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On the Movement of Water in Plants. By G. F. SCOTT
ELLIOT, M.A., B.Sc.

(Read 14th July 1887.)

There has been more discussion on the subject of the ascent of crude sap in the living plant than on almost any other botanical problem, and the literature is correspondingly large. I have intentionally confined myself to the more recent observations, and I have to thank Professor Dickson, Dr Macfarlane, and Mr John Ratray for the very kind assistance they have given me in this respect.

The question naturally falls under two heads. First, the path by which the sap ascends; and, secondly, the moving causes. The first of these questions is regarded by most German and French botanists as practically decided, but as Mr Vines (1), in his recent work on the physiology of plants, has dismissed their view in small type of a short paragraph, it may be of service to bring some of the evidence together.

The older view of Sachs (2) and Unger that the water travels *in the walls* of the lignified vessels, and not in their cavities, rests mainly on the supposed fact that these vessels contain air and not water. It was for exactly the same reason that arteries were long supposed to conduct air and not blood; and there seems to be as little foundation in both cases. Von Höhnelt (3) showed long ago that the cavities of the vessels were *not* in communication with the intercellular spaces or stomata. Moreover, the same observer, as well as Scheit (4), Boehm (5), and Russow * (6), have shown that cell-walls, when wet, are practically impervious to air. Scheit (4), for instance, was unable, even with a pressure of 120 cm. of mercury, to expel air from a piece of the stem of *Abies balsamea*.† There is no evidence to show that the air can enter by the roots. There is therefore some difficulty in understanding how the air can enter the vessels except accidentally.

Sachs lays stress on the fact that freshly-cut wood floats

* See also Weisner, *Sitz. d. k. Akad. d. Wiss.*, Abt. i., 1879; Schwendener, *Schutzscheiden*, Berlin, 1882.

† Klebahn's (7) experiments can only be held to prove the existence of air in intercellular spaces.

on the surface of the water, only sinking when the contained air was driven out by water. He does not, however, take into consideration the possible entrance of atmospheric air at the section surface. I tried the experiment with the addition of cutting in every case two pieces of wood;—one of these was cut under water to exclude atmospheric air, the other cut in the usual way and then dropped into water. I found in many cases that both twigs sank. In two cases, however, I found that the twig cut under water never rose to the surface, while the one cut in the air floated. The difference in these cases was therefore clearly due to the entrance of atmospheric air. This experiment, however, is far too rough to be worth working out, for, as Sanio (8) points out, air in the intercellular spaces would account for the floating. Sachs' experiments cannot therefore be regarded as conclusive.

Direct experiments by cutting sections of wood under oil or glycerine,—Hartig (9), Elfving (10)—particularly if conducted with specially constructed apparatus,—Volkens (11), Schwendener (12),—certainly appear to show that there are bubbles of air in the vessels and tracheids. Scheit (4) maintains that these bubbles are not air-bubbles, but simply empty spaces, because in glycerine these cavities quickly disappeared. This last view requires confirmation, but the presence of air does not show that there is no water. Hartig (9) gives the proportion of air and water as varying from one volume air to three volumes of water to from nine volumes to ten volumes water; Schwendener (12) gives air 0.33 mm., water 0.19 mm. in the vessels.

Most observers—Hartig (9), Von Höhnelt (3), Boehm (5), Volkens (11)—seem to think that the vessels and tracheids are full of water at night, and that it is only during the day, at the time of most active transpiration, that air enters (according to Scheit (4) the vessels are emptied). The air is also at an extremely low tension. Boehm (5) found that if a twig of *Robinia* is cut under mercury, the mercury rises in the vessels to a height of 116 mm.; cf. also Von Höhnelt (3). Vesque (13) found in one or two cases that the contained air was at a pressure equal to that of the atmosphere; but in his experiments it is not easy to see how the air in the intercellular spaces can be distinguished from that in the

vessels. No one supposes that water is ever entirely absent from the vessels.

There are also some anatomical objections to the view of Sachs. Sachs acknowledged that in some Monocotyledons and Dicotyledons, there is not enough lignified tissue in the bundles to conduct the water, and suggested that as sclerenchyma resembles true wood, it probably conducts the water to some extent in its walls. This, however, is not the case. Elfving (10) tested this view with the stem of *Chamædorea*. He covered the section of the stem with paraffin, and then removed this paraffin first *from the peripheral sclerenchyma*, in which case no water passed through (even with a pressure of 120 cm. Hg.), then *from the vessels*, and found that water passed through abundantly.

Moreover, Russow (6) pointed out that in that part of the haulm of grasses which is protected by the leaf there is practically no lignified or sclerenchymatous tissue at all, and the water certainly travels through it.

There are also other objections. First, on Sachs' view there is no known reason why the water travelling in the wood walls should not pass with equal ease in every direction. Elfving (10) and Boehm (5), however, found that it is quite easy to force water through pieces of coniferous wood cut tangentially, and impossible to force it through pieces cut in the radial direction. As the disc thickenings are on the radial walls only, this is what one would expect if the water travels by the lumina.

The method of causing the roots or cut surfaces of plants to suck up coloured solutions has been very largely used (*e.g.*, La Baisse, in 1733; Reichel, in 1758; and Herbert Spencer (14), in 1866). The substances used are very different. Professor MacNab (15) (see *Transactions* of this Society), used lithium salts. Van Tieghem (16) used either fuchsin or a double treatment—first with potassium cyanide, then with ferrous sulphate. The best substance, however, appears to be eosin,—Darwin and Phillips (17).

Sachs himself used this method, but considers it unsatisfactory, as the salt may not travel as rapidly as the water. He uses, however, an identical method—viz., non-passage of cinnabar particles, to show that coniferous cells are not in open communication for water. Van Tieghem ignores Sachs'

view, on the ground that if you cut a plant close to the root you can see, on rapidly applying blotting-paper to the section, water oozing out of the section. All who have used this method are against Sachs' view. Elfving (10) gives what is tantamount to a direct proof of its incorrectness. Eosin stains some substance in the cell-walls of coniferous wood, as can easily be seen in a transverse section; but if a branch of *Taxus* is made to suck up coloured solutions, *the walls are not coloured*, according to Elfving, while the cavities are full of eosin.

There are also some indirect ways of getting at the truth. Sachs and Dufour (18), and latterly Darwin and Phillips (17), tried the effect of making incisions in the stems. The latter observers made two incisions, each as far as the pith on opposite sides, and some distance apart. They found that in *Helianthus* (where such treatment would cut almost all the vessels) the transpiration was greatly diminished; while in *Taxus*, where continuity by the tracheids would not be affected, there was practically no difference.

The same observers (17) and also Kohl (18) and Vesque (13), have found that when a stem is strongly squeezed together in such a way that the cavities of the vessels may be considered obliterated, no water can pass through; though, on Sachs' view, it is quite possible.

Another method, on which Sachs appears to rely, has been adopted (at Würzburg) by Dufour (18). If a twig is bent at a very sharp angle, Dufour found that transpiration is not stopped. He considered that in this twig the vessel cavities must be closed, as he could not inject twigs bent in this way when separated from the tree. This conclusion is quite fallacious, however. Russow (6) clearly shows that the cavity of the vessels in this case is not closed, and Scheit (4) has shown that if Dufour had cut the bent twigs under water they could have been injected; see also Vesque (13).

A very ingenious proof is given by Weber (20), who found that vessels whose walls were apparently changed by heat into a gummy substance still continued to conduct water.

Some remarkably conclusive experiments of Elfving (10) appear to me to prove the point. His method consisted in closing or rather filling up the cavities of the vessels by melted coco-butter injected by the cut surface. The lumina

being filled and the fat hardened, he cut a thin section from the cut surface, to take away the ends of the cell-walls which might be affected by the fat, and he then attempted to force water through. This was in every case impossible. On Sachs' view there is no reason why the water should not travel by the walls. His experiments have been repeated, always confirmed, and made absolutely free from all objection by Scheit (4), Vesque (13), and specially by Errera (21), who used a mixture of 40 per cent. gelatine instead of coco-butter. It seems to me one must conclude from this evidence that the crude sap travels in the cavities of the vessels.

Now, with regard to the forces employed, Sachs, followed by Pfeffer (22), considers that it is the force of *imbibition*, a force quite different from capillarity, which causes the water to mount in the cell-walls. We have scarcely the right to assume that imbibition is different from capillarity; *cf.* Haberlandt (23). Moreover, I fail to see how the water can easily move upwards through imbibition, and at the same time be strongly held in the walls through the same force. Also, the water does not travel in the walls. The theories held by other observers are almost as numerous as the observers.

It is best to classify them according to the forces supposed to be effective. The first force, which certainly has great influence, is *osmosis*. There are two different ways in which this acts. Namely, the *osmosis* of the cells of the root, or *root pressure*, and the *osmosis* of all the cells of the stem and leaf which a vessel supplies. First, as to root-pressure. Von Höhnelt and Scheit (4) consider that it is the only force in action. This is, however, probably doubtful, as most observers do not consider that the root-pressure could lift the water to a greater height than six metres. There is, however, so much variation in the measurements given for the root-pressure that one must take all such figures with great reserve. Leclerc du Sablon (25), for instance, found a difference of 180 mm. in manometers only 8 or 10 cm. apart on the same tree. There is no doubt, however, that it has some influence.

The importance of the *osmosis* of the cells of the leaf and stem was first pointed out by Westermaier (24). The following experiment is worth giving to show the effect:—A circular disc of 6 mm. radius was cut out of a leaf of *Peperomia*. This was placed in a salt-solution, and weights

were placed on the upper surface. He was able to place a considerable weight on the upper surface without producing subsidence of the epidermis cells. From this he calculated that a whole leaf could lift 180 kg. a short distance. This is the only attempt at exact measurement of this force that I know, but if we consider the number of living cells that a vessel encounters on its course from the root to the leaf, we must consider it as probably the most important agent in the ascent of water.

Capillarity would be, according to Scheit (4), able to raise the water to a height of 1.25 to 1.69 m. Vesque (13) gives, on the other hand, ten metres. But there are three distinct theories as to the contents of the vessels and tracheids, which would modify the action of capillarity. First, Scheit holds that the vessels are full of water-vapour during the day, and at night contain water. Secondly, Vesque (13) and Elfving (10) hold that the vessels contain air-bubbles, which are suspended in water (not touching the sides of the vessels). Thirdly, Boehm holds that the air-bubbles are in contact with the sides of the vessels. Taking Scheit's view first, it must be remembered that the main loss of water occurs during the day. Van Tieghem (26) gives the loss of water by the evaporation due to the action of chlorophyll "chlorovaporisation" as 168 g. to every 2 g. produced by the ordinary evaporation, which takes place both day and night. If we imagine a vessel filled during the night with water, and suppose that as the water evaporates, the empty space is filled with water-vapour, there is no difficulty in seeing that the process of emptying can go on, the continuity from the leaf to the root being kept up by the water-vapour; but the difficulty consists in seeing how the vessel is filled up with water at night, and here Scheit gives no assistance, and we are obliged to take capillarity and root-pressure alone, and these two forces appear to be insufficient.

Secondly, if the air-bubbles are supposed to be floating freely in a vessel full of water, and if we suppose that capillarity can raise a column of water to a height of 10 metres, and that the amount of air is equal to the amount of water, then in this vessel capillarity can raise the water to a height of 20 metres, because the water is exactly half

as heavy on account of its contained air-bubbles. And if we take Hartig's figures, nine volumes of air to ten of water, there is no difficulty in seeing why water should not rise to as great heights as are found in nature. If, on the other hand, the air-bubbles are in contact with the walls of the vessel, their presence is simply an obstruction, and the water will have to get round them by the neighbouring cells. Boehm's view that the relative tensions of such air-bubbles assists in the elevation of water has been disproved by Zimmermann (27). The surface tension of every bubble must be a resistance in addition, and the resistance must therefore depend on the number of air-bubbles of Zimmermann (27).

The difficulty of the question is that the premises, namely, the contents of the vessel, at all times of the day, are quite unknown. If we assume that the second view of Vesque and Elfving is correct, we can say that the water rises through the following forces:—first, osmosis (*absorbent activity of Vines*), both of the cells of the leaf and root; and, secondly, capillarity; possibly the pressure of the atmosphere may be set down as a third force (Vesque), but we have no data to show what the several influences of these forces may be, and must keep the conclusions open till the premises are satisfactorily settled.

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Facts regarding the Morphology and Affinities of certain Genera of the Order Scrophulariaceæ. By P. SEWELL.

(Read 14th July 1887.)

Systematists have noticed with considerable detail the different modifications in the flowers of Scrophulariads, and made use of such for the purpose of distinguishing one genus from another. They have, indeed, rather attempted to detect differences than to see resemblances.

In this way they have somewhat overlooked the *natural series* of such modifications which afford the most important evidence of relationship and common ancestry.

The following notes instance a few of these series which have come under my notice in an attempt to determine the relationships of certain genera of Scrophulariaceæ.

In regard to the *gynæcium*, we may notice that fewer ovules occur in *Veronica* than in the less specialised genera of the order. This reduction, entirely in keeping with the condition of the calyx and corolla, serves as one of many examples that might be brought forward to show that reduction is an almost constant concomitant of specialisation.

A feature of very considerable interest has been observed and shown by Mr W. E. Fothergill in regard to the placentation. In young ovaries of *Digitalis*, he noticed that instead of an axile placentation towards the apex, it was very often parietal—suggesting the similar series of modifications in Saxifrageæ. In *Datura*, also, the four cells are at times not apparent near the apex of the ovary, where, owing to the cessation of growth in two of the septa, the ovary appears