REPORT

OF A DISCUSSION ON THE ASCENT OF WATER IN TREES

*Held in Section K at the Meeting of the British Association,
Liverpool, September 18, 1896.*

MR. FRANCIS DARWIN read the following paper :—

WITHIN the last few years the problem of the ascent of water has entered on a new stage of existence. The researches which have led to this new development are of such weight and extent that they might alone occupy our time. It will be necessary therefore to avoid, as far as possible, going into ancient history. But it will conduce to clearness to recall some of the main stepping-stones in the progress of the subject.

The two questions to be considered are :—(1) What is the path of the ascending water? (2) What are the forces which produce the rise.

I. The first question has gone through curious vicissitudes. The majority of earlier writers assumed that the water travelled in the vessels. This was not, however, a uniform view. Caesalpinus, 1583, seems¹ to have thought that water moved by imbibition in the 'nerves.' Malpighi and Ray held that the vessels serve for air, and the wood-fibres for the ascent of water. Hales², who believed in the 'sap-vessels' as conduits, speculated on the passage upwards of water between the wood and the bark. Also³, that water may travel as vapour, not in the liquid state. In the present century Treviranus⁴, 1835, held that water travelled in vessels; De Candolle, 1832, that the intercellular spaces were the conduits. In Balfour's Manual of Botany, 1863, vessels, cells, and intercellular spaces are spoken of as transmitting the ascending water.

The change in botanical opinion was introduced by the great

¹ Sachs' Hist. of Bot. (English Trans.), p. 451.

² Vegetable Staticks, p. 130.

³ Loc. cit., p. 19.

⁴ Sachs' History.

authority of Sachs¹, who took up Unger's view² that the transpiration current travels in the thickness of the walls as water of imbibition.

Then followed the reaction against the imbibitionists—a reaction which has maintained its position up to the present time. Boehm, who had never adopted the imbibition theory, must have the credit of initiating this change; his style was confused and his argument marred by many faults, but the reaction should in fairness be considered as a conversion to his views, as far as the path of the travelling water is concerned. Nevertheless, it was the work of others who principally forced the change on botanists—e. g. von Höhnelt³, Elfving⁴, Russow⁵, R. Hartig⁶, Vesque⁷, Godlewski⁸, and others.

II. The second question has a curious history, and one that is not particularly creditable to botanists generally. It has been characterized by loose reasoning, vagueness as to physical laws, and a general tendency to avoid the problem, and to scramble round it in a mist of *vis à tergo*, *capillarity*, *Jamin chains*, *osmosis*, and *barometric pressure*.

An exception to this accusation (to which I personally plead guilty) is to be found in Sachs' imbibition theory, in which, at any rate, the barometric errors were avoided, though it has difficulties of its own, as Elfving has pointed out.

But the most hopeful change in botanical speculation began with those naturalists who, concluding that no purely physical causes could account for the facts, invoked the help of the living elements in the wood. To Westermaier⁹ and Godlewski¹⁰ is due the credit of this notable advance, for whether future research uphold or destroy their conclusions, it claims our sympathy as a serious facing of the problem by an ingenious and rational hypothesis¹¹.

¹ *Physiol. Végétale* (French Trans.), 1868, p. 235, and more fully in the *Lehrbuch*. Sachs also partially entertained Quincke's well-known suggestion of movement of a film of water on the surface of vessels.

² *Sitz. k.k. Akad. Wien*, 1868. Dixon and Joly's paper in the *Annals of Botany*, September, 1895, gives evidence in favour of a certain amount of movement of the imbibed water.

³ *Pringsheim's Jahrb.*, xii, 1879.

⁴ *Bot. Zeitung*, 1882.

⁵ *Bot. Centr.*, xiii, 1883.

⁶ 'Ueber die Vertheilung,' &c., *Untersuchungen aus dem Forst. Bot. Inst. zu München*, ii and iii.

⁷ *Ann. Sc. Nat.*, xv. p. 5, 1883.

⁸ *Pringsheim's Jahrb.*, xv, 1884.

⁹ *Deutsch. Bot. Ges.*, Bd. i, 1883, p. 371. ¹⁰ *Pringsheim's Jahrb.*, xv, 1884.

¹¹ It is of interest to note that Hales, in speaking of the pressure which he found to exist in bleeding trees, says: 'This force is not from the root only, but must also proceed from some power in the stem and branches.' *Veg. Statics*, 1727, p. 110.

We may pass over the cloud which arose to witness for and against these theories, and proceed at once to Strasburger's great work¹, in which, with wonderful courage and with the industry of genius, he set himself to work out the problem *de novo*, both anatomically and physiologically. In my opinion it is difficult to praise too highly this great effort of Strasburger's.

Strasburger's general conclusion is now well known. He convinced himself that liquid can be raised to heights greater than that of the barometric column, in cut stems, in which the living elements have been killed. Therefore, the cause of the rise could not be (1) barometric pressure, (2) nor root pressure, (3) nor could it be due to the action of the living elements of the wood. His conclusions may be stated as follows:—

(a) The ascent of water is not dependent on living elements, but is a purely physical phenomenon.

(b) None of the physical explanations hitherto made are sufficient to account for the facts.

Strasburger has been most unjustly depreciated, because his book ends in this confession of ignorance. I do not share such a view. I think to establish such distinct, though negative, conclusions would be, in this most nebulous of subjects, an advance of great value. Whether he has established these conclusions must of course be a matter of opinion. To discuss them both would be to go over 500 pages of Strasburger's book, and will not here be attempted. Conclusion (a) that the ascent is not dependent on living elements must, however briefly, be discussed, because it is here that the roads divide. If we agree with Strasburger, we know that we must seek along the physical line; if we differ from him, we are bound to seek for the missing evidence of the action of the living elements.

Schwendener's Criticism.—Perhaps the best plan will be to consider the most serious criticism that has been published of Strasburger's work, namely, Schwendener's paper 'Zur Kritik' &c.²

Schwendener objects that although a continuous column of water cannot be raised by air pressure to a greater height than that of the barometric column, yet when broken into a number of columns, as in the case of a Jamin chain, that a column considerably over 10 m., even as much as 13 or 14 m., of water can be suspended. This, though

¹ Leitungsbahnen, 1891.

² K. Preuss. Akad. 1892, p. 911.

not fatal to Strasburger's conclusions, is no doubt a serious criticism. For if 13 m. can be supported, some of Strasburger's experiments are inconclusive. He finds that a branch can suck up a poisonous fluid to over 10 m., and, as above explained, argues that all ascent above that height, not being due to barometric pressure or to the living elements (since the wood is poisoned), is for the present inexplicable. But, if Schwendener is right, the effect above 10 m. may have been due to atmospheric pressure. Askenasy (loc. cit. infra, 1895, p. 6) objects to Schwendener that the supposed action cannot be continuous. By repeating the diminution of air pressure at the upper end, the movement of water becomes less and less, and sinks to almost nothing. Askenasy adds, moreover, that the amount of water which could be raised according to Schwendener's theory would be very small.

One difficulty about Schwendener's theory is that the result depends on the length of the elements of which the chain is made up (such element being a water-column, *plus* an air-bubble). In his paper, 'Ueber das Saftsteigen¹,' he finds that the elements of the chain in *Fagus* equal in round numbers 0.5 mm. In his paper², 'Wasserbewegung in der Jamin'schen Kette,' he finds the element in *Acer pseudo-platanus* = 0.9 mm., in *Acer platanoides* and *Ulmus effusa* = 0.2. But the calculation (1892, p. 934) is based on the existence of a chain in which the water-columns are each 10 mm. in length, a condition of things which he allows does not occur in living trees.

But even if we allow Schwendener to prove theoretically the possibility of a Jamin chain being raised to a height much greater than that of a barometric column, I do not think he invalidates Strasburger's position. Schwendener's idea necessitates the travelling of a Jamin chain as a whole, i.e. the translation not only of water, but of air-bubbles. But this cannot (as Strasburger points out) apply to his experiments on Conifers, in which the movement of air to such an extent is impossible³. And for the case of dicotyledonous woods, Strasburger has shown that the movement of air is excluded by the fact that transverse walls occur in the vessels at comparatively short distances. In *Aristolochia* the sections may be as long as 3 m., but in ordinary woods according to Adler⁴ we get: *Alnus* 6 cm.; *Corylus*,

¹ K. Preuss. Akad., 1886, p. 561.

² K. Preuss. Akad. Sitz., 1893, p. 842.

³ 'Ueber das Saftsteigen,' Hist. Beiträge, v. 1893, p. 50.

⁴ As quoted by Strasburger.

11 cm.; *Betula*, 12 cm.; *Quercus*, 57 cm.; *Robinia*, 69 cm. These facts seem impossible to reconcile with Schwendener's views.

Action of the Poisonous Fluids in Strasburger's Experiments.—The question whether the living elements are killed in Strasburger's experiments is of primary importance in the problem.

Schwendener does not criticize it at length; he seems to assume¹—as far as I can understand—that since the death of the tissues extends gradually from the cut end upwards, there are living cells in the upper part which may still be effective. He also doubts 'whether the cells were always killed at once.' The first objection of Schwendener's may or may not be sound, but in any case it does not (as Strasburger points out) account for the experiment² in which an oak stem was poisoned by picric acid, and three days afterwards was placed in fuchsin-picric. The second reagent had to travel in tissues already killed with picric acid, yet a height of 22 m. was reached.

The question whether the reagents kill the cells in Strasburger's experiments does not lend itself to discussion. It is difficult to see how they should escape, and we have Strasburger's direct statement that the living tissues were visibly killed. It must not be forgotten that in some of his experiments the death of the tissues was produced by prolonged boiling, not by poisons³. Thus the lower 12 m. of a *Wistaria* stem were killed in this way, yet liquid was sucked up to a height of 108 cm. In the *Histolog. Beitr.* v. p. 64, he has repeated his air-pump experiment, using a boiled Yew branch, and found that eosin was sucked up from a vessel in which almost complete vacuum was established, so that the action of living elements and of atmospheric pressure was excluded.

On the whole, the balance of evidence is, in my judgment, against the belief that the living elements are necessary for the rise of water. In other words, I think we should be justified, from Strasburger's work, in seeking the cause of ascent in the action of purely physical laws.

Strasburger's general argument from the structure of wood.—It seems sometimes to be forgotten that, apart from the physiological or experimental evidence, there is another line of argument founded on the structure of wood. Strasburger's unrivalled knowledge allows him to

¹ Zur Kritik, loc. cit., 1892, p. 935.

² Hist. Beitr. v. p. 12.

³ Leitungsbahnen, p. 646.

use this argument with authority, and he seems to me to use it with effect. Thus¹ he points out that though in coniferous wood the action of the living elements in pumping water is conceivable, yet this is far from being universally the case. He points out that in the Monocotyledons such theories meet with almost unconquerable difficulties. This is, he says, especially the case in *Dracaena*. He goes on to point to difficulties in the case of such Dicotyledons as *Albizzia*. The case may perhaps best be put in the generalized manner that Strasburger himself employs². If the living elements are of such importance as Godlewski, Westermaier, and Schwendener hold, we ought not to find these difficulties; we ought rather to find structural peculiarities pointing distinctly to the existence of such functions. For instance, we ought to find the tracheal water-path actually interrupted by living elements, which might act like a series of pumping stations one above the other. It should, however, be remembered that if we deny the importance of the medullary rays and other living elements in raising water, we ought to be able to point more clearly than we can at present to the function of the medullary rays and to structural adaptations to these functions.

The work of Dixon and Joly and that of Askenasy.—I now pass on to recent papers in which Strasburger's indications to search along a purely physical line have been followed. In 1894 Messrs. Dixon and Joly³ first enunciated an entirely new theory, depending upon the quality which water possesses of resisting tensile stress. To most botanists the existence of this quality is a new idea. To believe that columns of water should hang in the tracheals like solid bodies, and should, like them, transmit downwards the pull exerted on them at their upper ends by the transpiring leaves, is to some of us equivalent to believing in ropes of sand. Meanwhile Askenasy had independently hit on a similar theory which was published⁴ after the appearance of Messrs. Dixon and Joly's research.

Askenasy has earned the gratitude of his botanical readers by giving some of the evidence which demonstrates the existence of this property of water⁵. A tube a metre in length was filled by Donny with water,

¹ Hist. Beitr. v. p. 17.

² Loc. cit., p. 20.

³ Proc. Roy. Soc., Vol. lvii, No. 340 (1894). Also Annals of Bot., Vol. viii; Phil. Trans., Vol. 186, 1895 (B).

⁴ Verhand. a. d. naturhist. med. Vereins Heidelberg, N. F., Bd. v, 1895; and N. F., Bd. v, 1896.

⁵ He gives references to Donny, Poggendorff's Annalen, 67. Bd. (143. Bd. d. g. R.)

and the remaining space was as far as possible freed from air. When the tube was placed vertically, the water-column at the upper end hung there, and could not be made to break or free itself from the glass by violent shaking. Berthelot filled a thick-wall capillary tube completely with water at 28° – 30° C.; it was allowed to cool to 18° , so that the space left by the shrinking of water was filled with air. It was then sealed up and again warmed to 28° – 30° , so that the air was dissolved in the water. When it was allowed to cool again it retained its volume, filling the tube completely. A slight shake, however, allowed the water to break and return to its proper volume at 18° with the appearance of a bubble of air. In this experiment the water contained air, yet it seems to have been until recently assumed by some physicists that to show cohesion, water must be air-free. If this were the case, the application of the principle to plants would be impossible. Dixon and Joly have, however, proved that this is not so, and this forms an important part of their contribution to the subject.

They also¹ investigated the amount of tension which water under these circumstances will bear, and found it about equal to seven atmospheres. If, therefore, the leaves at the top of a tall tree can exert the requisite upward pull on the water in the trunk, it seems certain (if no other conditions in the problem interfere) that the pull can be transmitted to the level of the ground. This opens up the question whether the leaves can exert this traction on the water in the tracheals, and what is equally important, Are there any factors in the problem incompatible with the theory?

1. *The sucking force of the leaves.*—In Dixon and Joly's first paper² they assume that tractional force is given by the meniscuses 'formed in the membranous *réseau* of the evaporating cell-walls,' as well as possibly by the osmotic action of the cells of the mesophyll. We shall take these theories in order. Our knowledge of the cell-wall does not allow us to believe in the existence of pores visible with even the highest powers of the microscope. Dixon's more general expression³, 'surface tension forces developed in the substance of the

1846, p. 562; Berthelot, *Annales de Chimie et de Physique*, S. 3, t. 30, 1850, p. 232; Worthington, *Proc. Roy. Soc.*, Vol. 1., 1892, p. 423.

¹ *Phil. Trans.*, Vol. 186, p. 570. With ethyl alcohol Worthington records a tension of 17 atmospheres. See *Proc. R. Soc.*, Vol. 1.

² *Phil. Trans.*, pp. 563, 567.

³ *Proc. Roy. Irish Acad.*, Jan. 13, 1896, p. 767.

walls of the evaporating cells,' is therefore preferable. But Askenasy seems to me to put the matter more conveniently by using the term 'imbibition¹.' The force with which vegetable membranes, e. g. the thallus of *Laminaria*, absorb water, has been demonstrated by Reinke and others, and the existence of such a force is familiar to botanists.

Both Askenasy (*loc. cit.*) and Dixon and Joly² have pointed out that the force of imbibition, or the surface tension forces, as the case may be, can exert a tractional effect on the water in the tracheals, when the turgescence of the mesophyll has been destroyed. But Askenasy in his original paper (1895), Dixon in the January 1896 paper, and again Askenasy in his second paper (March, 1896) have also considered the imbibitional or surface tension forces in connexion with the turgescent cell. In his 1896 paper Dixon in fact gives up the view published in the *Phil. Trans.* and adopts the view given by Askenasy in his original paper, that the tractional force is supplied by the osmotic suck of the leaves. It must clearly be understood that this does not remove imbibition from the problem. It is one of the chief merits of Askenasy's work that he clearly sees and states the important relation between these forces³. The sun's heat causes the evaporation of the water with which the walls of the mesophyll cells are imbibed; this water is replaced by imbibition from the cell-sap. The concentration of the cell-sap so produced maintains the osmotic force of the cell, which again exerts suction on the water on the tracheals⁴.

I have now given, in its simplest form, the modern theory of the rise of water. Apart from the main idea, it combines the points of several familiar views. Imbibition becomes a factor of paramount importance, though not in the way that Sachs employs it. The suspended threads of water remind us of Elfving's capillary theory, while the living-element factor is represented by the turgescent mesophyll cells.

Resistance.—It is not possible to discuss the question whether the tractional forces in the leaf are sufficient for the work imposed on them until we know what is the resistance to the passage of water through wood. For it is clear that the work done by the leaf includes

¹ *Loc. cit.*, 1895, p. 10.

² *Annals of Bot.*, Sept. 1895.

³ Askenasy, 1895, p. 11.

⁴ Sachs' Text Book, edit. iv, Eng. Tr., p. 679, describes evaporation taking place in the cell-wall, which makes good the loss by imbibition.

not only the lifting of a given column, but the overcoming of the resistance to its flow.

The resistance to the flow of the transpiration-current is in want of further investigation. Janse¹ has discussed the question, and points out (loc. cit. p. 36) that two kinds of resistance must be reckoned with. The first (which he calls statical) is illustrated by means of a cylinder of *Pinus* wood fixed to the short arm of a J-tube filled with water, when it was found that in five days the level of water in the long arm was only one mm. above that in the short arm². That is to say, when time enough is given, the resistance is practically nothing. Janse has also investigated the resistance to the passage of water flowing through wood at the rate of an ordinary transpiration-current. His method seems to me open to criticism, but this is not the place to give my reasons. His experiments give a wide range of results. With *Pinus Strobus* a pressure of water equal to ten times the length of the wood was required to force water through at a pace equal to the transpiration-current. In *Ginkgo* the pressure was twenty-one times the length of the wood. Strasburger³ has repeated Janse's experiment, and finds a column 'several times the length of the object' necessary. Nägeli⁴ found that 760 mm. of mercury were needed to force water through fresh coniferous wood at the rate of $\frac{1}{21}$ mm. per second, i.e. at 180 mm. per hour. If we allow one metre per hour as a fair transpiration rate⁵, we get a pressure of 5 atmospheres required to produce such a flow. To return to Janse's experiments: even if we assume that the resistance (expressed in water)=5 times the length, it is clear that with a tree 40 m. in height, the resistance of 20 atmospheres has to be overcome. This would not be a pressure greater than that which osmotic forces are able to exert, but when we come to a tree of 80 m. in height, and a resistance of 40 atmospheres, the thing becomes serious⁶. A great difficulty in the question of resistance is that the results hitherto obtained are (though here I speak doubtfully) much greater than those obtained by physicists for the resistance of water flowing in glass capillaries.

¹ Pringsheim's Jahrb., xviii. 1887, p. 1.

² Strasburger (Leitungsbahnen, p. 777) observed equilibrium established a good deal quicker.

³ Leitungsbahnen, p. 779.

⁴ Das Mikroskop, 2nd edit., p. 385.

⁵ Sachs, Arbeiten, ii. p. 182.

⁶ Schwendener's experiments, K. Preuss. Akad. 1886, p. 579, do not particularly bear on this question.

Until this discrepancy is explained, it is rash to argue from our present basis of knowledge ¹.

Is the osmotic suck sufficient?—The osmotic force of a turgescent cell is usually measured by its power of producing hydrostatic pressure within the cell. Thus, De Vries ² investigated the force necessary to extend a plasmolyzed shoot to its original length; Westermaier ³ the weight necessary to crush a tissue of given area; Pfeffer ⁴ the pressure exerted by growing roots; Krabbe ⁵ the pressure under which cambium is capable of maintaining its growth.

The figures obtained by these naturalists have a wide range; it may be said that the hydrostatic pressure varies between 3 and 20 atmospheres.

Another method is to ascertain the osmotic strength of the cell-sap in terms of a KNO_3 solution, and calculate the pressure which such a solution can produce. According to Pfeffer ⁶, 1 per cent. KNO_3 with artificial membrane gives a pressure of 176 c.m. = 2.3 atmospheres. De Vries ⁷ calculates that in a cell, a 0.1 equivalent solution (practically = 1 per cent.) gives a pressure of 3 atmospheres. We may therefore take it as between 2.5 and 3 atmospheres. Now, De Vries found that beetroot requires 6–7 per cent. KNO_3 to plasmolyze it; this would mean 15–21 atmospheres. I do not know what is the greatest pressure which has been estimated in this way. Probably Wieler's ⁸ estimate of the pressure in the developing medullary ray cells of *Pinus sylvestris* at 21 atmospheres is the highest. It is clear that investigation of the osmotic capacity of leaves for high trees is wanted, also investigations of the variation in osmotic power produced by varying resistances in the flow of the current. The experiments of Pfeffer and others ⁹ show that the osmotic strength of cell-sap is capable of great adaptation to circumstances—cells respond by

¹ It is possible that the rate of the ascending water is much less than is usually assumed. Thus Schwendener (K. Preuss. Akad. 1886, p. 584) calculates from an observation of v. Höhnelt that the transpiration-current in the stem of a tall beech was only two metres per day.

² Untersuchungen über d. mechanischen Ursachen der Zellstreckung, 1877, p. 118.

³ Deutsch. Bot. Ges. 1883, p. 382.

⁴ Abh. k. Sächs. Ges. 1893.

⁵ K. Akad. Berlin (Abhandlungen), pp. 57, 69, 1884.

⁶ Pfeffer, Phys. i. p. 53.

⁷ Pringsh. Jahrb. xiv. p. 527.

⁸ Pringsh. Jahrb. xviii. p. 82.

⁹ Pfeffer, Abhandl. der k. Sächs. Ges. xx. p. 300; Eschenhagen, Untersuchungen aus d. Bot. Inst. z. Tübingen, 1889; Stange, Bot. Zeit. 1892.

increased turgescence to various stimuli. Whether they can respond sufficiently to account for the ascent of water is another question.

My own opinion is that the question of resistance to the flow of water is a difficulty which the authors of the modern theory have not sufficiently met. Unless it can be shown that the resistance to the flow of water in wood is less than that indicated by existing researches, we must face the fact that we do not at present know of osmotic forces which we can suppose capable of raising water to a greater height than 40 metres.

Continuity of the water in the tracheals.—The theory we are considering apparently requires that there shall be continuous columns of water from leaf to root, because a break in the column means a collapse of the machinery. This seems at first sight a fair assumption, though I doubt its complete correctness. It is in any case worthy of discussion. It has been constantly insisted on by Sachs and others that at the time of most active transpiration the vessels contain air, and not water. It is therefore a violent disturbance of our current views to believe in continuous columns of water.

For evidence on this point we are chiefly indebted to Strasburger. It is a remarkable fact that he should, without any theory to encourage such a view, have come to the conclusion that approximate continuity of water columns is a condition of primary importance, and that he should have made out the cognate fact that the whole of the *alburnum* need not be simultaneously occupied by a transpiration-current; parts of it may be so occupied, while parts of it are filled with air, and do not function as waterways. This is a valuable contribution to knowledge, and to the adherents of the new theory it is priceless; the very existence of their hypothesis may depend on it.

Strasburger's statements and reasoning are by no means accepted by every one; for instance, Schwendener refuses to take them seriously¹.

Strasburger has microscopically examined the condition of the tracheals as regards air². He found in the Spruce Fir in July 'almost no air bubbles' in the wood of the current year, but air in considerable

¹ K. Preuss. Akad., 1891, p. 931.

² Leitungsbahnen, p. 683 et seq.; Russow in 1882 (Bot. Centr., Vol. xiii. 1883) observed similar facts in the distribution of water and air.

quantity in four-year-old wood. In the same month *Pinus Salzmanni* (*Laricio*) showed scattered bubbles in the spring wood of last year, and more in the autumn wood. In a Larch there were only very occasional bubbles in the two last years' wood. In the Silver Fir the current year's wood was practically free from air: the air increased in the inner rings. *Tsuga canadensis* had no air in this year's wood, only a little in last year's, and an increasing quantity in the older rings, the fifth being very rich in air. In February, *Pinus Strobus* had hardly any air in this year's wood, and the Silver Fir was all but free from it in the youngest ring. *Robinia* in July had the youngest wood almost air-free. *Ficus elastica* and *spuria*, various *Acacias*, and willows gave vessels not entirely free from air, but nearly so. He concludes¹ that the path of the transpiration-current is not absolutely free from air. The younger wood, which especially functions as the water-carrier, is the most free.

Dixon and Joly quote Strasburger's results, which they consider sufficiently favourable to their views. They rely, in addition, on the impermeability of wet cell-walls to air isolating the conduits in which air has appeared; and on the possibility that the air may be redissolved under root pressure², an idea well worth testing.

I think Strasburger's facts are not so favourable to their theory as these authors believe; in the same way it seems to me that Askenasy is rash in saying³ that the tracheals in many cases contain continuous columns of water. It is true that this statement does not affect the validity of his general argument, since he faces the undoubted occurrence of air bubbles in many cases. This is undoubtedly necessary, and fortunately we can once more turn to the Leitungsbahnen. Strasburger states that he has seen water creep past the air-bubbles⁴ in coniferous tracheids. The best evidence for this seems to be the fact mentioned⁵ that the part of a single tracheid in front of an air bubble gets red with absorbed eosin, though the neighbouring tracheids are colourless. This clearly suggests the creeping round the bubble which Strasburger believes in. Schwendener⁶ has been unable to confirm Strasburger's microscopic observations, and moreover denies the physical possibility of the phenomena. I am unable to judge of the

¹ Loc. cit., p. 688.

² Phil. Trans., p. 572.

³ Verhand. naturhist. med. Vereins Heidelberg, 1895, p. 15.

⁴ Leitungsbahnen, pp. 704, 709. See also Hist. Beitr. v. p. 76.

⁵ Ibid., p. 79.

⁶ Zur Kritik, &c., p. 921.

validity of Schwendener's theoretic objections, and must leave this point. It is a question of great importance whether it is possible that on the breaking of a column of water a film of water remains surrounding the air bubble, and capable of holding the two columns together. If this is impossible, we must suspend our judgment until we know more of the contents of the tracheals.

To sum up this part of the subject, we may believe that the tracheals in their youngest condition may contain water in continuous columns, since the cambium cells from which they arise certainly contain fluid. But we know also that this condition is not absolutely maintained, since Strasburger has shown that the young wood contains air, though in small quantity. We must therefore believe either (1) that the transpiration-current is able to travel past the air bubbles, or (2) that tracheals partly filled with air may again become continuous waterways by solution of the air. If we adopt the first alternative, we must believe that the film of water between the bubble and the wall of the vessel is able to bear such a tensile stress that it can serve to link the column above with the column below the bubble. But this is analogous to trusting a rope so nearly cut through that only a few threads remain intact. With regard to the second alternative, we have at least indications from Strasburger's work that a tracheal, partly filled with air, does not necessarily remain permanently functionless (see *Leitungsbahnen*, p. 692).

The isolation of the tracheal.—There are a number of points connected with the structure and properties of wood which ought to be considered in relation to the modern theories. Want of space forbids my doing more than referring to two of them.

The resistance which the wetted cell-wall offers to the passage of undissolved air is a point on which many writers have laid stress. It is clear that on any theory of the movement of water in the tracheals it is essential that air should not filter into the waterway. This necessity is not, however, stronger in the case of the modern theories we are considering. The pressure tending to fill the tracheals with air from outside cannot be greater than atmospheric pressure, and since the wetted cell-walls of gymnospermous wood can resist the passage of air under a pressure of about an atmosphere¹, we need not fear criticism of the theory on this ground. The above remarks

¹ *Leitungsbahnen*, p. 722. Nägeli and Schwendener, *Das Mikroskop*, 2nd edit., p. 367, give 225 cm. of mercury.

seem, however, to be needed in face of the frequently recurring statement that wetwood membranes are impermeable to free air. Schwendener has some good remarks on this head¹.

Strasburger has called attention to the important subject of the localization or isolation of vessels or of certain lines of tracheids. When this is possible we may have one set of tracheals containing continuous water-columns, while neighbouring ones contain air at negative pressure². This is especially important in connexion with the theory of Dixon and Joly and of Askenasy, since, if there were no such isolation, a functioning tracheal containing a continuous column of water would give up its water to one which was not functioning. In other words, the inactive tracheals would, by negative pressure, suck water from the active ones. In the coniferous trees the young wood is cut off by the absence of pits in the tangential walls³ from free communication with the older wood, where air is more frequent.

In the same way the valve-like closure of the pits by the aspiration of the pit membrane comes to be a subject of much importance.

At present I merely wish to show by a couple of examples the necessity of a complete study of the minute structure of wood in relation to the modern theories. It is at least a hopeful fact for the authors of these views that we cannot point to anything in the anatomy of wood which is absolutely inconsistent with their views. Finally, with regard to the question at large: Whether we are friends or opponents of the new theory, the broad facts remain that water has the power of resisting tensile stress, and that this fact must henceforth be a factor in the problem. There are difficulties in the way of our authors' theory, but it is especially deserving of notice that many of these difficulties are equally serious in the case of any theory which excludes the help of the living elements of the wood, and assumes a flow of water in the tracheals. The authors have not only suggested a *vera causa*, but have done so without multiplying difficulties. There is therefore a distinct balance in their favour.

Huxley, quoting from Goethe, makes use of the expression *thätige Skepsis*. It is a frame of mind highly appropriate to us in the present juncture if we interpret it to mean a state of doubt whose fruit is activity, and if we translate activity by experiment.

¹ Zur Kritik, p. 943.

² See Histolog. Beiträge, v. p. 87.

³ Strasburger discusses, in this connexion, the existence of tangential pits in the autumnal wood: see Leitungsbahnen, p. 713.

PROFESSOR VINES said :—

It must, I think, have come as a surprise to many of the general public here present, that we are not yet in possession of a coherent theory as to the mode in which water is conveyed to the leaves from the roots of trees. It is almost incredible that though this problem has been the subject of research for more than a century, it still remains, as Mr. Darwin has pointed out, without its solution. But after the admirable account of the history of the subject to which we have been listening, there is no occasion for me to say anything about the past. My object in taking part in this discussion is to give some account of observations which I have been recently making, in the endeavour to carry the subject a step further onwards.

The particular feature of the problem which seemed to me to specially call for investigation is what is termed the *suction-force* of branches. I may explain what I mean by *suction-force* by referring to an experiment which has, I feel sure, been performed by every one in this room. When a gathered flower is placed in a glass of water, it sucks up a certain amount of the liquid; and it does so with a certain force, as can be proved by appropriate means: this force is the suction-force of the flower. Many have already measured the suction-force of various branches, &c., but it does not appear to me to have been done so systematically as to afford any important body of evidence on the subject. With this end in view, I have devised an apparatus¹ which combines simplicity with sensitiveness. I may briefly describe it as a system of tubes, partly glass, partly thick india-rubber pressure-tubing, completely filled with water, connected airtight on the one hand with the branch under experiment, and on the other with a Bourdon's vacuum-gauge: the readings on the dial of the gauge are in inches of mercury, and indicate the suction-force exerted by the branch. I thought at first that I had succeeded in devising an apparatus which possessed the special advantage that it indicated suction-force without the intervention of atmospheric pressure, and that therefore my results were different in kind from those of previous observers. I am glad to have this opportunity of distinctly stating that I was mistaken in this conclusion: as a matter of fact, the atmospheric pressure does contribute to the readings given on the dial. I was misled by the fact that the readings of the gauge are due to the withdrawal of very small quantities of water; so small,

¹ Described and figured in *Annals of Botany*, Vol. x, No. 39, September, 1896.

that I was led to believe that the branch did not absorb any water at all from the apparatus, but merely exerted a tensile stress upon it.

I am not now going to inflict upon you an account of the observations which I have already published; I will merely state the conclusions to which they led. I was struck with the relatively high degree of suction-force which can be developed by a branch after its leaves have been removed; and this led to the consideration that it is important to investigate the suction-force of stems quite independently of the leaves in the first instance. I cannot but think that hitherto the problem has been obscured, rather than otherwise, by introducing considerations based on the action, real or supposed, of the leaves in the development of the suction-force of branches. I would urge that it is of primary importance to study the stem, and to ascertain what it is capable of effecting by itself.

In the second place, I was struck with a fact upon which Mr. Darwin has laid stress, namely that the suction-force of a branch is not essentially dependent upon the life of the branch. I found that if a branch be killed by the injection of sulphate of copper, it still can develop a very considerable suction-force. Now in a branch thus injected, the normal conditions of osmosis must be altogether upset, and yet water reaches the evaporating surface: hence osmosis does not appear to be an essential condition to the conduction.

I now pass on to observations which I have since made. The logical outcome of the preceding considerations was to institute observations on dead leafless branches. For this purpose I used dead hazel-branches (which had served in the garden as pea-sticks during the summer); branches, that is, which, if I may so say, had died a natural death. I found that, in order to make satisfactory experiments with these sticks, it is necessary to previously inject them with water, and to cover all exposed cut surfaces with melted paraffin. In illustration of the results attained, I may mention that the best result was a suction-force of $19\frac{1}{2}$ inches of mercury developed by a piece of stick 18 inches long. This establishes the fact that a very considerable suction-force is developed by a branch independently of leaves or of life; and this is a fact which demands complete investigation. The problem of the travelling of the transpiration-current is here presented in its simplest form. We have a small piece of dead branch, without leaves, without osmosis, developing a force which would probably suffice to raise a column of water to a height

of about twenty feet. The problem is a purely physical—as distinguished from a physiological—one. What are the physical forces active in this stick? When we thoroughly understand the physics of a piece of dead stick, it will be easy to explain the physiology of the transpiration-current in a living tree—but not till then.

The suction-force developed by pieces of stick is very variable, and I must admit that I have not yet succeeded so far as to be able to control or account for the variations which I have observed. In illustration I may cite the following experiments made with different lengths of the same piece of stick, the duration of the experiments being nearly equal:—

Stick=36 in. long:	max. suction-force=16½ in.:	duration=28 hrs.
„ =18 „ :	„ „ =19½ „ :	„ =27 „
„ =9 „ :	„ „ =16½ „ :	„ =26½ „
„ =4½ „ :	„ „ =6½ „ :	„ =33 „

I am quite unable to explain these results; but no doubt they are susceptible of some simple physical explanation—the factor of resistance being taken into account—for which the data are not at present forthcoming.

It is a matter of congratulation to botanists that the question of the transpiration-current is again attracting the attention of physicists. The firstfruits of this renewed interest are already in our hands in the form of the papers published by Messrs. Dixon and Joly; and we shall have the privilege, as I understand, of hearing more about their work from one of the authors this morning. It is not my intention to attempt a criticism of the theory of the transpiration-current which they propound: but I would venture to say this, that the observations of which I have given you some account lead me to associate myself with Mr. Darwin in the opinion that these authors do not seem to attach sufficient importance to the part played by the imbibition-force of the cell-walls. Messrs. Dixon and Joly assert, indeed, that in the transpiring leaf the operative force is given by the menisci ‘formed in the membranous *réseau* of the evaporating cell-walls’; but surely if the physical properties of the cell-wall are of so much importance in these superficial cells, they must be equally important in the case of more deeply placed cells; for these too are receiving and giving up water like the superficial cells, though not by evaporation. Whilst

these observers prove that water can travel in the cell-walls of branches the wood of which has had its lumina injected with paraffin, their paper fails to suggest what relation, if any, this property of the cell-walls bears to the upward passage of water in the lumina under normal conditions. It seems to me that it may be fairly demanded of any proposed theory on this subject, that it should explain the relation between the characteristic physical properties of the walls of the wood-vessels and the passage of water through their lumina, more especially with reference to the question as to whether or not imbibed cell-wall may be regarded as maintaining continuity of liquid between, say, the upper and lower portions of a tracheide, the central portion of which is occupied by a bubble of air. However, it is to be hoped that some light will be thrown on this point in the course of Professor Joly's contribution to this discussion.

PROFESSOR JOLY read the following paper :—

I deem it necessary to preface any contribution which Mr. Dixon and I may make to this discussion by some remarks of the nature of claims to priority. Claims to priority are distasteful writing and distasteful reading, and I will hurry over them. I, at the same time, ask your indulgence as one acting under obligations which may not be shirked.

Our paper *On the Ascent of Sap*¹ was received by the Royal Society on October 16, 1894, and read November 15, 1894. It was written before the *Abstract*², which appeared November 15, 1894.

A considerable portion of our paper was excised by desire of the Publication Committee of the Royal Society; and after many delays it appeared in the *Philosophical Transactions* with the note 'Revised April 20, 1895,' at the head of it.

A restatement of the principal matter in the *Abstract* from the pen of Professor Askenasy³, appeared February 12, 1895; about four months after our complete paper was received by the Royal Society. Professor Askenasy's paper is prefaced by the remark that its publication was hastened by the appearance of our *Abstract*. The writer admits he had made no researches of his own upon the subject, and accounts for his inactivity by the statement that he had considered

¹ *Philosophical Transactions*, Vol. 186 (1895) B.

² *On the Ascent of Sap (Abstract)*, *Proc. R. S.*, Vol. lvii, No. 340, Jan. 1895.

³ *Ueber das Saftsteigen*, Heidelberg, 1895.

Strasburger's experiments to present sufficient data in themselves to solve the problem. I think it will presently be seen that in this view Professor Askenasy was mistaken; meanwhile I may remark that Professor Askenasy himself appears to have changed his opinion upon this point, as in his second paper¹ (April, 1896) he appears before us actively engaged upon experiments similar to, and having the same teaching as, some of our earlier ones.

The leading idea of our theory suggested itself to us at an early stage in our investigation. The following difficulties naturally presented themselves:—

(1) Is water containing air in solution and under such tension as must obtain in high trees (according to this hypothesis) stable?

(2) Will this stability also exist in presence of wetted wood?

(3) Is the leaf capable of exerting such a lifting force as will suffice to raise the column of water in high trees?

Of these questions, the first had previously only been quite inadequately considered, observers treating the presence of dissolved gas as detrimental to success in experiments on the behaviour of liquids in tension; the second, so far as I am aware, had never been previously considered, nor had the third received any attention. These questions are obviously inseparably connected with the admissibility of the theory, and admit of being answered only by experiment. Their consideration occupy a large part of our paper as published, and (over and above experimental work relating to the consideration of other hypotheses, most of which was excised from our paper) called for many months of careful investigation.

We, on our part, conceived of our theory quite originally, being unaware of any suggestion even remotely resembling our explanation of the cause of the ascent of sap in high trees. In this connexion I gladly repeat our expression of indebtedness to Professor Fitz-Gerald for many valuable suggestions in the course of our investigations.

Lest I be misunderstood I will state definitely that in this matter I have no cause of complaint whatever against Professor Askenasy. It is, indeed, only fair to quote his full acknowledgment. A few lines from his second paper will suffice:—‘As I have remarked in my first paper, Dixon and Joly are the first who have clearly recognized

¹ Beiträge zur Erklärung der Saftsteigens, Heidelberg, 1896.

and formulated the significance of the cohesion of water in the ascent of sap.'

A further matter for consideration suggested itself over and above those enumerated; a collateral question, it is true, but one nevertheless of great interest and importance:—What is the *nature* of the suction-force in the leaf?

Our earlier ideas led us to the view that capillary actions and the phenomena of evaporation were mainly concerned with the upholding and raising of the sap, as will be more fully gone into further on. I gather from Professor Askenasy's papers that, in so far as we regard capillary phenomena (or as he prefers to call them 'imbibition' phenomena) as upholding the sap, we were then in accord with his present views. He claims priority for these views, however, giving as his reason that they are not so definitely stated in our Abstract as in our full paper, and, perhaps misled by the term 'revised' occurring at the head of our complete paper, insinuates that we borrowed them, in their more pronounced statement, from his paper of February, 1895. (See pp. 19, 20, Beiträge zur Erklärung des Saftsteigens.)

This accusation is easily disposed of. I quote (translating) in full from Professor Askenasy's paper:—

'I come now to the imbibition of the cell-wall, the other¹ chief factor in the ascent of sap, from which the true (eigentliche) sucking action proceeds. The imbibition force of the cell-wall is in fact the so long vainly sought for source of the suction-force concerned in the ascent of sap in the plant. I believe myself to be the first to point out clearly the importance of imbibition in the ascent of sap, since Dixon and Joly speak of it in their first communication in a quite uncertain manner:—"Whether the draught upon the sap established at the leaf during transpiration be regarded as purely capillary or not, their experiments lead the authors to believe that it alone is adequate to effect the elevation by direct tension of the sap in tall trees."

'In the complete communication which appeared after my first work it runs for the first time thus:—"The meniscuses are formed in the membranous *réseau* of the evaporating cell-walls, while the columns of liquid supplying the evaporation loss exist in the functioning conduits."

It will be seen that the quotation from our complete paper is advanced

¹ Refers to the stability of a liquid in tension and containing gas in solution.

by Professor Askenasy as representing his views. I have here a type-written copy of our original manuscript, and the original is in the possession of the Royal Society and doubtless quite accessible. Reference to either will show that the sentence which Professor Askenasy quotes as representing his views on the matter occurs in our original manuscript, and was published from it without change of a syllable. The priority, for what is, at most, but a shade of meaning, is thus given away by his own decision.

After what I have quoted from Professor Askenasy as to imbibition-force of the cell-wall being 'the so long vainly sought for source of the suction-force concerned in the ascent of sap in the plant,' it will perhaps appear surprising that Mr. Darwin interprets Professor Askenasy as advancing the view 'that the tractional force is supplied by the osmotic suck of the leaves'; and, taking this view, dismisses Dixon's paper of 1896¹ as a reversion by Dixon to Professor Askenasy's views of 1895. The quotation from Professor Askenasy which I have given above is, indeed, from his second paper; but in his 1895 paper we find Professor Askenasy asking leave to modify a statement that osmotic forces are responsible, when he recalls how in dead trees the imbibition force alone can accomplish this, and proceeds to quote at a length of several pages experimental evidence in support of this view. Professor Askenasy does indeed refer to osmotic force as active in transferring the sap from the bundles into the cells of the leaf; but we ourselves, in our original paper, suggest as probable that this action occurs. In dwelling upon the great importance of osmotic pressure, Dixon advances alike beyond the views contained in our original paper and those put forth by Professor Askenasy. As will be seen presently, for the explanation of the active lifting forces in the leaf, we have not to go beyond our original statements that this is referable to the phenomena of evaporation in the leaf so far as our knowledge definitely extends².

¹ Note on the Rôle of Osmosis in Transpiration, Proc. Royal Irish Academy, January, 1896.

² 'Although osmotic actions may be concerned with the evaporative functions of the leaf, i. e. in the transference of water into the protoplasm-filled cells; still it is very probable that surface-tension forces developed upon the surfaces of walls coming in direct contact with air diffusion currents are responsible principally for the tensile forces displayed by the leaf. The fact that transpiration is not only accelerated by direct sunshine, but even more influenced by warm dry winds, supports the view that evolution of vapour at the leaf obeys the general laws

The nature of each phenomenon concerned must be clearly kept in mind with regard to whether it is of a static or of a kinetic nature ; whether merely a sustaining action or one actually giving rise to motion. It will tend to clearness to cite from Dixon's paper of 1896 (on the 'Rôle of Osmosis in Transpiration,' pp. 773-74) the model or system which he imagines as diagrammatically representing the rôle of osmosis in transpiration.

A porous pot rendered semi-permeable is attached, water-tight, to the upper extremity of a glass tube. Pot and tube are filled with water, and the lower end of the tube opens into a vessel of water. Above, a bladder or other semi-permeable membrane is supposed to inclose the porous pot loosely, the mouth being closed by a water-tight binding around the tube below the pot. We suppose an aqueous solution of potassium nitrate in the space between the bladder and pot. We call the region inside the pot A ; the space occupied by the osmotic solution B ; the external atmosphere C. The following actions I will now suppose to occur, and may be described as the teaching of the model :—

(1) If B is at first not quite filled with liquid, the osmotic attraction upon the water in A, or, according to recent views upon the nature of osmotic action, the osmotic pressure, will gradually suffice to quite fill it. Water will consequently ascend the tube. In this operation the membrane is at first loose and, of course, any force located in it is clearly unable to exert any independent lifting pull upon the water in A ; nevertheless water ascends. This is the case of the revival of a drooping leaf in which upon an adequate supply of water turgescence is re-established.

(2) The bladder becomes tense under increasing pressure in the space B.

I will assume now that a capillary or imbibition attraction of the membrane alone acts, and suffices to keep the external surface of the membrane moist. Evaporation now progresses upon the surface, and the current of water upwards in the tube is maintained. What

of evaporation from a moist surface' (Phil. Trans., Vol. 186 B, p. 567). The paragraph which follows refers to the 'sorting demon' nature of evaporation and the inflow of thermal energy at the evaporating surface in support of the view that to evaporation phenomena the elevation of the sap is to be ascribed. The same views are urged throughout the Abstract, and we admit that 'other physiological phenomena' may act (p. 5).

rôle does the imbibition or capillary attraction of the membrane play in this system? Once the steady state of supply and demand with regard to evaporation loss is established, it can play no *active* part. The attraction upon the water as much acts to retard evaporation as to elevate the sap. It is a purely static and undirected stress, and does no work. Without any more accurate knowledge of its physical nature than we at present possess we are safe in saying this much.

In this system, therefore, we have an osmotic pressure keeping the membrane tense and the cell filled with water (and we assume, for the present, doing no more); an imbibition force located in this membrane keeping the membrane permeated with water; and finally, on the boundary of the system evaporation progressing. Clearly in such a system the only kinetic action effective in actually lifting the water—in fact the only directed action—is that derived from the directed energy of those water molecules which escape from the evaporating surface or meniscuses; their loss being made good by molecular attractions and diffusion forces acting within the liquid. These are the actual lifting forces; the work done in lifting the water against gravity and viscous resistance being but small compared to the normal work of evaporation. The energy expended by the liquid is finally restored by the inflow of heat at the evaporating surface.

Again, from another point of view, the movement of water across the osmotic cell may be broadly referred to the difference of aqueous vapour pressure in the conduits and in the intercellular spaces.

Of the two static forces—osmosis and imbibition—how are we to single out one as especially *the* upholding force? We find osmotic pressure, indeed, in the drooping leaf actually playing an active part and functioning as a directed force. In the steady state we have not assumed it to do so any longer. Again, the imbibition force is located in a membrane owing its rigidity entirely, it may be said, to osmotic pressure. Are we justified in selecting the imbibition force as the long sought for source of the suction-force concerned in the elevation of the sap? I see no reason for doing so.

But this does not exhaust the question; a matter of much interest remains over. The actions enumerated above do not in point of fact suffice for the phenomena concerned with the ascent of sap in the living leaf. It happens that it is possible to test one of the static forces concerned independently of the other—that of imbibition independently of osmosis. If a leafless stick of some considerable length

is injected with water and left standing in a vertical position, the lower end dipping in water, it is found, after some time, to dry back from the upper cut surface. Here imbibition of the cell-wall shows itself inadequate to draw up water against gravity and the viscous resistance of the liquid. How then is it able to functionate in the leaf? Again, a cut branch fed with a liquid injurious to osmotic action shows, first, diminished transpiration, ending in complete drying up of the leaf. The same effect may be brought about by exposing the leaf to a temperature sufficient to kill the protoplasm: a 'damp heat' of 80° C. Lastly, we must consider that in some cases individual cells show themselves capable of effecting an actual extrusion of water by internal actions. The unicellular Fungus, *Mucor*, shows this in a marked degree. *Pilobolus* and *Phycomyces* may also be mentioned. The phenomenon of the extrusion of water by certain cells at the base of the petiole of the sensitive plant (*Mimosa pudica*), when responding to stimulation, is probably another case.

All this suggests that the actions progressing in the turgescient cells actually assist the extrusion of water. Indeed, we may go further and state more positively that the inadequacy of imbibition when unaided to maintain the moisture at the surface of the cell-wall on the one hand, and the evidence for the existence of extrusive forces in the turgescient cell on the other, at once forbid us to close the question as settled, and suggest where to look for the answer.

But what is the nature of the extrusive forces?

It would be a matter of profound interest if it turned out that 'vital' actions entered into this question. Or, if 'vital' processes in the primordial utricle are not responsible, can we refer the action to osmotic pressure alone? If we do so, we certainly find ourselves in the difficulty of ascribing to this force the opposite effects of securing the entrance of the sap into the cell against the tension in the conduits, and its subsequent expulsion through the cell-wall.

While this appears hardly admissible it is very certain that the osmotic pressure in the cell is effective in largely promoting the evaporation in so far as its action upon the flexible membrane results in the distension of this. This distension may amount to as much as from 10 per cent. to 20 per cent.¹ We may imagine the elastic shrinkage of the wall and its reduction in volume under the tensile

¹ Strasburger, Lehrbuch der Botanik, p. 138.

abstraction of water, when unsupported by osmotic pressure, to largely increase its resistance to the passage of water and at the same time diminish its effectiveness as an evaporating area, not only because of the diminution of this area, but also because of its increased fineness of grain and consequently increased capillary retentiveness. The stretching of the wall by the osmotic pressure, on the other hand, increases both its permeability and its evaporating effectiveness. This result of osmotic pressure in the cell permits us to regard this force as maintaining the water upon the outer surface of the turgescient cell against the elastic force of the cell-wall and the tensile pull of the sap. When the steady state is reached, it is however none the less a static force.

While something of what I have already said is, I hope, a contribution to this discussion, and over and above personal matter, I turn with pleasure to the unalloyed scientific interest of some points mentioned in Mr. Darwin's paper.

Mr. Darwin points out the want there is for observations on the osmotic pressure of the cells of leaves of high trees, in order to account for the high tractive forces required to elevate the water against gravity, and the viscous resistance of the ascending column of liquid. I am glad to say that Dixon has already done something towards supplying the want and is actively engaged in pushing the matter further.

In a paper of his read June 8, 1896, before the Royal Irish Academy, he gives an account of his preliminary researches. This paper is not yet published: I have the proof sheets here, however.

The mode of experimenting is already described in our full paper (pp. 564-66) and need not be re-described. The method is based on the assumption that a collapse of the leaf under a high external gaseous pressure will indicate the limit of the osmotic resistance of the turgescient cell; the water is then supposed to be forced back into the conduits and ejected from the cut end of the branch, which, from the nature of the arrangements, is not exposed to the high gaseous pressure.

In Dixon's experiments it is important to note, first, the pressure at which what we may call the *saturated* osmotic cell begins to eject water into the conduits; and secondly, the higher pressure at which the leaves begin to collapse and lose their turgescence.

Similarly to the manner described in our paper in the Philosophical Transactions, the first phenomenon is observed by observation, at

intervals of time and at different pressures, of the weight of a small phial of water surrounding the cut stem of a branch which, previous to experiment, has been left standing for some time in water.

The pressure first giving rise to the ejection of water under these circumstances assigns a limit to the functioning of the cell as one holding the maximum quantity of water which its voluminar distension admits.

The second phenomenon is observed directly in the curling up of the leaves, which roll slowly inwards from the edges and simultaneously droop upon the petiole. By relieving the pressure the leaf will in many cases recover its original form in the course of a few minutes. It may, in fact, be caused to curl up slowly and open out repeatedly like a Bourdon tube. The pressure giving rise to crumpling is that which assigns a limit to the ultimate tractive force of the cell and to its functioning as a healthy organ.

A striking fact is revealed in the course of these experiments:—The use of carbon dioxide as the agent for producing the pressure gives a markedly lower result than the use of air. In fact the limits of resistance fall to about one-third or one-fourth of their value.

In the case of *Cytisus Laburnum* a pressure of between 6 and 8 atmospheres of carbon dioxide will cause the crumpling of the older leaves, although the younger ones will still remain turgescient: in fact 16 atmospheres of carbon dioxide were attained without crumpling of the younger leaves being observed. First at 26.6 atmospheres of air the older leaves of *Cytisus* began to curl up. At 20 atmospheres of air the saturation limit of the osmotic force was reached.

In the case of *Tilia americana* a pressure of between 7 and 8 atmospheres of carbon dioxide gave slight collapse, while, according to Dixon's most recent experiments, a pressure of 20 atmospheres of air did not produce collapse. The saturation limit for this tree was reached, when carbon dioxide was used, at 4 atmospheres. With the use of air it was reached at 15 atmospheres upon a branch which had been already experimented with. A prior observation upon this branch gave no loss of water at 15 atmospheres of air.

In the case of *Helianthus multiflorus* 20 atmospheres of air produced collapse, the rolling up and flagging of the leaf being beautifully marked. At 13 atmospheres it held out. The osmotic limit of resistance may therefore be taken between 13 and 20 atmospheres in this plant.

The experiments are still in progress; but we have sufficient in these results to indicate an enormous potential osmotic tractive force in the case of tall trees such as *Tilia*. In this case the limit of this force *was not reached* at 20 atmospheres.

Following Mr. Darwin in assuming that the resistance to motion at the transpiration velocity is given by a hydrostatic pressure equivalent to five times the length of the branch, this minor limit of osmotic pull suffices for a lime tree 100 feet high. The limit of height recorded for *Tilia americana* is sixty feet. In the case of the Laburnum, this tree might, so far as Dixon's results indicate, flourish to a height of 130 feet. Its recorded limits are between thirty and forty feet. Similarly the Sunflower might attain a height of eighty feet or thereabout. It appears therefore as if it was not osmotic conditions which limited the heights of trees; although the limit, in the case of the lower growing plant, is the lowest observed.

I may mention here that, so far, conditions of sunshine or shade have not been observed to notably alter the results. If not freely supplied with water, however, the branches might indicate differently. Dixon hopes yet to make an observation upon the branch *in situ*.

The following table shows the weights of water transpired by similar branches exposed to like conditions, as far as possible, save that one was immersed in carbon dioxide and the other surrounded with air. The pressure on each was the normal atmospheric pressure:—

Helianthus multiflorus.

Normal pressure.

Surrounding medium.	No. of leaves.	Time.	Weight transpired.
A. Air.	10	90 mins.	0.302
a. Co ₂ .	10	90 mins.	0.257
B. Air.	10	60 mins.	0.372
b. Co ₂ .	10	60 mins.	0.108
B. Air.	10	180 mins.	0.598
b. Co ₂ .	10	180 mins.	0.236
B. Air.	10	24 hrs.	2.862
b. Co ₂ .	10	24 hrs.	1.979
C. Air.	12	24 hrs.	5.230
c. Co ₂ .	12	24 hrs.	2.240

In this table the letters prefixed indicate the identity of a branch used a second or third time. The branches B and b were, it will be seen, used in three succeeding experiments.

As regards the condition of the leaves at the conclusion of the experiments, it is to be remarked that but little difference was to be detected in the degree of flagging exhibited by specimens which had transpired in air and in carbon dioxide; on the whole the latter were the fresher.

I do not think that any one considering these results can fail to be struck by the inference that the great differences in the rate of transpiration may in a great measure be due to a lowering of vital activity in the one case. But of course, pending further and more varied experiments on this complex matter, the question hardly admits of profitable discussion.

The question has been raised as to what may happen in a tracheid containing air bubbles. I may say that our views on this subject are as follows:—

There will be a critical size for the bubble corresponding to the prevailing tensile stress. If below this dimension, the surface-tension force of the bubble will be adequate to cope with the tensile stress of the sap and the vapour and air pressure within it. It will then retain its minute dimensions and no more interfere with the circulation of water than would an equally minute solid body. If, on the other hand, it is of a dimension incapable of withstanding the expanding forces enumerated, it will yield and expand so as to occupy all but the sharp corners of the conduit or deep depressions upon the walls. Except within the cell-wall, we think that, under these circumstances, there will be no motion of water past the bubble in the conduit under consideration. Increase of tension will not tend to further a free current past the bubble, rather it will cause this to expand still further and carry the gaseous space deeper into the surface of the cell-wall.

In this connexion I may observe that the manner in which a hydrostatic tension is transmitted through the column of sap in the tree is sometimes a subject of some misconception, and many appear to regard our theory as postulating the existence of hanging thread-like filaments of water in tension, which must be supposed extending in continuous lengths from leaves to root in order to be effective. Hence, it is argued, the presence of a bubble anywhere in the path of one of these threads, by interrupting its continuity, destroys its

effectiveness, and the entire transpiration current is reduced in cross section throughout its length by the absence of one of the elementary filaments. Such a view greatly exaggerates the effect of the presence of free gas here and there in the lumina. It should be remembered that the vessels and tracheides are not merely laid end to end with intercommunication confined to the conduit above and below, but that where a lumen is occupied by a bubble the path of the current from the conduit beneath, for example, is simply deviated into an adjoining conduit. Thus by the presence of an idle lumen, the transpiration current experiences an opposition which is evaded somewhat in the manner in which a river evades the opposition of a stone in its bed. Or, if the idle lumina are numerous, the retardation effect might be compared to that of sand opposing the percolation of water. The hydrostatic tension is transmitted virtually in all directions, the lumina communicating as they do through the closing membranes of the pits.

The rarity of the occurrence of a liquid in tension (we do not know if hydrostatic tension has been detected anywhere else in nature) almost justifies the misconception which ascribes different laws to hydrostatic tension and hydrostatic pressure. Essentially the laws are the same, substituting for the idea of a pull, the idea of a push.

I would like to say a word as to some views which appear to us to commend themselves regarding the nature of the root-action in withdrawing water from the soil. The tensile stress transmitted to the root has ultimately the effect, we may say, of drying up the root surface. We suggested this in our first paper. The dry surface has the same power of condensing water as dry oatmeal, paper, or flannel would have if buried in damp earth; not necessarily by mechanical contact with damp particles, but by absorption of aqueous vapour. As a matter of fact the aqueous film which overlies solid bodies is so immobile that it is hardly conceivable that a root-hair in contact with a particle of silica, for example, could get more water than what immediately adjoined its point of contact. The quantity of water taken up by trees appears to be often so large, even from dry soils, that this older view of the phenomenon would we think be inadequate. Of course a great deal is taken up in the liquid form, and the necessary salts thus brought into the plant. Professor Askenasy seems to misconceive our ideas on this matter¹. Taking this view of

¹ Beiträge, p. 5, 1896.

the root-action, we can regard the whole phenomenon of the ascent of sap to depend broadly upon a difference of vapour pressure in the atmosphere surrounding the roots and in the atmosphere surrounding the leaves¹.

In reference to the doubt suggested by Mr. Darwin (p. 641) as to the re-solution of air by root-pressure sap, we would say that the *onus probandi* would rather lie with those who question such action. The root-sap contains only a small quantity of dissolved air, and, except the laws of absorption of gasses by liquids differ inside the tree from elsewhere in the world, we expect that it will be willing to take up more. Here too we may recall what Strasburger quotes² from Volkens and Vesque as to the appearance and disappearance of air bubbles in the conduits of herbaceous plants.

In regard to the general considerations of the stable properties of a dust-free liquid under tensile stress, it is interesting to notice the analogy with the behaviour of a dust-free vapour under pressure. In the first case an enormous stress is required to initiate a bubble of vapour, for the surface tension of this bubble will be the greater proportionately as its radius of curvature is smaller. In fact without actual fracture of the liquid, only a dry particle (exposing already a free surface of appreciable radius of curvature) can initiate the bubble. In the case of the vapour it requires a high pressure to initiate the precipitation or formation of drops, because the vapour pressure of these will be the greater as the radius of curvature is smaller. Here, too, we require a particle to initiate a wet surface of appreciably great radius of curvature. The increased vapour pressure at sharply convex surfaces may not be without influence in the evaporation at the surface of the minute mesophyll-cells, when these present a wetted surface to the intercellular space. I may remind you, in connexion with these remarks, of Aitkin's experiments on the counting of dust particles, and Maxwell's remarks on how small drops of rain are unstable in the presence of big ones³.

Reviewing the whole matter in a few words:—

We have in the tracheal system of the plant a water-way which is freely open to water-movement, while closed to the movement of free gas. Every bordered pit is an open door to the sap and a closed

¹ Ascent of Sap, Phil. Trans., pp. 574-75.

² Leitungsbahnen, pp. 696-97.

³ See Tait's Properties of Matter, Chapter on Capillarity.

one to the gas bubble, and one which locks and bars itself against the exit of an imprisoned bubble. In a word, it is a structure semi-permeable towards matter in its three states, the solid, the liquid, and the gaseous. Taking the nature of this structure into account; the observations on the swamped condition of a great part of it; the experimentally proved fact that water containing air and in presence of wet wood is stable under high tension; and that the phenomena occurring in the leaf are capable of giving rise to the necessary traction, it is not too much to say that one who questions the existence of tensile stress in the sap (when root pressure is inactive), because it has not been directly demonstrated, is in the same position as one who questions the existence of pressure in the deepest part of the ocean because observation there had never demonstrated it.

I may perhaps be permitted to remark more clearly here—in view of a misconception referred to early in this paper—that the mention of revision at the head of our complete paper in the *Phil. Trans.*, refers to no change of opinion or modification of views expressed in our original manuscript. The term refers solely to excisions.

In conclusion I desire to express how cordially Mr. Dixon and I concur in Mr. Darwin's remarks upon the work of Strasburger. Whatever the fate of our hypothesis—and the clearest evidence may deceive; the strongest convictions err—*his* name must ultimately be for ever associated with the true theory of the ascent of sap.

PROFESSOR G. F. FITZGERALD, in continuing the discussion, spoke of the difficulty of drawing distinctions between the physical nature of 'imbibition' and capillary forces; and the risk the use of the first term involved of substituting the word for the idea.

He did not consider that the supporters of Messrs. Dixon and Joly's theory required necessarily to prove the existence of tractive forces in the leaf equivalent to a hydrostatic head five times the height of the tree, in order to meet the viscous resistance of the sap. The estimate of the viscous resistance to be accounted for must be based on the velocity of the transpiration current in the higher parts of the tree under normal conditions of supply; and this, probably, was not ascertained. The actual movement of water in the higher parts of the tree might be very slow under normal conditions, and hence the viscous resistance very small.

The principles determining the permeability of a septum by the

medium in which it was immersed might be illustrated by the cases of a wet and dry fabric; the first freely permeable to water, the second freely permeable to air. Capillary resistance destroys the free permeability when it is sought to pass through the fabric a medium differing in physical properties from that already contained in the openings or meshes of the fabric. The fact that the wet fabric was not permeable by air illustrated the properties of the cell-wall in retaining a bubble developed within the lumen.

After some remarks from PROFESSOR MARSHALL WARD, the discussion closed.

Darwin, Francis. 1896. "Report of a discussion on the ascent of water in trees." *Annals of botany* 10, 630–661.

<https://doi.org/10.1093/oxfordjournals.aob.a088636>.

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