The Suction-force of Transpiring Branches¹.

BY

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OF all the still incompletely solved problems of the physiology of plants, none has received so much attention of recent years as that of the means by which a current of water is maintained in a lofty tree between the absorbing roots on the one hand, and the transpiring leaves on the other. Without entering upon a discussion of all the various theories which have been proposed to account for this fact, it may be pointed out briefly that, according to prevalent opinion, it cannot be satisfactorily explained on the imbibition-theory of von Sachs², nor on the gas-pressure theories of Hartig³ and Boehm⁴, nor on the vitalistic theory of Godlewski⁵; and that it is not merely a phenomenon of capillarity. It would appear, from the researches of Dixon and Joly⁶ and of Askenasy⁷, that the motive power is the suction-force of

¹ I have published a brief note on this subject in the last (June, 1896) number of the *Annals*, p. 292.

² *Vorlesungen ueb. Pflanzenphysiologie*, 2^{te} Aufl., 1887, p. 221. (Eng. Ed., p. 241.)

³ *Die Gasdrucktheorie*, 1883.

⁴ *Warum steigt der Saft in den Bäumen*, Wien, 1878; also *Ann. d. sci. nat.*, sér. 6, t. 6, 1878.

⁵ *Pringsheim's Jahrbücher*, XV, 1884.

⁶ *Annals of Botany*, Vol. viii, 1894; *Proc. Roy. Soc.*, Vol. lvii, 1895; *Phil. Trans.*, 1895.

⁷ *Verhandl. d. naturhist.-med. Vereins zu Heidelberg*, Neue Folge, Bd. v, 1895 and 1896.

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the transpiring surfaces. The former make the following definite statement of their conclusion¹:—‘Our theory is that this (the suction-force, *Saugkraft*, of the leaf) is the all-sufficient cause of the elevation of the sap, not however by establishing differences of gas-pressure, but by exerting a simple tensile stress on the liquid in the conduits’: and Askenasy says²,—‘the warmth of the sun causes evaporation at the external surface of the mesophyll-cells, the imbibition-force of the wall of these cells sucks water from their contents, thus increasing their osmotic capacity: this gives rise to a pull which, in virtue of the cohesion of the water (we assume for the moment the existence of continuous columns of water in the conducting tissues, which is certainly true in many cases), is propagated to the root, and thus affects the living cells of the root: here it is reconverted into osmotic force which promotes absorption by the roots, provided that they are in contact with water.’

Such being the current views on the subject, it becomes a matter of importance to study and measure this suction-force; to determine the relation of the force to the transpiring leaf-area and to variations in external conditions; and to analyse it into its ultimate physical factors.

Experiments of this sort are by no means new. So long ago as 1726, Hales³ instituted ‘experiments whereby to find out the force with which trees imbibe moisture’; and the same has been done since by Meyen⁴, Unger⁵, von Sachs⁶, von Höhnelt⁷, Boehm⁸, and others. In all cases the method of experimentation has been essentially the same. A cut-off branch was attached air-tight to a glass-tube filled with water,

¹ Phil. Trans., p. 563.

² Loc. cit., 1895, p. 11.

³ Statical Essays, Vol. i, 4th ed., 1769, p. 84.

⁴ System der Pflanzenphysiologie, 1838, Vol. ii, p. 70.

⁵ Beiträge zur Anatomie und Physiologie der Pflanzen, XIII; in Sitzungsber. d. k. Akad. d. Wiss., Wien, Vol. 50, 1864.

⁶ Experimental-Physiologie, 1865, p. 260.

⁷ Ueb. den negativen Druck der Gefäßluft, Inaug. Diss., Wien, 1876.

⁸ Ber. d. deut. bot. Ges., VIII, 1889; Bot. Centralblatt, 42, 1890; Ber. d. deut. bot. Ges., XI, 1893.

the other end of the tube dipping into an open vessel containing mercury : as the water at the upper part of the tube was absorbed and transpired by the branch, the mercury rose in the tube from below.

But it is clear that an experiment thus arranged is not well adapted to demonstrate and estimate the suction-force generated in connexion with transpiration : for it is obvious that the rise of the mercury in the tube, up to a height of thirty inches (760 mm.) or so, is not the result of a tensile stress exerted by the transpiring branch on the liquid in the tube, but is due to the atmospheric pressure acting upon the mercury in the open vessel. It is surprising how small were the results obtained by this method. Thus Hales observed, with an apple-branch two feet high, a rise of twelve inches of mercury in the tube : Meyen, with a shoot of *Vicia Faba*, seven inches in four hours : Unger, with a shoot of *Eupatorium cannabinum*, a rise of 110 mm. : von Sachs, with a small branch of *Aesculus Hippocastanum*, a rise of 20 mm. in nine hours ; and with a Cabbage-leaf, a rise of 30 mm. in twenty-four hours : von Höhnelt, with a small branch of *Syringa vulgaris*, a rise of 300 mm. Boehm alone appears to have succeeded in observing a rise of the mercury in the tube above the height attributable to the atmospheric pressure : in his most recent (1893) account of his work, he mentions two experiments in which this occurred, both being made with branches of *Thuja* : in the one the mercury rose to a height of 864 mm., with the barometer at 751 mm. ; in the other it rose to 906 mm., with the barometer at 745 mm. Hence, in the one case, the suction-force of the branch alone was (864-751) 113 mm. ; in the other it was (906-745) 161 mm.

This mode of experimentation has the disadvantage that the conditions under which the water is absorbed by the branch differ materially from those obtaining in nature, in that the atmospheric pressure intervenes ; whereas in the uninjured plant the atmospheric pressure does not directly affect the absorption and transmission of water by the wood which constitutes an air-tight system. It occurred to me that

a mode of experimentation in which the conditions should more nearly approach the normal, would be one in which the water in contact with the cut-off branch was enclosed in an air-tight vessel, thus excluding the intervention of the atmospheric pressure. Moreover, in such a case, any measurements which might be obtained would have reference solely to the suction-force of the branch. In the first experiments, made last year, the air-tight tube, entirely filled with water, to which the branch or shoot was attached, communicated with a mercurial barometer as a means of measurement, the fall of the mercury in the barometer indicating the suction-force of the branch. By this means I obtained values for the suction-force, which were much higher than any I have met with recorded elsewhere. In these experiments I used the Cherry-Laurel (*Prunus Laurocerasus*) as representing woody plants, and the Sunflower (*Helianthus annuus*) as representing herbaceous plants: with the former I obtained as a maximum a fall of 320 mm. of the mercury in the barometer-tube, and with the latter a fall of 116 mm. I cannot, however, attach great importance to these results, as the experiments were few in number, for they had to be brought to an abrupt conclusion.

This spring I resumed experiments on the subject, but with an important alteration in the apparatus, namely this, that for the mercurial barometer I substituted a Bourdon's vacuum-gauge. The apparatus, as used, is represented in the accompanying Woodcut 1, where a branch is attached to an india-rubber tube connected with one arm of a T-tube at *B*, the two other arms of which are respectively connected by india-rubber tubes with the gauge *C*, and with a glass tube leading into the water-reservoir *A*. The water-reservoir is closed by an india-rubber stopper, through which pass two glass tubes, the one of which is connected with the T-tube, whilst the other carries a small piece of india-rubber tubing at its free end, and can therefore be hermetically closed by means of a pinch-cock at *a*. In preparing for an experiment the branch is attached to its india-rubber tube under such

conditions that the cut surface is maintained in contact with water : in some cases I removed the cortex from the portion of the branch introduced into the india-rubber tube, in others I simply attached the branch as it was, without any perceptible difference in behaviour. When all the connexions are made, the tubing is filled with water by raising and inverting the water-reservoir *A* ; then the reservoir itself is completely filled by raising the tube *a* so that its lower end does not project beyond the lower surface of the india-rubber stopper, and then pouring water down it from a wash-bottle, when all the air escapes up the tube : the tube *a* is then lowered so that its lower end is about on a level with that of the other tube

Woodcut I.

in the reservoir ; and, finally, the india-rubber tube attached to its free end is closed at *a* by two stop-cocks whilst still full of water. The apparatus, if properly set up, is now entirely free from gas ; it is air-tight, and the indicator of the vacuum-gauge stands at zero. It should be mentioned that the india-rubber tubing must be provided with an internal spiral wire to give it strength to withstand the atmospheric pressure from without, so as not to become occluded ; or, better still, it should be thick-walled pressure-tubing ; and the water used must have been boiled, so as to render it as nearly as possible air-free. The dial of the gauge is divided into thirty parts, representing inches of mercury, so that a complete revolution of the indicator would mark a perfect vacuum.

As the branch begins to exert stress on the water in the apparatus, the indicator moves round the dial, marking the degree of tension to which the water in the tubes is being subjected.

I have found, like my predecessors, that gas is evolved, sooner or later, from the cut end of the branch into the tubing. This does not occur, however, until the gauge indicates considerable tension: for instance, in the case of the Beech-branches, at tensions varying from 5–21 in.; and in the case of *Helianthus*, at a tension of about 5 in. But in this apparatus, the evolution of bubbles of gas from the branch does not affect the indicator of the gauge, provided that the gas is not allowed to accumulate between the branch and the T-piece so as to interrupt the continuity of the water in the tube. The evolution of gas by branches freshly cut from the tree is frequently so rapid that I found it impossible to keep the tube clear: consequently I was obliged to abandon freshly cut branches of Beech, and to use only such as had been kept standing in water for twenty-four to forty-eight hours after having been cut. The Yew gives off gas much less readily, so that in this case freshly cut branches might be used: one such branch did not begin to give off bubbles until a tension of over $17\frac{1}{4}$ in. had been reached: another similar branch which had been kept standing in water for forty-eight hours after having been cut from the tree, did not give off bubbles until a tension $19\frac{1}{4}$ in. had been attained: moreover the volume of gas evolved was small in both cases.

If at any time during an experiment a leakage develops in the tubing so that air enters, the indicator goes backward on the dial; and if the leakage is considerable, or if the stop-cock be opened, the indicator at once returns to zero, and the water sinks in the tube *a*.

I may now pass to an account of some illustrative experiments, beginning with the Beech (*Fagus sylvatica*) and the Yew (*Taxus baccata*), as representing woody perennial plants. The branches used were cut from large trees. The experiments were carried on in a well-lighted room facing south:

the branches lay in a horizontal position on a table close to a window.

June 4, 1896.—Beech-branch (*A*) with about 1,150 leaves: diameter of cut end = $\frac{5}{8}$ in.: standing 24 hours in water: rather hot, sunny:—

1.20 p.m.	indicator	= 0 in.	1.50 p.m.	indicator	= 17 in.
1.25 "	"	= $6\frac{3}{4}$ "	2 "	"	= $18\frac{1}{4}$ "
1.30 "	"	= $11\frac{3}{4}$ "	2.10 "	"	= $19\frac{1}{4}$ "
1.33 "	(first bubble)	= 13 "	2.20 "	"	= 20 "
1.40 "	"	= $15\frac{3}{4}$ "			

Readjusted apparatus, removing gas and refilling with water:—

2.40 p.m.	indicator	= 0 in.	3.10 p.m.	indicator	= $20\frac{1}{2}$ in.
2.50 "	"	= 14 "	3.20 "	"	= $20\frac{3}{4}$ "
2.55 "	(first bubble)	= $16\frac{3}{4}$ "	3.35 "	"	= $21\frac{1}{4}$ "
3 "	"	= $18\frac{1}{2}$ "	3.40 "	"	= $21\frac{1}{4}$ "

July 1.—Branch of the Yew: freshly cut: about 3 ft. 6 in. long: diameter of cut end = $\frac{1}{2}$ in.: weather cloudy, temp. 64° F.:—

July 1.			July 2.		
1.15 p.m.	indicator	= 0 in.	Gas accumulated in tube during the night; gas removed.		
1.25 "	"	= 1 "	9 a.m.	indicator	= 22 in.
2.30 "	"	= $13\frac{1}{4}$ "	10 "	"	= 22 "
3.30 "	"	= $15\frac{1}{2}$ "	10.30 "	"	= $22\frac{1}{4}$ "
4.30 "	"	= $16\frac{3}{4}$ "	11 "	"	= $22\frac{1}{4}$ "
5 "	"	= $17\frac{1}{4}$ "			

The following is the record of an experiment with the Sunflower (*Helianthus annuus*) as representing herbaceous plants:—

June 8.—Pot-plant 2 ft. high, with 13 leaves of various sizes: kept in dark room and well watered for 40 hours previously to the experiment: stem cut off under water: the remaining stump shows strong root-pressure: weather hot, sunny: plant began to flag visibly at 11.45 a.m.:—

11 a.m.	indicator	= 0 in.	1.30 p.m.	(bubbles)	= $5\frac{1}{4}$ in.
11.15 "	"	= $\frac{1}{2}$ "	2 "	indicator	= $6\frac{1}{4}$ "
11.30 "	"	= $1\frac{1}{4}$ "	3 "	"	= $7\frac{1}{2}$ "
Noon	"	= $2\frac{1}{2}$ "	4 "	"	= $9\frac{1}{2}$ "
12.30 p.m.	"	= $3\frac{1}{2}$ "	5 "	"	= 11 "
1 p.m.	"	= $4\frac{1}{2}$ "			

The question now arises as to the significance of such figures as these; what is it that they represent? This question may be met with the reply that they represent the

suction-force of the branch under experiment. But this is no real answer, for the further question at once arises, what is the nature of this force?—can it be definitely shown to be of the nature of a tensile stress; or is it merely a measure of the tension of the gases in the wood, a measure, that is, of the negative pressure developed in the branch?

The first step towards a solution of this somewhat difficult problem is to obtain a clear idea of what is going on in the branch whilst the experiment is in progress. It must be understood that, so long as no gas-bubbles are evolved from its cut surface, the shoot is not absorbing any water from the apparatus. If any direct proof of this obvious physical fact is necessary, it is afforded by the rapid flagging of the leaves and younger parts of the shoots of *Helianthus* when under experiment: their cells very soon lose their turgidity, in consequence, no doubt, of transpiration uncompensated by absorption. When bubbles are evolved, however, each bubble displaces a corresponding volume of water from the apparatus, so that water is then absorbed by the shoot; in an experiment with an actively transpiring branch, a considerable proportion ($\frac{1}{3}$ – $\frac{1}{2}$) of the water in the reservoir may eventually be replaced by gases evolved from the cut end of the stem.

These are the actual facts; but how are they to be explained? What is the active cause of the escape of bubbles of gas from the cut end of the stem? This gas cannot be air leaking through the shoot, for were it so there would necessarily be a fall of the tension indicated on the dial: it is gas derived from the tissue of the stem, some of it, possibly, escaping out of solution in the water of the tissues. Various explanations of the escape of this gas might be suggested: but as the matter is a purely physical one, I will not attempt to discuss it in detail. For my own part, I incline to the view that the escape of bubbles is due to a stress exerted upon the water in the tube by the suction-force of the branch, with the result that water is absorbed and gas expelled in corresponding volume; and that, consequently, the tension indicated on the dial is not a measure of the tension of the gases (negative

pressure) in the branch, but is a measure of a tensile stress exerted by the branch.

The escape of bubbles of gas from the cut surface of the shoot into the apparatus does not, at the moment, affect the position of the indicator on the dial, because the gas is at the same tension as the water in the apparatus: but as the gas evolved at lower tensions is removed from the tubes and accumulates in the reservoir *A*, it will gradually expand as the tension increases, and thus lowers the absolute measurements of the tension obtained.

A point of interest is the consideration of the different tensions at which gas-bubbles begin to escape from the cut surfaces of the shoots. In the case of the Beech I have the following tensions recorded:—13, $16\frac{3}{4}$, $21\frac{1}{4}$, 16, 5, $9\frac{3}{4}$, $13\frac{1}{2}$ inches; and in the case of *Helianthus* 5– $7\frac{1}{2}$ in. The tension at which bubbles begin to escape would seem to be determined by the degree of tension of the fluids in the shoot at the beginning of the experiment; for I found that the tension was relatively high when the shoot had been previously well supplied with water, and relatively low when this was not the case. For instance (June 18), a branch of Beech which had been standing in darkness with its cut end in water for twenty-seven hours began to evolve bubbles at a tension of 5 in.: but after remaining all night connected with a tube by which water was injected into its cut surface by a slight siphon-action, it did not evolve bubbles next morning (June 19) until the tension reached $9\frac{3}{4}$ in. In most cases no gas was evolved by shoots from which all the leaves had been removed, in consequence, probably, of the low tensions attained.

The highest tensions which I have observed are 23 inches of mercury with the Beech, and $23\frac{3}{4}$ in. with the Yew, tensions which would raise water to a height of about 24–25 feet, in the case of relatively small shoots. This important fact being established, it becomes necessary to distinguish the factors which co-operate in developing so considerable a force.

In the first place, the enquiry may be made as to the relation between the bulk of a shoot, as a whole, and its suction-force; and for the purposes of such an enquiry the following data, referring to four different branches of Beech, are available :—

<i>Branch.</i>	<i>A.</i>	<i>B.</i>	<i>C.</i>	<i>D.</i>
Length of main shoot . . .	7 ft.	5 ft.	6 ft.	5 ft.
Diameter of cut surface . . .	$\frac{5}{8}$ in.	$\frac{3}{8}$ in.	$\frac{1}{2}$ in.	$\frac{1}{2}$ in.
Number of leaves . . .	1150	320	755	594
Maximum tension observed . .	21 $\frac{1}{2}$ in.	14 $\frac{1}{4}$ in.	16 $\frac{1}{4}$ in.	23 in.
Gas-bubbles evolved at tension of	21 $\frac{1}{4}$ in.	11 in.	11 in.	12 in.

Now the 'bulk' of a shoot includes the important factor of the leaf-area, a factor which might well be thought to be preponderant. But a consideration of the foregoing figures shows that no definite relation can be traced between the leaf-area of the four branches and their suction-force. This remarkable fact comes out even more strikingly when the leaf-area of one and the same branch is diminished at intervals by the removal of some of the leaves, as follows (the letters refer to the branches already mentioned):—

Shoot A.

<i>Time.</i>	<i>No. of leaves.</i>	<i>Indicator travelled.</i>	<i>No. of leaves removed.</i>
June 5. 11.10–noon . . .	1150	0–21 $\frac{1}{2}$ in. max.	(330)
12.10–1.5 p.m. . . .	820	0–20 „ „	(270)
1.20–2.35	550	0–18 $\frac{1}{2}$ „ „	(195)
2.45–3.40	355	0–20 „ „	(110)
3.50–5.40	245	0–18 $\frac{1}{4}$ „ „	
June 6. 10.35 a.m.–12.50 p.m.	245	0–20 $\frac{3}{4}$ „ „	(245)
1.10–3.50 p.m. . . .	leafless stem	0–4 $\frac{3}{4}$ „ „	

Shoot B.

June 9. 1–4.30 p.m. . . .	320	0–13 $\frac{3}{4}$ „ „	(81)
„ 11. 11.45 a.m.–6.15 p.m..	239	0–9 $\frac{1}{2}$ „ „	(94)
„ 12. 12.15 p.m.–5 p.m. . .	145	8 $\frac{1}{2}$ –12 $\frac{1}{4}$ „ „	(102)
„ 15. 3.50 p.m.–5 p.m. . .	43	0–5 $\frac{1}{2}$ „ „	

Shoot C.

June 19.	10.15-11.45 a.m.	.	755	0-15½ in.	(400)
	12-12.40 p.m.	.	355	0-16¾ „	(212)
	12.45-1.30 p.m.	.	143	0-15½ „	(82)
	1.50-5.20 „	.	61	0-16¼ „	(61)
	5.35 p.m.	.	indicator	= 16¼ „	
June 20.	3.5-9.45 p.m.	.	leafless stem	= 0-8½ „	

Shoot D.

June 24.	1 p.m.-5 p.m.	.	594	0-23 in.	(250)
„ 25.	9.50 a.m.-4 p.m.	.	344	0-18½ „	
	4.30 p.m.	.	indicator	= 18½ „	
	4.45 „	.	„	= 18½ „	

The bulk of the branches themselves, as distinguished from the leaves which they bear, seems to have some relation to the suction-force of a shoot. For instance, a shoot (C) of Beech, from which all the leaves had been removed, gave (June 22) a maximum tension of $8\frac{3}{4}$ in. Next day about 18 ft. of lateral branches were cut off, leaving a bare main axis about $3\frac{1}{2}$ ft. long, which gave a maximum tension of $5\frac{1}{4}$ in.: the two experiments were of about equal duration (23 hours).

In connexion with these observations it is worthy of note that in the earlier experiments on the effect of the removal of leaves, I was careful to close the cut surfaces of the branches by means of melted paraffin in order to exclude air; but in the later experiments I omitted this precaution (e. g. Beech shoot C) without any apparent effect upon the tension subsequently developed. This was also the case in an experiment with *Helianthus*: a shoot had developed and maintained for some hours a tension of $7\frac{1}{2}$ inches; I cut off the two largest leaves at 3.30 p.m., leaving the wounds open; at 3.45 the tension was still $7\frac{1}{2}$ inches. I then cut off all the remaining leaves, readjusted the apparatus to zero, and obtained the

following record from the bare herbaceous stem, about 2 ft. long:—

June 17, 3.50 p.m.	Indicator = 0 in.	June 18, 9 a.m.	Indicator = $7\frac{3}{4}$ in.
4 "	" = $\frac{1}{2}$ "	10 "	" = $7\frac{3}{4}$ "
5 "	" = $1\frac{1}{2}$ "	11 "	" = 7 "
6 "	" = 2 "	Noon	" = 7 "
		2 p.m.	" = 7 "

whence it appears that, in the Beech and the Sunflower at any rate, air cannot penetrate centripetally into the vascular tissues of the plant by means of open wounds at the surface. This I found to be true also of the Yew.

But to return to the question of the relation between leaf-area and suction-force. From the foregoing figures it would appear that the suction-force of a shoot is not immediately dependent upon the leaf-area; and in fact the case of *Helianthus* indicates that an herbaceous stem deprived of its leaves can develop almost as high a suction-force as when the leaves are present. Nor does it appear that the maximum tension is always attained more rapidly with a larger than with a smaller number of leaves. Considering the foregoing data from this point of view we get the following results:—

	No. of leaves.	Max. tension.	Time required.
Beech. Shoot A.	1150	$21\frac{1}{2}$ in.	35 minutes
	820	20 "	55 "
	550	$18\frac{1}{2}$ "	105 "
	355	20 "	55 "
	245	$18\frac{1}{4}$ "	110 "
	leafless stem	$4\frac{3}{4}$ "	160 "
Shoot B.	320	$13\frac{3}{4}$ "	210 "
	239	$9\frac{1}{2}$ "	390 "
	43	$5\frac{1}{2}$ "	70 "
Shoot C.	755	$15\frac{1}{2}$ "	90 "
	355	$16\frac{3}{4}$ "	40 "
	143	$15\frac{1}{2}$ "	45 "
	61	$16\frac{1}{4}$ "	220 "
Shoot D.	594	23 "	270 "
	344	$18\frac{1}{2}$ "	370 "

Results of a similar kind were afforded by the Yew. A branch (4 ft. long; diam. cut surface = $\frac{1}{2}$ in.) gave (July 3-4)

a maximum tension of $23\frac{3}{4}$ in.: on the morning of July 4, leafy twigs were removed from it so as to reduce its leaf-area by at least two thirds, and it then gave (July 4-5) a maximum tension of 23 in. On the removal of the whole of its leaves, the tension (July 5-6) reached $18\frac{1}{4}$ in.

However, these figures also show that in certain cases the reduction of the leaf-area did materially lower the maximum tension and prolong the time required to attain it, though not to the extent that might have been expected. The leaf-area is, then, a factor in determining the maximum tension attainable by a shoot, but it is not the only factor; what the other factors may be has yet to be ascertained. It seems to me probable that one other factor is the antecedent condition of the shoot. When the transpiration of a shoot, previously to an experiment, has been greater than its absorption of water, a considerable tension is set up within it; this tension appears to persist as an after-effect, and to enable the shoot to develop a high tension in a subsequent experiment, even though its leaf-area is largely diminished. This is the only way in which I am able to account for some of the observations tabulated on the previous page. The remarkable behaviour of the leafless stem of *Helianthus*, I attribute in part to the fact that the stem is itself an efficient organ of transpiration.

I come now to another enquiry, the enquiry, namely, as to the relation between the life of the shoot and its suction-force. I have not been able to make many observations in this direction, but such as they are, they give some indications.

A branch of Beech (*D*) with 344 leaves gave (June 25) a maximum tension of $18\frac{1}{2}$ in. It was left all night with 10% solution of copper sulphate (CuSO_4) being injected into it by a 3 ft. siphon: on the following morning, drops of the copper-solution were exuding from wounds where small branches had been cut off, but the leaves still looked fresh and green: that day a maximum tension of $14\frac{3}{4}$ in. was attained, and, after being left all night, the tension indicated next morning (June 27) was $14\frac{1}{4}$ in., the fall being due to an

accumulation of gas. It was then dismantled, and placed with its cut end in the copper-solution for forty-eight hours (till June 29). On this date the leaves were discoloured and shrivelled: the shoot was then placed in connexion with the apparatus, and after a prolonged experiment (9.50 a.m.—4.45 p.m.) a maximum tension of $4\frac{1}{4}$ in. was registered. In a subsequent experiment (July 2–3) with the same branch, after all the leaves had been removed, the maximum tension observed was $4\frac{1}{4}$ in. Again, a vigorous shoot (*D*) of *Helianthus* gave (July 19–20) a maximum tension of $9\frac{1}{4}$ in.: it was then injected for twenty-four hours with copper sulphate solution, when it became discoloured and flaccid and gave a maximum tension of 5 in. Hence it appears that the suction-force of a dead shoot is very much less than that of a living one; and more especially that dead leaves contribute but little to the development of suction-force in a shoot, a result which is confirmatory of conclusions recently arrived at by Dixon¹.

When, however, the suction-force of living and dead *leafless* branches is compared, the difference is less considerable; in one case the difference was in favour of the presumably dead branch. The following are illustrative experiments:—

Taxus (Shoot *B*).

- a.* Bare branch after injection with water (24 hours):—
July 7, 9.30 a.m.—July 8, 9.30 a.m.—Max. tension = $16\frac{1}{2}$ in.
- b.* Same branch after standing in and injection with CuSO_4 solution (80 hours):—
July 11, 7.45 p.m.—July 15, 10 a.m.—Max. tension = 19 in.

Taxus (Shoot *C*).

- a.* Bare branch after injection with water (16 hours):—
July 28, 9.15 a.m.—3 p.m.—Max. tension = 9 in.
- b.* Same branch after injection with CuSO_4 (16 hours):—
July 29, 9.30 a.m.—4.30 p.m.—Max. tension = $7\frac{3}{4}$ in.

Helianthus (Shoot *C*).

- a.* Leafy shoot injected with water (12 hours):—
July 18, 9.30 a.m.—6.30 p.m.—Max. tension = $8\frac{1}{4}$ in.
- b.* Same shoot, deprived of leaves, injected with water (14 hours):—
July 19, 11 a.m.—7.30 p.m.—Max. tension = $6\frac{1}{4}$ in.

¹ Note on the rôle of Osmosis in Transpiration; Proc. Roy. Irish Acad., III, No. 5, 1896, p. 767.

- c. Same bare shoot, injected with CuSO_4 (14 hours) :—
 July 20, 11 a.m.—July 21, 9 a.m.—Max. tension = $4\frac{1}{4}$ in.

Fagus (Shoot *F*).

- a. Bare branch, after injection with water (21 hours) :—
 July 24, 9.30 a.m.—6 p.m.—Max. tension = $9\frac{1}{4}$ in.
 b. Same branch, after injection with CuSO_4 (13 hours) :—
 July 25, 9.15 a.m.—7.30 p.m.—Max. tension = 8 in.

It may be explained that the reason for injecting with water in several of the above observations was to remove any possible after-effect from previous transpiration ; and, further, to render the results of these observations strictly comparable with those obtained with branches injected with solution of copper sulphate.

The question as to the influence of external conditions (heat, light, &c.) on the suction-force of branches is one to which I have been unable as yet to give much attention. I have, however, observed in many experiments that the tension increases more rapidly when a branch is directly exposed to the sun, but I have not specially investigated the point ; I hope to return to it on a future occasion.

In conclusion, I may perhaps venture upon some suggestions as to the bearing of my observations upon the theory of the transpiration-current in entire plants. Whilst it must be admitted that the ultimate motive power is the transpiration of the living or the evaporation from a dead branch, it is by no means clear what the intermediate or subsidiary forms of force may be. Both Askenasy and Dixon attach importance to osmotic processes taking place in the tissues intervening between the conducting wood and the evaporating surface : but it would appear that these processes cannot be of primary importance, since, as my observations prove, a high suction-force can be generated by a branch which is saturated with solution of sulphate of copper. Facts such as this point to the importance of the imbibition-force of the cell-walls—to which Askenasy draws attention—rather than to that of the osmotic force of their contents. Then, again, Dixon and Joly—and Askenasy essentially agrees with them—state that the suction-force conveys water through the wood ‘by exerting a simple tensile stress on the liquid in the conduits,’ a statement which they cannot be said to have proved, however

plausible it may be. For my own part, I am at a loss to explain on this theory the results which I have obtained as to the suction-force of leafless branches, whether living or dead : for whilst the transpiration of a leafy branch may theoretically suffice to set up a considerable suction-force of the nature of a simple tensile stress on the water in its wood, it is, I think, questionable if the transpiration of a leafless branch would suffice to set up a tensile stress corresponding to the suction-force observed. I am, in fact, inclined to conclude that the imbibition-force of the wood plays a more important part in the conduction of the transpiration-current than is generally admitted at present. It may be that von Sachs' imbibition-theory does not afford a complete explanation of the mechanism of the transpiration-current ; but it seems to me that his theory includes some at least of the essential elements of a complete explanation.

But whatever may be the ultimate physical nature of the suction-force, my observations show how considerable is the force which a relatively small shoot can exert ; and though there are no data available for a conclusion as to the mode of summation of the suction-forces of the various branches of a tree, yet it is intelligible how that they together constitute a force which suffices to raise water from the roots to the topmost twig. At the same time, I do not consider it probable that the suction-force of branches such as I used, is ever so great in nature as I have found it to be. For in these experiments the branches continued to transpire for hours without absorbing any water ; whereas, in nature, the demand of the branches for water would doubtless be supplied by the roots long before the suction-force had attained anything like such dimensions. These experiments illustrate an extreme case.

I am conscious that these observations are by no means complete—in fact they are merely preliminary. I will therefore not at present attempt any further discussion, still less any more definite conclusion.

Vines, Sydney Howard. 1896. "The suction-force of transpiring branches."
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