 centim., the surface-tension pressure inside it would be  $\frac{1}{3}$  of an atmosphere, so that the pressure outside might be zero, while that in the bubble was  $\frac{1}{3}$  of an atmosphere.

A point of still greater importance is, that this pressure will tend to prevent the formation of air-bubbles in a liquid under stress, unless they have some nucleus around which they can form. Thus, suppose sufficient molecules of gas come together to form a bubble of  $10^{-5}$  centim. diameter at atmospheric pressure. Then the surface-tension pressure inside the bubble will be approximately 15 atmospheres. Hence, a liquid might be under a tension of 14 atmospheres, and yet contain air-bubbles of  $10^{-5}$  centim. diameter under a positive pressure of one atmosphere. Such a condition would not be stable however, since any coalescence of the bubbles would result in their rapid expansion coincidently with a rapid fall of the surface-tension pressure acting on them.

#### *Section 24.—The Osmotic Pressure in Leaves Transpiring at Different Levels.*

If in tall trees the upward pull of water was mainly or entirely due to the suction exerted by the transpiring leaves, then we should expect to find differences in the osmotic pressure of the leaves at different levels corresponding to the various degrees of suction required. Accordingly, leaves were taken in the afternoons of bright sunny days from different levels on trees, at once placed in corked bottles, and examined for the osmotic pressure in the leaf-cells by sectionising and placing in solutions of salt, potassium nitrate, and grape-sugar of increasing strength, until incipient plasmolysis was noticed.

Preliminary experiments made with the leaves of the apple, pear, and elm, showed that the osmotic concentration in the leaf-cells reaches unexpectedly high values at the close of a day's active transpiration and assimilation, often 6 per cent., and in some cases 8, or even 10 per cent., solutions of  $\text{KNO}_3$  (10 grammes per 100 cub. centims. of solution) being required to produce incipient plasmolysis. The highest pressure previously observed (in the beetroot, and in the developing medullary ray cells of *Pinus sylvestris*)\* was equivalent to about 6 per cent.  $\text{KNO}_3$ , or 21 atmospheres. In addition, the osmotic concentration in the different cells of the same leaf may vary by 1 or 2 per cent. of  $\text{KNO}_3$ , i.e., by 3·5 to 7 atmospheres under the above conditions. At first sight it may not seem clear how the osmotic pressure may be different in neighbouring, or even contiguous cells, and yet all of them exercise the same suction upon the water in the vessels. The plasmatic membranes are, however, impermeable to the osmotic materials in the cell-sap. These draw in water with forces equivalent to the concentration. This force of suction is partly antagonised by the stress up to 1, or perhaps 2, atmospheres, exerted upon the water in the wood vessels. The remaining force of suction maintains the hydrostatic pressure in the cell, which acts against the cell-wall. Hence, all the leaf-cells exert the same

\* DE VRIES, 'Pringsh. Jahrb.,' vol. 14, p. 527; WIELER, *ibid.*, vol. 18, p. 82.

upward pull, which will be that of the cell with the lowest osmotic concentration, while the different cell-walls will be distended by dissimilar internal pressures, some being more stretched than others.

The leaf-cells being small can easily withstand the high pressures which may act on them, although relatively thin-walled. Curiously enough, the osmotic concentration in the palisade parenchyma-cells appears to be usually distinctly higher, being often over 1 per cent.  $\text{KNO}_3$  more than that in the more actively transpiring spongy mesophyll cells, at least, at the close of a bright sunny day. In the early morning the osmotic concentration appears to be more uniform, and is distinctly lower all round.

Test experiments were performed in the same way as the above with an elm 18 metres high, the selected levels from which the leaves were taken being 250 centims. and 1350 centims. above ground. This difference of level in water is equivalent to a head of an atmosphere, and, with the normal rate of flow, a difference of pressure of from 4 to 8 atmospheres would be required according to previous calculations for this portion of the stem. The lowest concentration required to produce incipient plasmolysis in any leaf-cell was noted in each case, *i.e.*, the lowest concentration at each level. The maximal difference observed was equivalent to 3 per cent. of grape-sugar (18 and 15 per cent.), but the usual difference was below 2 per cent. ( $2\frac{1}{4}$  atmospheres). Although these values are not as high as would be required by DIXON and JOLY's theory, the fact that they do exist, and appear to be fairly permanent, is of considerable interest, even although they may be in the first instance merely due to the more rapid assimilation in the more exposed leaves at the higher level. The plant itself, however, can vary the osmotic concentration of the sap in case of need, and can, if necessary, produce the required concentration in a non-assimilating cell as well as in an assimilating one.

As far as these observations go, however, they do appear to indicate that, although the leaves may exert suction approaching 1 or 2 atmospheres, actions go on in the trunk itself which raise the water upwards, and maintain it in a mobile condition, ready to flow to any region where even a small suction is exercised upon it. Full and satisfactory proof will, however, only be obtained by observations made upon trees of 50 or more metres height, and having healthy leaves near their bases as well as at their apices. It is worthy of note that, if a pressure of 100 atmospheres is required to pull water up a tree 150 metres high, this would need a concentration of 144 per cent. of cane-sugar, 30 per cent. of grape-sugar, or 28 per cent. of  $\text{KNO}_3$ , without taking into account the amounts required to maintain the turgidity of the cell, and prevent it from collapsing. These are altogether impossible concentrations, which no known plant protoplast can produce or maintain within itself.

*Section 25.—The Evidence against the Existence of any Surface-tension Pumping Action may be grouped under the following heads.*

(1) The rapid rate of diffusion of dissolved solids required through the medullary ray cells, and the powers of selective absorption and re-excretion needed by them.

(2) The fact that this action is no longer possible in vessels completely filled with water, and that hardly any plants immediately exhibit bleeding if the stem is cut when transpiration is active.

(3) The fact that when water is driven through under pressure, the flow is most rapid through those vessels which are completely filled with water.

(4) The fact that the flow of water through short lengths of stem under pressure or suction is always less than would be expected from a viscosity calculation, and not greater, as might be expected if any pumping action were at work.

(5) The fact that, *ceteris paribus*, the flow is as rapid up a stem as down it.

(6) The fact that STRASBURGER\* has found that long lengths of stem (often 12 metres) remain capable of conducting sufficient water to keep the upper parts fresh for several days after the stem has been killed by heat or poison, and that the conductivity may be temporarily restored by injection with water.

With regard to this last objection, the mere fact that the trunk and branches of a tree when saturated, may contain sufficient available water for a few days to two or three weeks' average transpiration, suffices to show that STRASBURGER's experiments have by no means the finality usually ascribed to them. Further, there is no disputing the fact that the leaves may exercise an osmotic suction upon the water in the vessels, which will be proportional to the difference of concentration in the two cases, less the minimum amount required to maintain turgidity in the leaf (over three atmospheres). Owing to the high breaking strain of water, a tension of five atmospheres can be transmitted through the vessels as long as they contain no bubbles larger than 0.00005 centim. diameter (surface-tension pressure =  $5\frac{1}{2}$  atmospheres). This would theoretically suffice to raise water to a height of 180 feet, but in the wood of a tree, owing to the internal friction which has to be overcome, and owing to the rapid appearance of large bubbles in actively functioning vessels, less than one-third of this force would be available for raising the water, even when the rate of flow was slow. As a matter of fact, we have seen that the greatest differences between the minimal osmotic pressures of leaves at different levels, approximated to two atmospheres. The temporary restoration of the conductivity of dead wood by injection with water, is partly the result of providing supplies of water close at hand, and is partly due to the removal of air enabling the osmotic suction of the transpiring leaves to be transmitted further down the stem, and also lessening the resistance to flow. As bubbles appear in the vessels, the conductivity is rapidly lost

\* STRASBURGER, 'Bau u. Verricht. der Leitungsbahnen,' 1891, p. 1645; 'Ueber das Saftsteigen,' 1893, p. 11. Similar results had been previously obtained by BÖHM and HARTIG.

in the absence of any surface-tension pumping action in the wood. To prove conclusively that no pumping action is exerted in the wood, it will be necessary to kill at least 100 feet of an upright actively transpiring stem, and the leaves above should remain fresh and turgid for more than three weeks. The other objections may be taken in the order given.

*Section 26.—The Rate of Diffusion in the Wood-parenchyma.*

The diffusion of liquids or of dissolved solids is usually regarded as an extremely slow process, and in PFEFFER'S 'Physiology' (vol. 1, p. 125 of Eng. Ed.) the idea is given that the rate of diffusion in a plant cell is too slow to be of much avail for the transference of soluble materials in the absence of streaming or mixing movements. Thus, it is stated, that by diffusion alone, it requires a period of 319 days to transfer a milligramme of salt from a 10-per-cent. solution through a distance of one metre of water, and unfortunately this impression is strengthened in the English Edition by the conversion of metre into millimetre (m. into mm.). In any case, either statement might be correct, since the amount transferred depends also upon the area through which the transference takes place, which is not given.

If diffusion is slow, then the wood-parenchyma cells would hardly be capable of so rapid a transference of dissolved material as is required by the foregoing theory. As a matter of fact, diffusion in small plant cells is not slow, but extremely rapid. Suppose a broad tube, a metre long, to be half filled with a strong solution of copper sulphate, and then filled up with water without mixing, it would take more than 10 years before a cubic centimetre at any point of the tube contained approximately the same amount of copper sulphate. The time required is, however, proportional to the square of the length of the tube, so that if the latter were 1 centim. long, not more than 10 hours would be required, while in a plant cell 0·01 centim. long, only 0·001 of an hour or 3·6 seconds are necessary. This is less than half the time required for the protoplasm to rotate once round such a cell, whereas in large cells like those of *Chara* and *Nitella*, the protoplasm could pass round the cell from 10 to 200 times during the time required for the complete diffusion of copper sulphate.

Each substance has its own specific rate of diffusion, which increases with rise of temperature and of concentration, though not proportionately. Under similar conditions, the time required for the diffusion of sugar is  $\frac{2}{5}$ ths, and for sodium chloride  $\frac{1}{3}$ th, that for copper sulphate, while diffusion occurs almost as rapidly through a colloid like protoplasm as through pure water. In small cells therefore, like those of the medullary rays, diffusion is rapid enough for all requirements, and furthermore, the diffusion of a dissolved solid or gas through a liquid is accelerated towards any point where it is continually removed or converted into some other substance, whether insoluble (sugar or glycerine into starch), or soluble (cane-sugar into grape-sugar or oxalic acid), since in this way a steep gradient of concentration of the primary diffusing substance is maintained.



A simple mode of showing how rapid the diffusion across short distances can be, is to pour melted 5- or 10-per-cent. gelatine, containing a trace of phenolphthalëin and of free alkali into a long glass cylinder, and after the gelatine has set, pouring on top dilute sulphuric acid of 3 N strength (147 grammes per litre) kept in gentle motion. The penetration of the acid is shown by the decolorisation of the gelatine.

Distances decolorised in millimetres.	Times in minutes.	Expected times from previous reading if $T \propto D^2$ .
1	2.5	—
2	6.5	10
3	12	14.5
4	17	21.3
10	85	106.2
14	150	166.6
31	1420	730
35	1865	1800

The chemical fixation makes the neutralisation progress at first more rapidly than in the case of pure diffusion, but, at a distance of 30 millims. below the surface of the gelatine, the amounts of acid reaching the neutral zone are so small as to be in part counterbalanced by the amounts of the extremely dilute alkali diffusing up from the zones beneath. Hence the neutral zone progresses downwards more slowly than would be expected.\*

*Section 27.—The Absence of Bleeding from Actively Transpiring Plants, and the Rapid Flow through Vessels filled with Sap, in which no Surface-tension Action of the kind described is possible.*

The absence of bleeding from transpiring plants is often only temporary, and is then due to the suction exercised by the leaves, for it is not until the negative pressure is converted into a positive one that the air drawn into the vessels can be driven out again by the ascending water. If the pumping action in the stem is only feeble, and the supply of water limited, the suction of the remaining leaves may prevent any positive pressure from being produced, or may delay it until the cut ends of the vessels become partially or completely blocked.

Furthermore, it is quite possible that the potential pumping action might only be

\* If neutral gelatine containing phenolphthalëin is dissolved in decinormal alkali, and an equal quantity of decinormal acid gelatine be poured above after setting, the neutralisation zone will only progress downwards if the acid diffuses more rapidly than the alkali. In this way it can easily be shown, for instance, that the rates of diffusion of HCl,  $\frac{1}{2}\text{H}_2\text{SO}_4$ , NaHO, and  $\frac{1}{2}\text{Na}_2\text{CO}_3$  solutions descend in the order named.

called into play when needed, that is, when the air in the vessels becomes considerably rarefied, and when the water columns become very short, or acquire a definite size in relation to that of the wood-parenchyma cells. Indeed, the power of pumping might conceivably only be developed in the later layers of wood formed on the older stems of tall trees, and in this way the danger of bleeding from cut branches would be avoided, since the last portion of the journey would only be performed, at least when transpiration was active, under the suction exercised by the leaves. The necessity of this suction at once explains how in drought trees can throw off portions of their leaves. Those leaves are usually thrown off which, from their position and condition, transpire most actively, and in which, therefore, so great osmotic suction is required that the concentration of the sap reaches limits which are either injurious, or which excite abscission.

PITRA\* has, however, shown that the leafy branches of trees (oak, etc.), if immersed under water, may show an exudation of sap from the cut end above water, and presumably the air in the vessels is, after a time, largely removed, so that no surface-tension action is possible. There is, however, a possible physical explanation, which may also apply, to some extent, to the generation of root-pressure. Suppose all the parenchyma cells of the leaf (or root) have absorbed water until fully turgid, and the whole of the osmotic pressure is acting against the cell-wall. If any sugar is excreted into the vessels by the wood-parenchyma cells, as is often the case, this will draw in water from outside through the surrounding turgid parenchyma as readily as if cells filled with pure water under no pressure at all intervened. This might continue until the sap in the vessels was raised to as much as 20 feet, if it contained 1 per cent. of cane-sugar or 0.2 per cent. of  $\text{KNO}_3$ . Further than this, if the medullary ray cells at the higher points absorbed the sugar from the vessels, and converted it into starch, a power which is often exercised, the sap escaping might be extremely dilute, though exuded under a pressure of an atmosphere, as is actually the case with the cut stems of vines. Hence a considerable pressure of exudation might be excited even when the escaping sap was very dilute, and when the vessels were filled with water, and the root-pressure may, indeed, be capable of supporting 10 to 20 feet of water.

Direct observations were made upon the terminal branches of tall trees, to determine whether these actually exhibited the power of bleeding at considerable heights when the vessels were more or less filled with sap. Manometer tubes, with the distal end bent downwards to avoid the entry of rain, were attached to the cut ends of terminal branches in March, and observed until the expansion of the foliage. In all cases the results were negative, except that a few drops of moisture appeared to condense within the tubes, especially in the case of the yew and oak. The trees

\* For lit., see PFEFFER'S 'Physiology,' vol. 1, p. 254, Eng. trans. KRAUS and WIELER have confirmed PITRA'S results, but I have repeatedly obtained negative results with branches of *Pinus sylvestris*. Possibly the pumping action is not always shown.

used, and the elevations of the branches were : elm, 36 feet ; yew, 32 feet ; apple, 26 feet ; walnut, 22 feet ; oak, 44 feet ; pear, 28 feet.

It is difficult to conceive of any way in which living cells can exert any direct continuous pumping action by an active exudation of water, although several theories have been propounded. Changes of osmotic pressure will simply cause to-and-fro movements of water. Alterations of permeability, although they can affect the rate of flow through particular cells, are unable to generate any propulsive force, except in so far as they may produce changes of osmotic concentration, and, although these may produce slight to-and-fro movements of water until a condition of turgid equilibrium is reached, they cannot continually propel it in a definite direction. With regard to one-sided filtration under pressure, it is only natural that, if water is forced into a permeable cell at one side, it should escape by filtration through the others, but this is of no aid in explaining how the forces required for the ascent of water in tall trees are generated.

*Section 28.—The more Rapid Flow through Vessels Completely Filled with Sap when Subjected to Pressure.*

This is the direct result of the removal of the JAMIN'S chain from the vessels with its high resistance to flow. The fact that even then the flow is always slower than it should be from a viscosity calculation, may be ascribed to the effect of the irregularities in the interior of the walls of the wood-vessels, and of the presence of more or less transverse partitions. These factors, together with the change of conductivity always shown in cut stems, would effectually disguise the existence of a pumping action aiding in the onward flow, for this would be relatively feeble in a short length of stem. The same applies to the fact that flow is possible down a stem as well as up it, while the experiments which showed that the resistance to acropetal flow was practically the same as to basipetal flow in horizontal stems under similar conditions, have only been performed on short isolated lengths of terminal branches.

Definite proof that a pumping action exercised by the wood-parenchyma is largely or mainly responsible for the ascent of water in trees, will only be obtained by experimenting with trunks at least 60 feet in height. The stems of tall tropical lianas, or of the giant bamboo, would afford material which could easily be handled. If it were found that water could be made to rise in an erect cut stem at rates approaching that of the normal transpiration current, by a suction less than the head of water due to the height of the tree, then we should have the required proof, for the presence of air in the vessels instead of accelerating the flow retards it, in the absence of any surface-tension actions favouring upward flow. Finally, if it were possible to fill all the vessels in an erect stem over 200 feet in length with water, and an ascent of sap was found to take place as usual, we should have positive evidence of the exercise of a direct pumping action by the wood-parenchyma cells as distinguished from their suggested surface-tension action.

29.—*Summary.*

The flow of water through open vessels filled with sap takes place in accordance with POISEUILLE'S formula for the flow through rigid tubes, divergences being due to the presence of irregular internal thickenings in the vessels.

Hence, the velocity of flow is directly proportional to the pressure and to the square of the radius of the tube, inversely proportional to the length of the tube and to the viscosity of the liquid. Large vessels, therefore, offer very much less resistance to flow than more abundant narrow ones, having the same total internal area of cross-section, and since viscosity is largely dependent upon temperature, the latter forms an important factor in regulating the flow, the viscosity and resistance falling with a rise of temperature.

With an average rate of flow, the total resistance due to the viscosity of the water flowing through the vessels, is always less, and in climbing plants with large vessels is considerably less than a head of water equal in height to the stem. The vessels of actively transpiring plants always contain air-bubbles, and these introduce a resistance to flow which is inversely proportional to the radius of the tube, and which becomes very great when the vessels are small and the air-bubbles numerous. Hence, in intact vessels containing air the rates of flow are proportional to a power of the radius lying between 1 and 2. The volume passing is proportional to a power of the radius lying between 2 and 4.

Estimations of the amount of flow made from the rate of flow and the diameter and number of the vessels, showed that the actual flow in the wood of Dicotyledons takes place almost entirely through the vessels. In young stems saturated with water, a considerable flow takes place under pressure through the pith, but practically none in intact transpiring stems. In a cut stem, apart from the blocking at the cut surfaces, a gradual diminution of conductivity occurs along the entire length after water has been passed through for some time. This appears in part, at least, to be due to the development of bacteria in the vessels, but may be aided by swelling or other changes in the walls of the vessels.

The length of the vessels in the woods examined, averages from 7 to 36 centims., the tracheides of the yew being from 0·2 to 0·5 centim. in length. The resistance to transverse flow through the wood is from 300 to 45,000 times greater than to longitudinal flow, the resistance to filtration under pressure, through a single partition wall, being from 2 to 10 times greater than that to the flow through the entire length of a vessel in the wood of the crab apple.

The total resistance to flow in the erect stems of actively transpiring plants appears to correspond to a head of water of from 6 to 33 (shrubs and small trees), or from 5 to 7 (large trees) times the height of a plant. Hence, in the tallest trees, the total pressures required to maintain active transpiration may be equivalent to as much as 100 atmospheres. No leaf could produce or maintain an

osmotic suction of this intensity, and, in the presence of large air-bubbles in the vessels, the strain transmitted in them from the leaves could never be as great as an atmosphere. If, however, the air-bubbles were exceedingly minute, they might be under a small positive pressure, while the water outside was under a maximal strain of 5 atmospheres. This would suffice to overcome the resistance offered during active transpiration by 30 to 80 feet of stem. The maximal osmotic suction exercised by the leaves, as determined by comparing the osmotic pressures during active transpiration of the leaves at the top and bottom of an elm 18 metres high appears to be from 2 to 3 atmospheres, and is usually less than this. At the same time, the total resistance to flow in the trunk of this tree might reach from 10 to 12 atmospheres.

It appears, therefore, that to maintain flow, a pumping action of some kind or other must be exercised in the wood, for which the presence of active living cells is essential. In support of this, it has been shown that the production of wood in a slowly-growing tree is greater than is necessitated by mechanical requirements. In other words, the production of new wood is determined largely by the length of time during which the wood-parenchyma can remain active.

There is no known means by which these cells can directly pump water in a definite direction, although the existence of a power of absorbing and exuding water under pressure has been proved in the living wood of cut branches. It is suggested that the wood-parenchyma cells, by the excretion and re-absorption of dissolved materials, may bring into play surface-tension forces within the vessels of sufficient aggregate intensity to maintain a steady upward flow, and to keep the water of the JAMIN's chains in the vessel in a mobile condition, ready to flow to wherever suction is exercised. The rapid rates of diffusion required for such action do actually exist in the wood-parenchyma cells.

It appears that the terminal branches of trees at heights of from 22 to 44 feet above ground exhibit little or no power of bleeding in spring. Possibly in such trees the pumping action is only used or developed in the wood of the older stems, or is only exercised when transpiration is active, and the water columns in the vessel attain a definite size relatively to the wood-parenchyma cells. The importance of the JAMIN's chain in the vessels is that it renders a staircase pumping action possible, and enables the water to be maintained in them in a labile condition, ready to flow to any point where moderate suction is exercised. This pumping action being a diffuse, and probably regulated action, need not produce any high pressure of exudation at the terminal branches of tall trees, which, in fact, appears always to be absent at high levels.

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