Botany. — *"Sap-raising forces in living wood."* By E. REINDERS. (Communicated by Prof. J. W. MOLL.).

Of the many theories, which have been advanced in explanation of the transpiration-current of trees, most are at present only of historical importance in the literature. The imbibition theory of SACHS [1]); BÖHM's atmospheric pressure theory [2]); the gas pressure theory of HARTIG [3]); the views of WESTERMAIER [4]), who regarded the xylem parenchyma as the water conduit and considered the vessels to be reservoirs; EWART's [5]) hypothesis that the living elements help te overcome the resistance, the cohesion theory of ASKENASY [6]). which neglected to adopt the continuity of water as a conditio sine qua non — all these have been given up. On the other hand opinion is still divided with regard to two hypotheses, the advocates of which combat the views of their respective opponents with remarkable asperity. GODLEWSKI [7]) and his supporters defend the view that the transpiration-current cannot be explained without postulating the cooperation of the living elements of the wood; DIXON and JOLY [8]) on the other hand advance the proposition that the living elements have not, and cannot have, anything to do with the process. They explain the phenomenon that water ascends up to the summits of the highest trees by assuming that in these trees the water, enclosed in the narrow water conduits, hangs like a thread from the surface of the leaf cells, where it is held by capillary or other physical forces. The thread does not break, because, as is supposed, it is nowhere in contact with air, and in these circumstances water can support a tension of 150 atmospheres. When the water evaporates in the leaves at the summit, this thread is drawn up through the tissues.

The keenness with which the two parties oppose each other is best illustrated by a couple of quotations.

SCHWENDENER [9]), an advocate of the more physiological theory, says:

"An der Vorstellung, dass die Lebenstätigkeit der Zellen irgendwie in die Saftbewegung eingreift ist . . . . unbedingt festzuhalten. Ohne dieses Eingreifen ist die Hebung des Wassers auf Höhen van 150-200 Fuss und darüber einfach unmöglich und alle Bemühungen, die vorhandenen Schranken mit unklaren physischen Annahmen zu durchbrechen, sind nicht viel mehr als ein Suchen nach dem Stein der Weisen".

In the same year 1909 DIXON [10]) writes:

"The adhesion of writers to the vital hypothesis . . . . is so

remarkable that we must devote some space to examine fully the grounds for their contention".

When we attempt to trace why opinions diverge so widely, the cause seems to lie principally in a different appreciation of certain experiments and in the somewhat adventurous aspect which the Dixonian explanation presents at first sight. It is necessary to become accustomed to the idea that the life of our trees hangs upon a water-thread, before we can become reconciled to it. GODLEWSKI [11]) indeed required a much more adventurous hypothesis in order to reconcile the anatomical structure of the wood with its power of pumping up water. This part of his theory has in consequence received adhesion from no one and so I will leave it out of discussion. In what follows below, "GODLEWSKI's theory" will therefore mean the view that the living wood must be regarded as the cause of the transpiration current.

In order to facilitate a judgment of the state of affairs I will tabulate the most important arguments of the two parties side by side and will then discuss them in pairs. From this table I omit everything relating to the question whether the cohesion of water is sufficiently great to account for the work which DIXON and JOLY attribute to it. I will assume, if I may put it thus, that there is no technical objection to their theory and I think this assumption may be made with safety.

GODLEWSKI c. s.	DIXON and JOLY.
1*a*. There is not sufficient continuity in the water columns of the wood to admit cohesion as an explanation [12]).	1*b*. There is no reason for doubting the continuity of the water columns [13]).
2*a*. The remaining available physical forces are insufficient to raise the water more than 14 metres [14]).	2*b*. STRASBURGER's experiments in which the water ascended in poisoned trees, prove the contrary [15]). The cohesion theory has at its disposal forces which would be able to provide a tree of 200 metres and more with water [16]).
3*a*. URSPRUNG's experiments, with branches which had been killed for part of their length, after which the	3*b*. In URSPRUNG's experiments the conduits become blocked and the leaves were poisoned because

leaves faded, prove that dead wood cannot transport enough water to balance the transpiration [17]).

they got a decoction of wood for their drink [18]).

4*a*. The structure of the wood is in favour of GODLEWSKI's theory [22]).

4*b*. "The very structure of the wood offers the strongest evidence against GODLEWSKI's theory" [19]).

Living wood offers the same resistance in either direction to the forcing through of water [20]).

5*a*. Arguments from analogy [22]).

5*b*. Arguments from analogy [21]).

6*a*. The distribution of pressure in living transpiring trunks is opposed to the cohesion theory [23]).

6*b*. The measurements of pressure are considered unreliable or are left out of account.

Point 1. The question of the "continuity of the water-threads" in the wood amounts to the following. The cohesion theory requires the assumption that the water in the tree forms one connected mass from the root to the leaves. Every xylem vessel in which there is an air-bubble has according to this theory become useless for the conduction of water, for in such a vessel the water cannot be under negative pressure; it is at once sucked empty by the adjoining vessels. Every bubble of air therefore puts one vessel out of action.

Now if it could be shown that by far the largest proportion of vessels contain air bubbles, only a small percentage would remain available for the conduction of water, and perhaps here and there the required connection of the water would be entirely interrupted, so that there could be no question of the cooperation of cohesion.

It is of course difficult to prove the absence of air, for in the necessary manipulations preparatory to the examination there is always the chance that air bubbles in some way or other get into the vessels [24]). If air is found in the majority of the vessels this does not prove that it was already present in the living plant, for it may have penetrated during manipulation.

For the further course of my argument it matters little, however, whether DIXON and JOLY or whether their opponents are right on this point. I will not therefore discuss it any further.

Point 2. The proposition, that physical forces alone are insufficient [25]) to raise water higher than 13—14 metres is a very weak point in the defence of GODLEWSKI's theory, for STRASBURGER's intoxi-

cation experiments have proved in the most striking manner, that this proposition is untenable. He found that water still ascended to the highest tops of the p o i s o n e d trees, up to a height of 22 metres.

The attempts of GODLEWSKI's supporters to maintain their proposition in spite of this fact give a very unsatisfactory impression. STRASBURGER is attacked in vague terms[26]; he is accused of a want of critical insight, he is reproached for not making any attempt at explanation: the fact itself remains.

The following argument appears to be somewhat more weighty. It is said[27]: "with the help of a JAMIN chain atmospheric pressure may be imagined to force water up to 13—14 metres"; but fourteen is not twenty-two and moreover a JAMIN chain can by no way explain anything in this case. It might perhaps be applied to this purpose with some chance of success, if the vessels ran through continuously from the root to the leaf, but certainly not in a system of vesicles like the wood, where the bubbles cannot pass the partitions, dividing up the conducting tracts, to say nothing of the multitude of other clinching objections.

It is further adduced against STRASBURGER, that continuous liquid threads are formed when the trunk, having been sawn off, is placed in water[27]), but in the first place it is not clear what objection is really meant by this and in the second place it is difficult to imagine how these threads are supposed to originate. The water which is sucked up cannot remove the air present, for the air is enclosed; it is moreover saturated with air, and is more likely to give off bubbles than to absorb them, as soon as it is exposed to a lower pressure at a certain height. Sawing off the tree will hardly affect its air-content except to increase it; the air which enters does not, however, endanger the cohesion, as it cannot ascend.

Point 3. URSPRUNG's experiments[17]) with branches, which had been killed by steam over part of their length, in consequence of which the leaves faded, do not prove much for GODLEWSKI either. The steam not only kills the living elements, but also induces other changes.

For some time the vessels must conduct a decoction of wood instead of water and a blocking of the membranes or even of the lumina of the vessels may be the consequence, so that the resistance increases. The cells of the leaves are further more or less poisoned by this liquid, so that it is very doubtful whether the death of the leaves may be attributed to a want of water[18]).

These experiments are therefore not of much importance in deciding the question under consideration.

Point 4. The anatomical structure of the wood is 'a better argument for DIXON [19]) [20]) than for GODLEWSKI, for as yet it is quite impossible to imagine in what way the living elements could really exert any successful pumping action. The unidirectional resistance without which such an action can hardly be conceived, has never been observed, in spite of a careful search for it.

This argument is therefore no longer always adduced in support of GODLEWSKI.

Point 5. In critical cases the arguments from analogy are hardly more valuable than illustrations. I will therefore not discuss them here.

We see therefore that the arguments which have been advanced so far give little support to GODLEWSKI's theory. On the other hand the striking and conclusive result of STRASBURGER's intoxication experiments is in favour of DIXON and JOLY. If to this be added the great convincing power which proofs from analogy exert, when well presented (and here DIXON and JOLY are much more fortunate than their opponents), we may readily understand, that the cohesion theory has many supporters.

There are, however, two facts which are adduced against this theory with more success.

In the first place a second series of experiments by URSPRUNG [28]) in which he used ice instead of steam, in order to render part of a branch inactive. This series of experiments does not of course suffer from the objections which deprived the other series of its argumentative value. The fact, however, that fading only occurs after several days, makes the result less convincing.

Another objection is more important:

Point 6. The distribution of pressure in living trees is opposed to the theory [23]).

In a hanging water-thread the pressure decreases gradually as one ascends and the decrease is at least one atmosphere for an ascent of 10 metres. In living transpiring trees it has been impossible to demonstrate this; it was found on the contrary that manometers placed at different heights up the trunk, behave quite independently of one another. Sometimes one shows a lower pressure, sometimes the other.

It is true that objections can be raised against many of these measurements of pressure, but some of them in SCHWENDENER's opinion proved positively and undeniably that there can be no question of a regular decrease of pressure. For in this case it would be inconceivable, "dass ein Baumstamm der nach 2—3 Regentagen durch Nachschub von unten etwas wasserreicher geworden, in mittlerer

Höhe (wo vorher Saugen stattfand) Luft in das hier angebrachte Manometer hineinpreszt, während oben in der Krone und insbesondere unten am Stamm weder Saugung noch Pressung stattfindet" [23]).

It is remarkable that DIXON, in his review of the state of the problem in the "Progressus", does not at all refer to the ice experiments of URSPRUNG, nor to measurements of pressure, although he there considers at length and refutes much less important objections.

Thus we have traced the causes of the remarkable phenomenon mentioned in the introduction. The partisans of GODLEWSKI point to the measurements of pressure and maintain that STRASBURGER'S experiments are invalid, whereas DIXON points to STRASBURGER and is not concerned with pressure measurements.

As will be seen the position is somewhat confused. In my opinion no advance can here be made along a theoretical road. Experiments alone can lead us out of the confusion.

I think I am able to supply conclusive, experimental proof that the normal living wood is able to pump water actively.

In order to give this proof I started from the following preliminary conception. If the irregularity of the results of pressure measurements is really caused by a pumping action of the living wood, this irregularity must at once disappear as soon as the experimental trees are killed or paralyzed. This was indeed found to be the case. Moreover, as soon as the trunk was dead the differences of pressure followed the same rule as would be expected to apply to a glass tube. When the conditions became unfavourable to evaporation, as in the evening and when rain supervened, the indications of the manometers approached each other more and more. At midday, in sunshine, on the other hand they differed more. This becomes intelligible, when we consider that a more rapid evaporation requires a stronger current; for a stronger current larger differences of pressure are however necessary, in order to overcome the greater resistances.

First I will describe the experiments somewhat more in detail. Later I hope to publish the curves of the positions of the manometers, together with the result of a more extensive investigation of this subject.

Of a $\pm 2\frac{1}{2}$ metres high specimen of *Sorbus latifalia*, which divided a little above the ground into two almost equal, strong branches, one branch was left intact as a control; to the other I fixed above one another some U-shaped open mercury manometers, in the following manner. Some lateral branches were cut off from the main branch in such a way that a stump of 5 cm. length remained. A tube was slid over this stump, and to it the manometer was afterwards fixed

this tube was blown out in the middle to a small bulb, and was hermetically fixed to the stump with a piece of india rubber tubing. It was then half filled with water, and momentarily pumped empty that we may inject the cut vessels. I then left it open for half an hour and finally closed it with the perforated rubber stopper, through which the manometer was stuck. Once a day the bulb-tubes had to be replenished, for the wood always leaks a little from the intercellular spaces. The bark leaks still more and for this reason I always removed it at the place where the rubber tube was to come.

As long as the tree was alive, no regularity could be perceived in the indications of the manometers: they all showed a pressure, smaller than that of the atmosphere, but sometimes one "sucked" more, sometimes another. After a few days I killed the portion of the branch bearing the manometers over its whole length by means of steam. At once the manometers followed the rule indicated above, and did not depart from it. The differences of pressure became very considerable towards midday, showing that the dead portion offered a great resistance to the strong current.

The crown and the base of the branch remained intact during this treatment. The leaves showed only after 3 weeks, that they had suffered from the operation; up to that time they remained perfectly fresh. When at last they began to change, they gave the impression that they were diseased, rather than that they suffered from want of water.

Two manometers were attached to the small trunk of a *Cornus* and fixed to almost equal stumps of branches, the one 66 cm. above the other. The whole tree was 2 metres high. Before I cut off the branches, which were to yield the stumps, I killed the trunk at these two places with steam over a length of 10—12 cm. The manometers were thus attached to dead branch stumps on dead pieces of the trunk, separated by a living portion.

I wished to investigate whether the living intermediate portion did pump or not. If so, it would always be occupied in diminishing the difference of pressure between the two dead pieces of the trunk. If it was then suddenly cooled with ice, the manometers would have to diverge suddenly and would once more approach each other if the tree was left to itself. Finally if it was killed, the well-known regularity would be bound to appear.

The result was different, however. The intermediate portion evidently did not pump, for the manometers behaved exactly as in a dead tree. At midday they sometimes differed by 24 cm. of mercury. However — on the fifth day their behaviour changed fairly

suddenly and on the sixth day it was as irregular as in living trees!

Evidently the intermediate portion had suffered too much by this treatment, to function immediately, but on the sixth day it had so far recovered, that it could work again. It lived on until the end of December, as could be seen by the perfectly fresh bark. Now, at the end of January, it is dead. The crown, however, still looks healthy, as also do the buds.

Although those facts, as far as I can see, do not permit of an explanation other than the one given here, a proof may still be adduced that such phenomena cannot be attributed to a change in the resistances. Such a change would moreover have to be of a very remarkable nature to be of any use as an explanation.

Four manometers were attached to the trunk of a lilac tree (*Syringa vulgaris*) 2 metres in height, and they were numbered in ascending order 1, 2, 3, and 4. After a short time they all showed an approximately equal "suction", which oscillated with diurnal periods between 48 and 28 cm. of mercury. Although the differences were small, some times one was the highest, some times another. After 15 days, when I knew the course of the pressure curves sufficiently, stump 2 was killed, together with the piece of the stem to which it was attached. This was done by passing through it for an hour the discharges of an induction coil capable of giving a spark of 10 cm. long, without sparking in the secondary circuit. The stump and the portion of the trunk became heated to nearly 60° C.: a few pieces of glass cement of that melting point, which I had fastened to it, just began to melt.

While the induction current was being passed, the suction of stump 2 first diminished greatly, as a result of the heating, the other manometers remained constant. Soon the fall of the mercury in no 2 stopped and the suction increased again. After the interruption of the current the mercury rose higher than usual; this abnormally high suction subsequently persisted; no 2 afterwards followed the periods of the other manometers, which went on without hindrance, but sucked always strikingly more. How we can deduce from this the proof that this phenomenon is not caused by changes in the resistances, will be explained presently.

Thus far the description of the experiments. I will now consider what may be deduced from the results.

The course of the manometers in *Sorbus* proves that the water current in a living tree is caused by quite different forces from those of a dead one. The result cannot be attributed to the imperfectness of measurements. Most of these are the same before and after death

and we cannot suppose that the circumstances which are changed in the operation, are altered exactly in such a way as to bring to light the observed regularity. Thus the distribution of pressure before death can only be explained on the assumption that there are pressor factors, i.e. pumping actions in the wood.

This view receives important support from quite a different side, through the experiments of ZIJLSTRA[30]). He allowed a solution of Säureviolett to ascend living and dead branches and then examined them microscopically. In the living ones only the tori of the bordered pits were stained, together with a thin layer of the walls of the vessels; in the dead ones, however, the whole of the wood was coloured uniformly. It follows from this that the water current takes quite a different course in dead wood from that taken in living wood.

That in the lilac only the one manometer was affected, which was attached to the portion killed by induction shocks, cannot in my opinion, be explained in any other way than by the aid of GODLEWSKI's theory. If one imagines, with DIXON and JOLY, that the whole trunk behaves like a dead tube, the phenomenon cannot be explained. An increase of resistance cannot be the cause, for then the other manometers would have undergone this influence. If on the other hand, we imagine a tree-trunk to be a system of tubes in which everywhere small pumps occur, the phenomenon becomes intelligible. The death of the piece of trunk puts the pumps out of action locally and the suction must there be somewhat greater to get the water through the piece of dead wood. This would not necessarily be observed at the following manometers, since the intermediate elements bring the pressure back to normal.

I regard all the above as proof positive that the living wood has a hydromotory power. The experiment with *Cornus* already proves this very clearly: one could almost see the recovering intermediate portion suddenly begin pumping, as it were before one's eyes.

After thus having given the positive proof that the living wood assists in the ascent of the water I will again take up the theoretical considerations with which I started, and see to what extent this proof can modify the condition of affairs.

We encounter the difficulty that STRASBURGER's intoxication experiments prove that help of living elements is not necessary, whereas the only theory which is not adversely affected by these experiments becomes untenable on account of the pressure measurements. The solution is clear from the preceding.

The adherents of GODLEWSKI are wrong in asserting that water

cannot ascend more than 14 metres without the help of life, for STRASBURGER's experiments show that this is indeed possible. But that is not the question. The position is simply this, that in a living tree the water is pumped up by living elements, whereas in a dead one it also ascends, but through other causes e.g., with the help of cohesion.

Let us test this view by the data in the table:

Point 1. The question of continuity is only of importance for the cohesion theory. As soon as this has been refuted in another way, the question of the continuity of water, may be left untill it may perhaps arise again in connection with new questions.

Point 2. The intoxication experiments of STRASBURGER have been included in my thesis.

Point 3. Although the experiments of URSPRUNG do not prove anything certain in favour of GODLEWSKI's theory, they certainly prove nothing against it.

Point 4. The anatomical structure of the wood can never be adduced as an actual objection to the view here put forward. As soon as it has been proved that the living wood pumps, this fact cannot of course be weakened because we cannot at once imagine from its structure how this action may take place. The investigation of this point must simply be left for further research.

Point 6. The distribution of pressure is quite in agreement with GODLEWSKI's view. When pressor factors are everywhere present in the trunk, the distribution of pressure cannot be predicted as long as these factors themselves are not fully known.

We see therefore that the questions discussed here do not produce an objection to my view. In this preliminary communication I have of course limited myself to the most important matter; afterwards I hope to treat the same subject more completely.

I might have omitted the literature entirely, but it seemed desirable briefly to justify my quotations and references. The small figures in the text refer to the bibliography which is appended below.

I wish to conclude this preliminary communication by pointing out that the method which is here introduced, may also be of service in the solution of other questions. By its aid we might, for instance, ascertain whether the living elements cooperate, when a branch is made to transport water in the inverse direction; the influence of all sorts of stimuli (heat, cold, electricity, stimulant substances) on the activity of these elements can be examined. Should the intoxication experiments of STRASBURGER be repeated with manometers fixed to the experimental trees, they would at once constitute a

definite proof in favour of GODLEWSKI. A small tree would, however, be sufficient for this.

The method in which a living piece of wood is isolated between two dead portions is especially to be recommended. The portions to be killed should not, however, be heated above about 60°, in order to spare the intermediate position (compare the experiment with the induction current). If possible a leafy branch should be left attached to the intermediate portion, for otherwise it must soon die of hunger.

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