PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Relation between Transpiration and Stomatal Aperture

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IX. *On the Relation between Transpiration and Stomatal Aperture.*

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Contents.

§ 1. Introductory.

The subject of the present paper was briefly discussed in a former communication.* The porometer there described was used to estimate changes in stomatal aperture by observing the variations in the rate of flow of an air current drawn through the stomata of an uninjured leaf under a given pressure.

In § 3, p. 139, the porometer was compared with Stahl's cobalt method and my own horn hygroscope. It is superior to both these, which only give *indirectly* any information about the stomatal aperture. It is true that if the stomata close, *e.g.* in darkness, the readings of the horn hygroscope diminish, but, since transpiration is diminished by darkness quite apart from stomatal closure, the lower reading of the hygroscope may, indeed must, be partly independent of the closure of the pores. The same objection applies to the cobalt method, valuable though it is. The use of the porometer is in one way superior to Lloyd's† microscopic method, which consists in measuring the stomata in strips of cuticle forcibly removed from the leaf and fixed in absolute alcohol, since the porometer gives information about the living uninjured stomata. On the other hand, it does not tell us the dimensions of the stomata: it only gives variations in the rate of flow of air through these openings, which changes, however, must depend in some way on changes in the stomatal apertures. In our original paper‡ the use of the porometer was illustrated in various ways: the closure

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* F. Darwin and D. F. M. Pertz (3) (see Literature, p. 437).

† Lloyd (6).

‡ F. Darwin and D. F. M. Pertz (3).

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of the stomata in darkness and their re-opening in light; the effect of withering, *i.e.* the preliminary opening of the stomata followed by closure, etc. The problem which forms the subject of the present paper, *i.e.* the relation between stomata and transpiration, is but briefly illustrated in the paper. Only a single experiment was given to show the parallelism which occurs between the variations in aperture of the stomata and in the rate of transpiration. In the present essay I hope to establish the fact that this parallelism holds good within certain limits. There are, indeed, frequent irregularities in the experiments, as disturbing causes cannot be avoided; but when the general correspondence between the results of a large number of experiments is considered, it seems to me impossible to accept LLOYD'S dictum* with regard to stomata—that "their regulatory function is almost *nil*." It must in justice be said that he elsewhere modifies this sweeping assertion. He allows (p. 35) that "complete closure of the stomata, if this occurs, reduces transpiration to, or nearly to, cuticular rate." He also grants that the stomata give the upper limit of transpiration; that is to say, when the stomata are open to their utmost limit the highest rate of transpiration under these conditions is the maximum of which the leaf is capable. Anyone who has been familiar, as I have, with the *general* parallelism in the curves of transpiration and stomatal aperture in obedience to changing conditions cannot possibly give in to what must be called the illogical position just referred to, that in the intermediate conditions, when the stomata are neither shut nor widely open, the regulation is not chiefly stomatal but depends rather on other factors. I can only suppose that there is some flaw in Mr. LLOYD'S method which has escaped even his careful and conscientious manner of attacking the problem. He gives his readers every chance of estimating the accuracy of his results. The present paper shows the unavoidable uncertainties which attend the subject, and no one can read Mr. LLOYD'S account of the matter without realising the pains he took to get a trustworthy result.

As soon as it was obvious that the readings of the porometer were rapidly and greatly depressed by darkness and restored to their previous point by re-illumination, it was clear that here was a method of testing the relationship between transpiration and stomatal behaviour. In observations with the porometer and potometer, carried out simultaneously on a transpiring plant during alternate periods of light and darkness, it became clear that the rise and fall of the curve constructed from the readings of the porometer did not correspond in magnitude with the transpiration curve. It is true that the two curves rose and fell together, but the amplitude of the porometer curve was much greater than in the case of transpiration. When, however, the curve of stomatal behaviour was constructed from the *square roots of the porometer readings* a much closer approximation to parallelism was obtained. It seemed possible that here was a case in which the formula might apply which was suggested by Sir J. LARMOR and employed by Messrs. BROWN and ESCOMBE in their paper on

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* LLOYD (6), p. 45.

"Static Diffusion"*; I therefore applied to Sir J. LARMOR, who gave me his assistance in the kindest way.

He points out that: "(i) The speed of diffusion through a narrow aperture† between two open spaces is proportional to its diameter. (ii) The speed of a stream of air through such an aperture, between open spaces having different pressures in them, is proportional to its area if the effect of viscosity can be neglected, but proportional to the 3/2 power of its area if viscosity is preponderant. Which of these conditions prevails, or whether the circumstances are intermediate, in a given case, depends on the diameter of the aperture."

If we assume that viscosity is not important, we have diffusion proportional to the diameter and flow of air proportional to area of the stomatal pore; or, in other words, transpiration is proportional to the square roots of the numbers representing the rate of flow of air as measured by the porometer.

It seems to me, however, that stomata must, on the whole, be considered as tubes. Thus a widely open stoma of *Fouquieria splendens*, drawn by LLOYD,‡ has a tube-length roughly twice that of the width of the opening. We must therefore consider the case where the stoma is not to be reckoned an aperture in a relatively thin plate, but rather a tube whose length is greater than its diameter. "*Diffusion* through a long pipe or channel varies as the area, and *flow* through it depends on a reduced area owing to the flowing air adhering to the walls of the tube; in fact, it varies as the square of the area if the viscosity is predominant. Thus, if this is the case, provided the channels are of fairly uniform width,§ transpiration would be proportional to the square root of flow—the same law as that obtained for the case of holes in a thin plate."

Sir JOSEPH LARMOR was good enough to calculate the size of the stomatal pores in the ivy from the rate of flow of an air current through them, as indicated by porometer readings. The result was satisfactory, and will, I hope, be published when other similar calculations have been made.

§ 2. THE POROMETER.

A possible objection may be raised to the porometer, namely, that the rate of air-flow through the stomata is not directly proportional to the water-column in the apparatus. If this were the case it would be a source of difficulty. For instance, when the stomata are wide open it is better to use a low pressure, otherwise the column falls so quickly that accurate readings are impossible. Thus in bright light

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* BROWN and ESCOMBE (2).

† Sir J. LARMOR says that "a tube whose length is less than one-fifth of its diameter is practically an aperture for this purpose."

‡ LLOYD (6), p. 10.

§ The interstices between the cells within the leaf are wide irregular passages, so large that their exchanges with the outer air are regulated almost entirely by the narrow stomatal tubes which make the connection.

I might record the fall of the column from 12 cm. to 8 cm., *i.e.* the falling meniscus would be timed over 4 cm. at an average pressure of 10 cm., and let us assume that the result is 12 secs. As the stomata shut the number of seconds required increases, say, to 600. To avoid loss of time this can be diminished to 300 secs. by reading the fall of the meniscus from 11 cm. to 9 cm. This can again be reduced to 150 secs. by reading the fall of the column from 21 cm. to 19 cm., *i.e.* at an average pressure of 20 cm. When this is done in the course of an experiment it is quite clear from the graphic representation of the result that no error is introduced by sudden change of pressure. Nevertheless, it seemed worth while to test the matter with an artificial stoma, *i.e.* a capillary glass tube. With this in place of a plant it was found that the flow of air (for the rates of flow employed) is directly proportional to the height of the water column forcing air through the capillary.

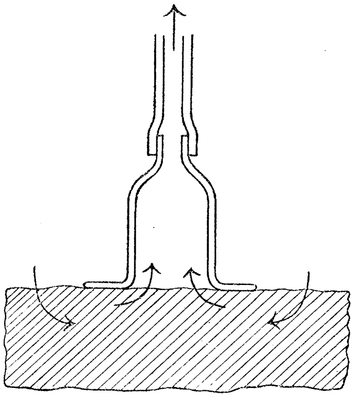

Fig. 1.

Another question is, What is the exact course of the stream of air sucked through the leaf?

We know that inside the chamber the air must flow from all open stomata, and it can be shown that the flow is here uniformly distributed. For if one half of the surface is painted with vaseline the rate falls to half of what it was, and when the half of the ungreased portion is again painted a fall to half the rate again occurs as shown in Expt. 89.

Expt. 89. December 14, 1910. Laurel Leaf fitted to Porometer Chamber by a Gelatine Washer.

	Seconds.		Reciprocals.*	Or as
		Average.		
11.36	9·4	9·3	107·5	3·99
37	9·2			
39	Half the surface of the leaf within the porometer painted with vaseline.			
40	17·2	17·4	57·5	2·14
45	17·6			
	Painted half of the remaining half so that a quarter of original stomatal area is now in action.			
48	36·9	37·2	26·9	1
50	37·5			
52	Remaining quarter painted.			
54			0	0

* Reciprocal × 10,000.

Considering that the halving and quartering of the stomatal surface were done by eye, the result is satisfactory.

But when we ask where lie the entrances of the streams of air indicated by the outer arrows in fig. 1 which emerge inside the chamber, the answer is not clear. It is certain, I think, that the stomatal surface of the leaf outside the porometer provides ample inflow,* since cutting the leaf through close to the porometer chamber does not seem to increase the rate of flow, and this can only mean that the fall of the column of water is ruled by the capacity for outflow and not by inflow. However this may be, there remains the fact that the flow of the air is through intercellular spaces. This raises the question whether or no these passages can be supposed to vary in size under changing conditions. From what is known of the varying turgor of leaves† it does not seem impossible that this is so. In any case, the intercellulars are huge passages in comparison with the stomata, which must, I think, be held to be masters of the situation.‡

A fault in the method used by me is that the illumination of the stomata within the chamber is necessarily not so good as that of the rest of the leaf, or of the other leaves on the branch, so that a comparison between the transpiration of the whole branch and the porometer readings is not accurate. The plan followed by BALLS§ and by Miss STEIN|| is free from this defect. In my experiments the leaf is supported on a glass plate with the stomatal side upwards, the flange of the chamber pressing on a washer or perforated disc of 20 per cent. gelatine (not shown in fig. 1) which makes the air-tight connection. BALLS§ and Miss STEIN|| attach the leaf by pressing it on to melted paraffin. In this way the upper surface of the leaf is fully illuminated as in a state of nature, though the lower stomatal surface is probably not so well lighted as it is under natural conditions.

§ 3. THE ERRORS INTRODUCED BY CUTICULAR TRANSPIRATION AND THE DIRECT EFFECT OF LIGHT.

In all our earlier work on the relation between transpiration and the readings of the porometer we assumed that a roughly trustworthy result might be obtained without taking account of either the *direct effect of light on transpiration* (*i.e.* the effect of light on the tissues apart from the reaction of the stomata) or the effect of cuticular transpiration. We merely recorded the relative changes in the rate of transpiration and in the square root of the porometer rate and compared them. It is not possible now to apply the necessary corrections to these experiments; nevertheless, they seem to me to be worth giving, for reasons which will appear later. In my paper¶ on the effect of the humidity of the atmosphere on transpiration I employed leaves, chiefly those of the laurel (*P. laurocerasus*), of which the stomata

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* Provided of course that there are more stomata outside the chamber than within.

† THODAY (8).

‡ The experiment of cutting the leaf is, in fact, a proof (as above suggested) that the stomata and not the intercellulars dominate the flow.

§ BALLS (1).

|| STEIN (7).

¶ F. DARWIN (4)

are closed by a coating of vaseline, while the intercellular spaces are connected with the outer air by cutting the lamina into strips. In this way the well-known fact of transpiration in saturated air was demonstrated, and a rough method of correcting transpiration for varying hygrometric conditions was pointed out. This method has been used throughout my work.

The transpiration of a greased and slit leaf has also been used for investigating the *direct effect* of light on transpiration.* The intensity of the light was not measured, the plants being simply exposed to a north, or in some cases east, light of the same varying character as that of the ordinary porometer experiments. It was found that with the laurel (*P. laurocerasus*) the direct effect of light varied much, the average being Light/Dark = 132/100, with ivy Light/Dark = 136/100. In order to get a convenient approximate number, I have assumed that the direct effect of light for ivy and for laurel is to introduce a factor 133/100, or 1·33.

With regard to cuticular transpiration—which was also neglected in my earlier experiments—I am not aware that any data exist for laurel or ivy. I have therefore, with the help of Miss PERTZ, made a series of observations on these plants. Although it is easy to block the stomata by rubbing the surface with vaseline, it does not follow that transpiration from the cuticle surrounding the stomata is entirely checked, though no doubt it is enormously diminished. It seemed, therefore, necessary to provide a thick layer of a greasy nature, and this was done by using detached leaves firmly pressed into a layer of vaseline contained in a shallow metal tray. The transpiration from the upper surface was thus obtainable†; the total cuticular evaporation could only be estimated by multiplying the amount by two. This is not satisfactory, since the character of the cuticle is not necessarily the same on the upper and lower surfaces. We may set aside the objection that a detached leaf does not transpire normally, for the series of weighings do not show any clear falling off, such as might be expected if loss of water-content affected the rate of transpiration.

In Table I we have the result of two days' observation on 12 ivy leaves, the transpiration being expressed in milligrammes per hour per 100 cm.^{2} at 60 per cent. ψ.‡ To get the total loss the averages 2·82 and 2·68 are multiplied by two as above mentioned. Thus, in saying that the cuticular transpiration of ivy is 5·5 mgrm. per hour per 100 cm.^{2}, I mean that this is the loss of a leaf whose outline encloses 100 cm., the actual surface exposed under natural conditions being, of course, 200 cm.^{2}.

The average cuticular transpiration is therefore 2·75 mg. in the dark for one surface of a leaf whose outline encloses 100 cm.^{2}. To get the whole cuticular transpiration of such leaf we multiply 2·75 by 2 = 5·5 mgrm. But since Expt. 428 A gives a relatively big result, I have thought it right to give transpiration calculated without 428 A; this works out at 3·9 mgrm. for two surfaces, upper and lower, each of 100 cm.^{2}.

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* F. DARWIN (5).

† The tray containing vaseline but without a leaf showed no loss of weight.

‡ Here and elsewhere the symbol ψ is used for the relative humidity of the air.

Table I.—Cuticular transpiration per hour of the upper surface of a single ivy leaf per 100 cm.^{2} at 60 per cent. ψ, in darkness.

Date.	No.	1st 24 hours.	2nd 24 hours.
		mgrm.	mgrm.
29.4.14	418 A	1·1	0·9
	B	1·4	0·9
1.5.14	419 A	1·3	1·1
	B	0·8	0·7
4.5.14	422 A	4·6	4·4
	B	3·0	2·6
7.5.14	424 A	0·8	1·0
	B	0·7	0·9
11.5.14	426 A	1·7	1·7
	B	2·3	2·0
13.5.14	428 A	11·5	11·5
	B	4·6	4·5
Sum		33·8	32·2
Average		2·82	2·68

The following Table (II) gives the cuticular transpiration similarly worked out for *P. laurocerasus.*

Table II.—Laurel. Cuticular transpiration per hour of the upper surface of the leaf per 100 cm.^{2} at 60 per cent. ψ, in darkness.

Date.	No.	Transpiration.	Date.	No.	Transpiration.
		mgrm.			mgrm.
18.11.13	N 18 . . .	3·3	7.4.14	A 7 i . . .	5·9
19.11.13	N 19 . . .	2·6		A 7 ii . . .	12·3
4.12.13		3·2	8.4.14	A 8 i . . .	11·9
24.1.14	386	3·9		A 8 ii . . .	18·4
2.2.14	388	5·9	19.5.14	431 A* . . .	6·0
27.3.14	410	2·1		B . . .	3·4
2.4.14	A 2	3·4	21.5.14	433 A . . .	7·4
3.4.14	A 3	4·1		B . . .	4·3
4.4.14	A 4 i . . .	10·8	25.5.14	434 A . . .	5·6
	A 4 ii . . .	7·1		B . . .	6·4
5.4.14	A 5 1 . . .	7·4	28.5.14	436 A . . .	5·7
	A 5 ii . . .	10·1		B . . .	12·9
6.4.14	A 6	3·3			
Average				6·70	

* The results of 431–436 are the averages of two successive days; the figures were :—

Day 1	5·9	3·4	7·2	4·2	6·7	7·2	5·4	12·5
Day 2	6·0	3·4	7·5	4·3	4·5	5·5	5·9	13·2

§ 4. The Correction of the Errors Discussed in § 3.

In this section I deal with the application of corrections for cuticular transpiration and for the "direct effect" of light, *i.e.* the relation between transpiration in darkness and in light *apart from the condition of the stomata.* As already stated, this difference is expressed by the fraction—

$$\frac{\text{Transpiration in light}}{\text{Transpiration in dark}} = \frac{133}{100}.$$

The correction for the effect of illumination is identical for laurel and ivy, but the values for cuticular transpiration are different for the two plants.

An example will illustrate the method of applying the corrections :

Ivy, Expt. 421. May 4, 1914.

	mgrm. per hour.
Transpiration, light	165·6
,, dark	48·2

The smaller value for cuticular transpiration is 3·9 mgrm. in the dark and 5·2 mgrm. in light.

$$165{\cdot}6 - 5{\cdot}2 = 160{\cdot}4$$
$$48{\cdot}2 - 3{\cdot}9 = 44{\cdot}3$$

The transpiration in light 160·4 must next be corrected by subtraction of a quarter of its value, corresponding to a diminution from 133 to 100. Thus the final value is 120·3/44·3 = 2·72, the original 165·6/48·2 = 3·44, thus the effect of correction is to reduce the value of Light/Dark from 3·44 to 2·72, *i.e.* from 126 to 100, or by 26 per cent. If a similar calculation is made with what is possibly a fairer value for cuticular transpiration, viz., 5·5 mgrm. in darkness and 7·3 mgrm. in light, the corrected value of the fraction 165·6/48·2 = 3·44 is 118·7/42·7 = 2·78, an amount which differs from the uncorrected value by 23 per cent. It seems, therefore, that correction for cuticular transpiration diminishes the error due to direct light effect, the diminution being greater when cuticular transpiration (in the case of ivy) is taken as 5·5 mgrm. in darkness, which is the result of the complete series of weighings. In what follows I have applied the above method of correction not to single experiments but to averages of series of results.

Table III gives in column I the transpiration in light divided by that in darkness, the values being uncorrected in both cases. Column II gives the fractions as decimals.

The numbers in column II fluctuate widely. On the whole, it seems that the abnormally high values belong to cases in which transpiration in darkness is small. In these cases accidental and unrecognised errors may largely influence the result, and the record becomes untrustworthy. The remaining data give a fairly consistent order of magnitude.

TABLE III.—Ivy, Experiments 421–452, May 4 to July 24, 1914.

No.	Date.	I.	II.
	1914.		
421	May 4 . .	165·6/48·2	3·44
423	,, 5 . .	19·8/17·3	1·14
429	,, 16 . .	110·5/46·4	2·38
432	,, 23 . .	141·5/31·3	4·52
435	,, 29 . .	65·9/16·9	3·90
438	June 2 . .	151·6/21·6	7·02
444	,, 8 . .	50·0/5·1	9·80
447	July 6 . .	119·2/10·4	11·46
449	,, 10 . .	76·3/33·0	2·31
450	,, 15 . .	142·6/5·8	24·59
451	,, 22 . .	78·8/12·2	6·46
452	,, 24 . .	89·6/3·3	27·15

The average of the fractions is obtained by dividing the average of the numerators by the average of the denominators, which in whole numbers is 101/21 = 4·81. When corrected for cuticular transpiration (5·5 mgrm. in dark or 7·3 mgrm. in light) the fraction becomes 93·7/15·5 = 6·05. This value corrected for direct light effect is 70·3/15·5 = 4·54, which differs from the uncorrected value (4·81) by 6 per cent.*

In another series with ivy, consisting of 14 experiments,† the uncorrected figures are Light/Dark = 74·4/25·9 = 2·87. When corrected for cuticular transpiration the value is 67·1/20·4 = 3·29. When corrected for light it becomes 50·3/20·4 = 2·47, which differs from the uncorrected fraction (2·87) by 16 per cent.

To recapitulate, the first series (421–452) consists of 12 experiments, the second of 14. In the first the difference between corrected and uncorrected results is 6 per cent., in the second 16 per cent.; the average error is 11 per cent. in round numbers. In my tabulated results (see § 6) the relation between potometer and porometer shows considerable irregularity, and an error of 11 per cent. is a comparatively small matter. We may therefore use "uncorrected" experiments without vitiating the conclusions.

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* The most divergent cases are Expts. 450 and 452: if these are omitted, the corrected result differs from the uncorrected by 3 per cent. instead of 6 per cent.

† Three (378–385) in December, 1913, and eleven (432–445) in June and July, 1914.

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TABLE IV.—Laurel. Transpiration Light/Dark, uncorrected.

No.	Date.	I.	II.
	1914.		
413	April 22 .	174/105	1·66
414	,, 23 .	144/21·4	6·68
415	,, 24 .	74·8/47·7	1·57
416	,, 27 .	66·7/21·4	3·11
417	,, 28 .	190/64	2·97
420	,, 30 .	79·5/55·6	1·43
425	May 11 .	116/47·3	2·45
427	,, 13 .	134/97	1·38

The average of the eight experiments is—

$$\frac{\text{Light}}{\text{Dark}} = \frac{122\cdot 4}{57\cdot 4} = 2\cdot 13.$$

Corrected for cuticular transpiration (13·4 mgrm. dark, 18·0 mgrm. light) we get 104·4/44 = 2·37.

Corrected for light this becomes 78·3/44·0 = 1·78. This is 20 per cent. less than the uncorrected result.

TABLE V.—Laurel, 7 Experiments, LA 10, etc., April 10–15, 1914.

No.	Date.	I.	II.
	1914.		
LA 10 (i)	April 10	250/57	4·39
LA 10 (ii)	,, 10	266/104	2·56
LA 11 .	,, 11	45/15	3·00
LA 12 .	,, 12	289/61	4·74
LA 13 .	,, 13	145/98	1·48
LA 14 .	,, 14	254/35	7·26
LA 15 .	,, 15	181/39	4·64

Average of seven uncorrected experiments Light/Dark = 204·3/58·4 = 3·50. Corrected for cuticular transpiration, 186·3/45 = 4·15. Corrected for light effect 139·7/45 = 3·10. Corrected result 11 per cent. less than uncorrected.

TABLE VI.—Laurel, 5 Experiments, 465–469 B, November 11–26, 1914.

No.	Date.	I.	II.
465	14.11.14	83·88/3·96	21·2
466	20.11.14	135·00/20·52	6·58
468	24.11.14	94·32/32·76	2·88
469 A	26.11.14	106·20/64·80	1·64
469 B	26.11.14	182·52/37·80	4·83

Here, as in Table III, we have, in one case, No. 465, a very high result in column II, correlated with a great closure of the stomata in the dark. This is not uncommon and cannot be treated as abnormal. The result is that the averages here made use of are not really trustworthy.

Uncorrected average, 120·4/32·0 = 3·76. Corrected for cuticular transpiration, 102·4/18·6 = 5·51. Corrected for light, 90·3/18·6 = 4·85. The corrected results are 22·5 per cent. *greater* than the uncorrected. The average error of the above 20 experiments on laurel is 18 per cent. in round numbers. This is greater than the error for ivy, but it is not so large as to vitiate seriously my uncorrected results.

§ 5. Graphic Representation of Results.

In this section the relation between transpiration and the condition of the stomata is given graphically by means of curves.

The line S gives in all cases the changes in the square root* of the porometer reading. Curve T gives the variation in the rate of transpiration. Where, as in fig. 2, the plant's loss of water was estimated by weighings, it is necessarily represented by a series of steps, whereas when the potometer is used to construct curve T we have illustration of the type of fig. 1A, in which T and S are of similar character. Weighing is no doubt the safer method, *i.e.*, more free from accidental undetected errors, but the potometer has countervailing advantages, and on it I have chiefly relied.

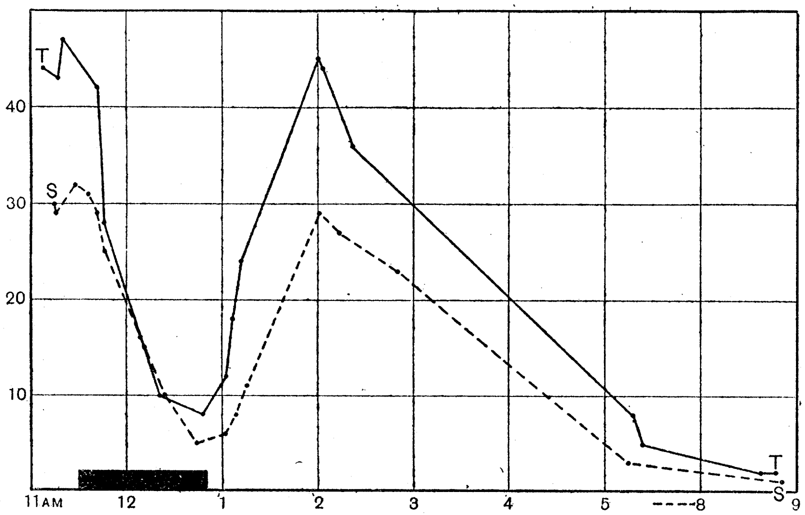

FIG. 1A.—Laurel, Expt. 76.

The potometer readings consist of the number of seconds in which the surface

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* As already stated, Sir J. LARMOR assumes that, in typical cases, the square root of the porometer reading is proportional to the size of the stomata, but for other forms of stoma some other function of the porometer readings would be more accurate. At any rate, it is certain that the square root of the porometer readings is far closer to the transpiration curve than are the actual porometer readings.

of the column of water travels over a given length of tube. The reciprocals give, therefore, a series of readings proportional to the absorption of water by the plant, and these, on the whole, must correspond to relative transpiration rates. The reciprocals were converted into whole numbers by multiplying them by some power of 10—generally by 1000. Thus in Expt. 76, p. 434, the first dot of curve T (11.8 A.M.) represents the flow of the water column through 1 centimetre in 22·8 secs., the reciprocal of 22·8 is 0·04386, which multiplied by 1000 = 43·86. This is given in the curve as 44·0.* In this instance, all the potometer readings were corrected to relative moisture of the room at 11.8 A.M., viz., 61 per cent.; the transpiration 43·86 therefore remains unaltered. The porometer readings are treated in the same way, *i.e.* the reciprocal of the number of seconds occupied by the fall of the water column is multiplied by a power of 10, and then the square root is entered in the appropriate place. One other change was occasionally made either for the sake of saving space in the diagrams, or of making the curves more comparable at a glance. Thus, if in fig. 1A (Expt. 76) each of the stomatal readings constituting curve S was increased by one-third of its value, the two curves would lie closer together: the first dot would be at 40 instead of 30, and their parallelism would be slightly more obvious.

Expt. 76.—*Laurel*, 14.10.10, branch having about 30 leaves. Temperature 13·9–16·1°. Relative moisture of air (= ψ)† = 58–69 per cent. Sunset 5 h. 9 m. P.M. Plant at east window and not exposed to sunshine.

A.M.	Potometer.	A.M.	Porometer.
11.8	43·9	11.15	29·6
17	43·1	16	29·1
22	46·5	28	31·8
31	Dark	31	Dark
42	41·8	37	31·2
46	27·5	43	28·6
12.11	15·1	47	24·6
22	10·3	12.9	15·5
48	8·3	24	10·2
51	Light	45	5·1
1.3	12·1	51	Light
7	17·5	1.2	5·6
12	23·8	10	7·7
2.0	44·9	16	11·4
3	43·8	2.1	28·9
23	35·8	14	26·5
5.17	7·8	50	22·9
24	4·9	5.13	3·1
8.38	2·2	8.50	1·3
47	2·4		

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* In most cases such a number would have been given graphically as 43·9, but in Fig. 1A whole numbers are given.

† The symbol ψ is used throughout for relative moisture of the air as determined by the wet and dry bulb thermometers, or occasionally by the polymeter. In all cases the transpiration is corrected for ψ.

Or if, instead of this, curve T were reduced by a quarter all through, the area of the figure would be reduced by bringing the curves closer to each other.

In what follows I have, on the whole, given figures without the details of the experiments on which they are founded: it seems desirable, however, to give two experiments fully, viz., those corresponding to figs. 1A and 2, in one of them transpiration being estimated by the potometer, the other by weighing.

The general similarity of curves S and T (*i.e.* the *stomatal* and *transpiration* curves) is very obvious in fig. 1A; thus there is a slight fall followed by a bigger rise in both before the great fall induced by darkness. The effect of darkness in T is a diminution from 47 to 8, in S from 32 to 5. These results, expressed in fractions, are: T = 47/8 = 5·88; S = 32/5 = 6·40. When the plant is brought back to light, T rises from 8 to 45, S from 5 to 29: or T = 45/8 = 5·63; S = 29/5 = 5·80. The final falls at 8.50 are T = 45/2 = 22·5; S = 29/1 = 29.

Expt. 7.—*Ivy*, 14.5.10.

In this experiment the ivy branch was cut the previous day and securely corked in a bottle of water, to which air was admitted by a capillary tube to allow for the absorption of water by the plant. The bottle had to be weighed without risk of disturbing the connection of the porometer chamber with the leaf, and, with this end in view, both plant and porometer were supported by an iron retort stand.

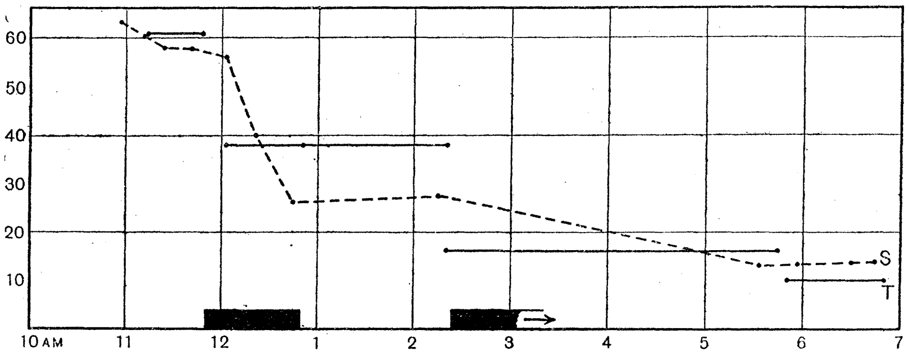

FIG. 2.

The weight was slightly over 8 kgrm., and the weighings, taken on one of Nemetz's balances, could only be made to 0·05 grm. Weighings were made at intervals of not much less than an hour and the loss reduced to grammes per hour, and as in all other cases corrected for relative humidity (ψ). During the experiment the temperature varied from 18·5° to 19·5° C., ψ (relative humidity) from 44 to 53 per cent.

It is not easy to compare the curves S and T, but if one imagines a line drawn through the centre of each of the horizontal lines it would clearly have a general resemblance to curve S. The most striking parallelism is in the complete absence of increased transpiration in light when the first dark period ceases, and the almost complete absence of change in the stomatal curve during the same time. The fall in transpiration in the whole experiment is clearly roughly similar to the fall representing stomatal closure, although, expressed arithmetically, it is not so close as it looks; thus transpiration T falls from 61 to 10 = 6·1, the stomatal curve S from 58 to 13·5 = 4·3.

A.M.	Transpiration.	A.M.	Porometer.
	grm. per hour.		
11.15	6·1	10.57	63·0
48		11.23	58·4
50	Dark	43	57·8
48	3·8	50	Dark
12.50		12.2	56·0
51	Light	22	40·3
50	3·8	44	26·3
2.23		50	Light
24	Dark	2.15	27·3
23	1·6	24	Dark
5.44		5.33	12·7
52	1·0	57	13·2
6.53		6.31	13·7
		44	13·5

Expt. 13.—*Ivy*, 10.4.10.

In this instance two ivy plants were used, one for transpiration, the other for porometer readings. In this and in the other weighing experiments in which pot-plants were used the pot was enclosed in a metal box, the lid being rendered vapour-tight by melted wax mixture, and the hole for watering the plant being closed with a rubber cork.

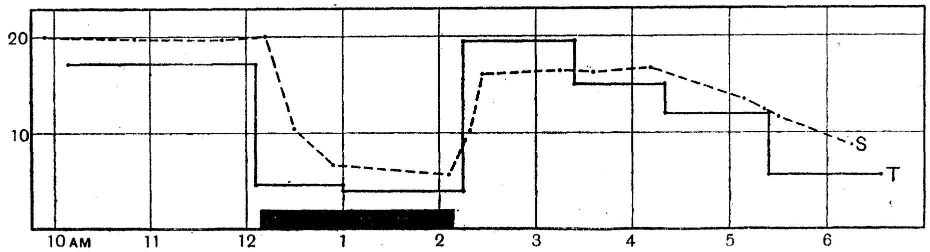

FIG. 3.

The general resemblance between S and T is obvious: the fall from the first to the third weighing period being approximately that of the fall in curve S, and the fall of both curves after about 4.20 P.M. being roughly similar. There is, however, no drop in S corresponding to the step between weighings 4 and 5 where T falls from 19·6 to 15·0 while S is practically horizontal. Also the rise in T when the plants are replaced in light at 2.15 is markedly greater, in about the proportion of 10 : 6.

Expt. 15.—*Ivy*, 3.4.10.

In this experiment the stomata were allowed to close naturally. The fall in curve T about sunset, *i.e.* 6·33, is obvious ; curve S also falls abruptly, shortly before 6 o'clock. It is clear that the curves S and T during the afternoon are roughly similar.

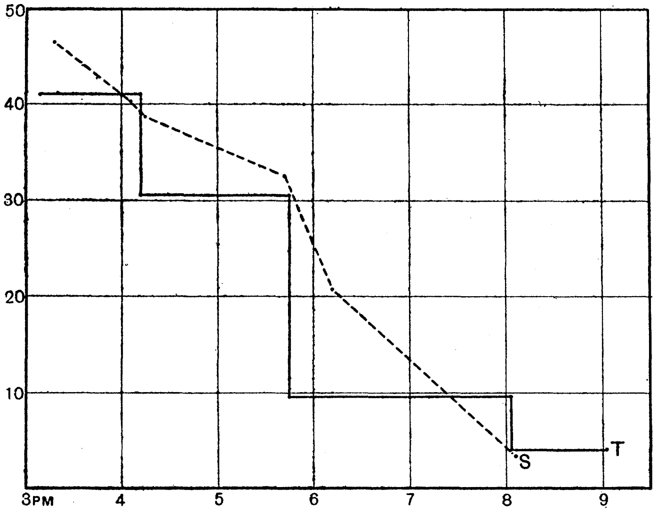

FIG. 4.

Expt. 34.—*Laurel*, 4.7.10.

For convenience of illustration the transpiration curve T is given in units equal to $\frac{1}{6}$ grm. instead of in decigrammes. In fig. 5 there is a striking discrepancy between the curves; from about mid-day to shortly after 1 P.M., S rises while T falls. The falls in the two curves when the plant was darkened are more congruous, though the drop in S from 28·3 to 11 (expressed as a fraction 28·3/11) = 2·57, the corresponding fraction for T being 3·66, a difference of about 40 per cent.

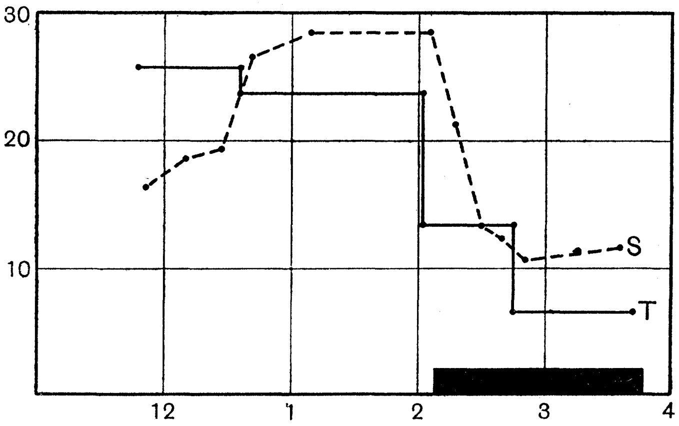

FIG. 5.

Expt. 50.—*Ficus elastica*,* 19.7.10 (fig. 6).

Curve T is given in units of $\frac{1}{3}$ decigramme. Here the fall and rise of S is clearly considerably less than that of T. Thus T falls from 28·8 to 4·2 (expressed as a fraction 28·8/42 = 6·8), while S falls from 22 (the average S-reading during the first weighing-period) to about 11; the fraction 22/11 = 2·0 being very small in comparison with 6·8, the corresponding value for T.

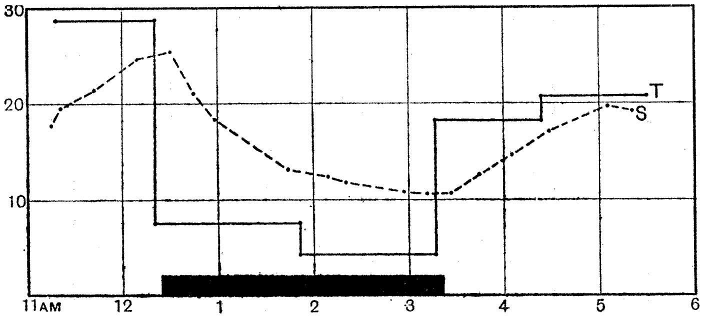

FIG. 6.

Expt. 50A.—*Ficus elastica*, 20.7.10 (fig. 7).

The final result is fairly satisfactory, *i.e.* if we compare the increase in transpiration (T) in the first and third periods with curve S for the corresponding times. But the rise in T at the beginning of the light period is clearly much more rapid than the rise in S.

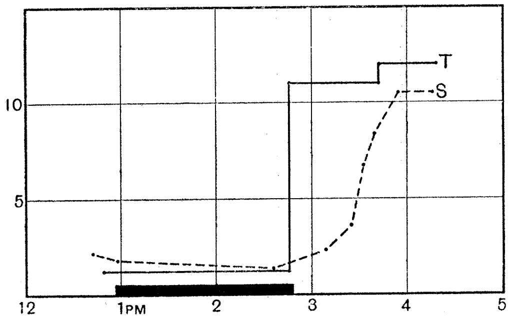

FIG. 7.

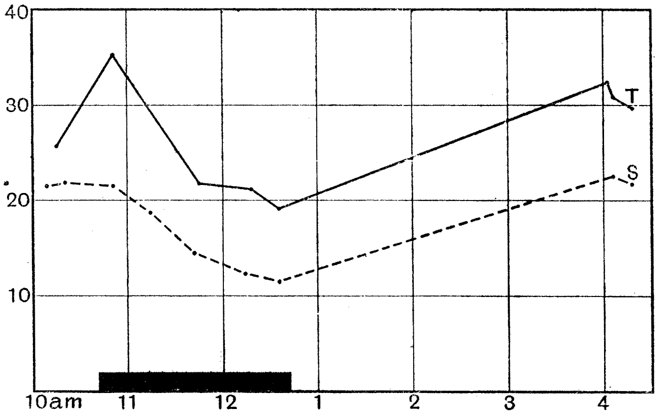

FIG. 8.

Expt. 22.—*Laurel*, 10.5.10 (fig. 8).

There is a clear general similarity in the patterns of curves S and T, but the rapid rise in T before the dark period is not represented in S.

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* It seems allowable to give two experiments on Ficus. They are not, however, included in the general statement in § 6, which is confined to ivy and laurel.

Expt. 23.—*Ivy*, 11.5.10 (fig. 9).

Here the general similarity between S and T is obvious. It is instructive to note that, nevertheless, the falls in S and T, numerically expressed, are by no means identical. Curve T drops from 45 to 13·5, and 45/13·5 = 3·33. If S is similarly treated we get 44/8·5 = 5·18, so that an obvious general resemblance may mask a difference of 56 per cent., since 5·18/3·33 = 1·56.

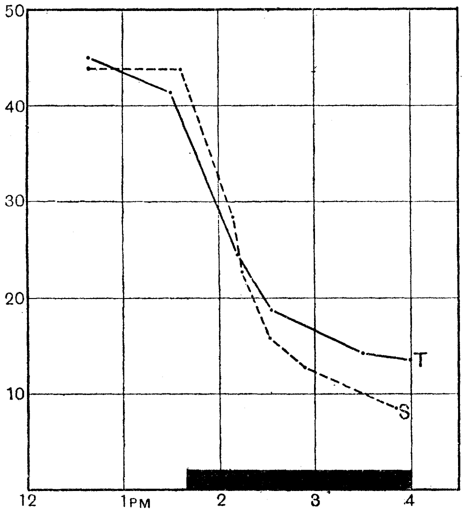

FIG. 9.

Expt. 35.—*Laurel*, 6.7.10 (fig. 10).

During the dark period there is a rough resemblance between S and T, for they both show a slackening in the rate of fall at 12.50. But the falls in the dark numerically expressed are discordant. T = 25·6/11·5 = 2·23; S = 20·0/12·2 = 1·64, *i.e.* a difference of 36 per cent. The chief error occurs at 1.50, when the light period begins, and S rises while T falls.

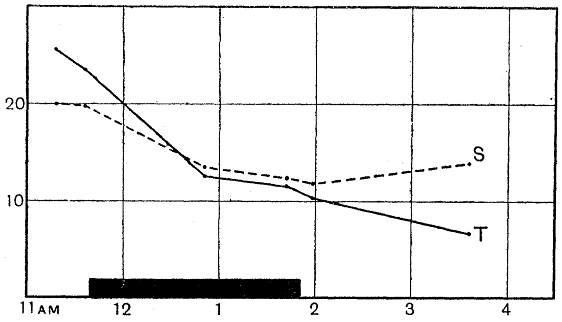

FIG. 10.

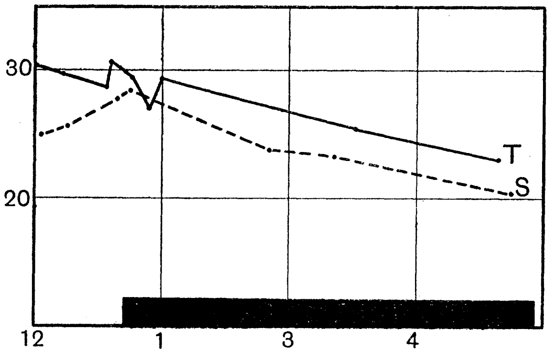

FIG. 11.

Expt. 90.—*Laurel*, 25.1.11 (fig. 11).

Here the effect of darkness is slight, but long continued, and is clearly similar in S and T. But before the dark period the curves run in contrary directions.

Expt. 94.—*Laurel*, 31.1.11 (fig. 12).

The curves are so far similar that S and T are both falling before the dark period, and both rise during an early part of that period, which is unusual. But the amplitude of T is markedly less than that of S. It is to be noted also that from 3 to 6 P.M. T rises very slightly, while S falls rapidly.

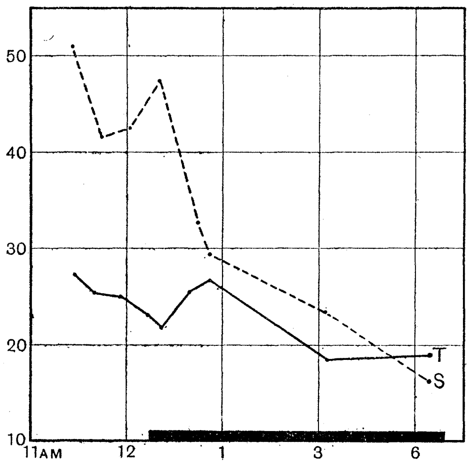

FIG. 12.

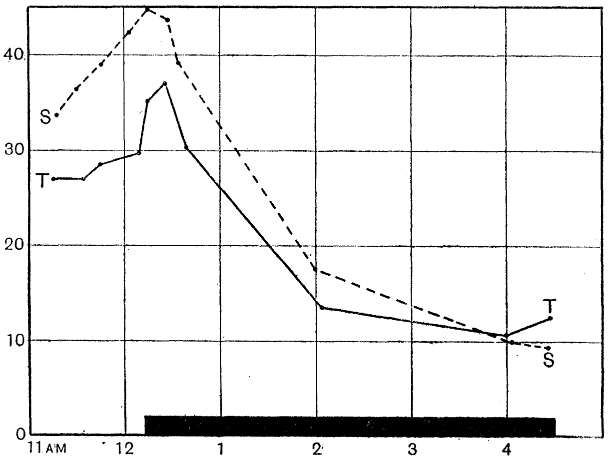

FIG. 13.

Expt. 95.—*Ivy*, 2.2.11 (fig. 13).

Here the general resemblance is striking, except during the final half hour; it should also be noted that the rise during the beginning of the dark period is continued longer in T than in S, but the first well-marked fall in S is contemporary with that in T.

Expt. 96.—*Ivy*, 3.2.11(fig. 14).

The chief feature here is that darkness produced no increase in the rate of diminution of T (transpiration), and that the contemporary fall of S, though perceptible, is slight.

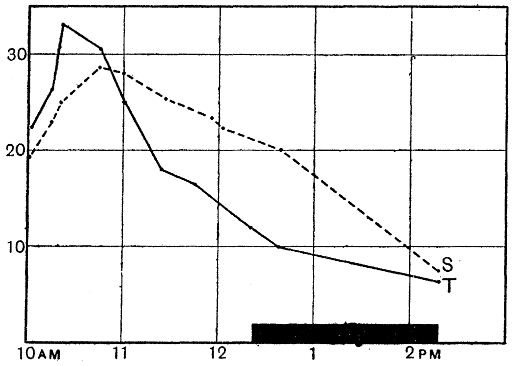

FIG. 14.

In both there is a well-marked rise between 10 and 11 A.M., followed by a fall long before the plant was placed in the dark room.

Expt. 98.—*Ivy*, 6.2.11 (fig. 15).

There is a close general resemblance between the curves during the dark period, namely, a rapid fall replaced by a slower one beginning in both S and T at noon. There is discrepancy in the light period, *i.e.* before 11.20.

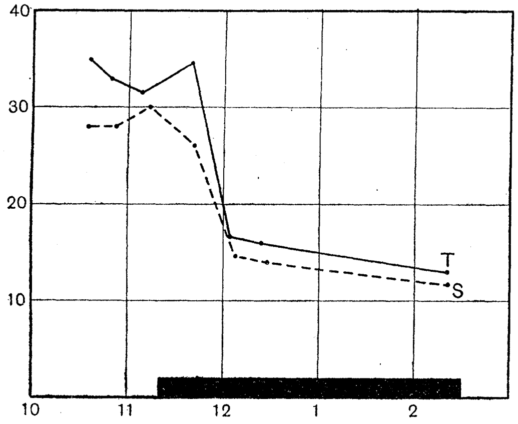

FIG. 15.

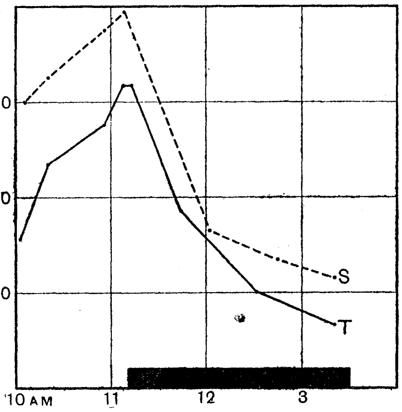

FIG. 16.

Expt. 100.—*Ivy*, 8.2.11 (fig. 16).

Here S and T are, on the whole, clearly similar. The chief differences are the steeper rise of T before darkness begins and the more sudden change of direction in S in the middle of the dark period.

Expt. 465.*—*Laurel*, 14.11.14 (fig. 17).

There is general similarity between the two curves, viz. : in both a slow rise from about 11 to noon, when both curves become horizontal; both fall suddenly in the dark; both become less steep just before 1 P.M. and become roughly horizontal about 3.30. If we express the darkening effect as a fraction (Light/Dark), we have $T = 23{\cdot}3/1{\cdot}1 = 21{\cdot}2$; $S = 25{\cdot}8/4{\cdot}1 = 6{\cdot}3$. Thus the drop in T is 3·4 times as great as that of S.

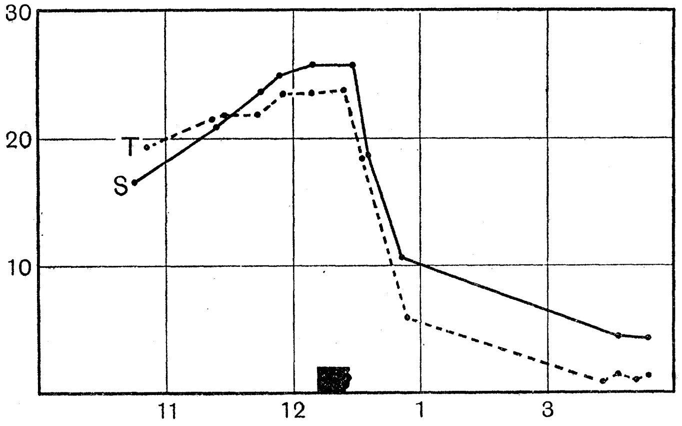

FIG. 17.

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* In Expt. 465 the curve of transpiration is accidentally dotted instead of curve S as in the other figures.

Expt. 106.—*Ivy*, 16.2.11.

Here the parallelism between S and T is sufficiently obvious almost throughout.

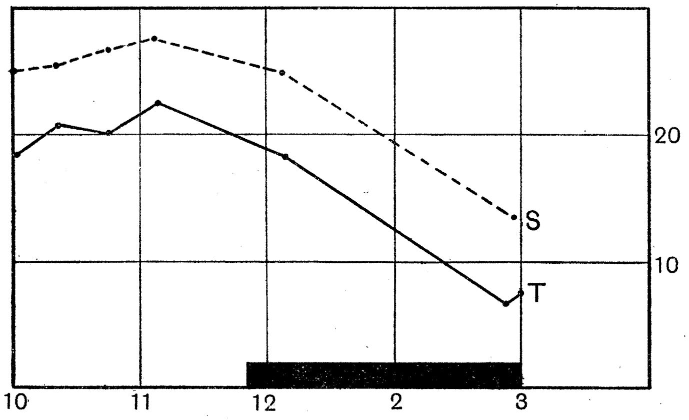

FIG. 18.

§ 6. THE RELATION OF TRANSPIRATION TO THE CONDITION OF THE STOMATA.

The present section gives in a tabular form the results of experiments on ivy and laurel. The experiments are selected as being trustworthy; the amount of variation in the results will show that many experiments are included which, taken by themselves, do not favour the thesis that transpiration varies as the stomatal aperture. The results are arranged in two columns, T and S, the first of these giving transpiration and the second the condition of the stomata as expressed by the square root of the porometer reading.

The numbers, *e.g.* the first in column T means that the transpiration in light (61·0) divided by transpiration in darkness (10·0) = 6·1, and a corresponding relation, 58/13·5, is expressed by the first number (4·3) in column S. If the fall in transpiration (column T) were exactly proportional to that representing the closure of the stomata (column S), it is obvious that the corresponding numbers in columns S and T should be equal to each other: this is clearly not the case, the relative transpiration being considerably bigger than the stomatal ratio.

TABLE VII.—Ivy. The following Table gives the relation between the effect of darkness on transpiration and on the condition of the stomatal aperture as revealed by the Porometer.

No.	Date.	T, Transpiration. Light/Dark.	S, $\sqrt{\text{Porometer}}$. Light/Dark.
7	14.5.10*	6·1	4·3
13	4.4.10*	4·3	3·3
15	3.4.10*	10·3	13·3
23	11.4.10	3·3	5·2
95	2.2.11	2·3	4·1
96	3.2.11†	2·0	2·3
97	4.2.11	2·8	4·5
98	6.2.11	2·4	2·6
99	7.2.11	4·0	10·0
100	8.2.11	4·8	3·4
101	9.2.11	2·5	1·0
102	10.2.11	3·4	6·2
103	11.2.11	4·1	8·5
104	14.2.11	7·3	4·1
105	15.2.11	3·5	2·4
106	16.2.11	3·0	2·0
107	18.2.11	2·1	2·9
N 8	8.11.11	5·4	4·5
N 11	11.11.11	5·3	4·8
161	23.6.11*	2·0	1·2
167	3.7.11	1·4	1·3
213‡	21.11.11	1·4	2·7
214	22.11.11	6·2	2·2
215	23.11.11	2·5	6·7
216	25.11.11	3·5	2·2
222	7.12.11	3·4	8·2
224	13.12.11	11·6	7·3
225	14.12.11	5·4	2·6
228 A	19.1.12	2·4	2·7
228 B	20.1.12	2·1	3·0
229§	24.1.12	18·7	3·4
230	25.1.12	1·7	1·3
231	27.1.12	2·0	1·2
232	29.1.12	1·0	1·5
233 A	30.1.12	1·6	1·2
234	31.1.12	1·9	1·2
235	2.2.12	1·7	1·6
237	7.2.12	4·1	1·3
238	14.2.12	1·7	1·6
240	26.2.12	5·0	4·2
241	27.2.12	2·1	1·2
242	29.2.12	6·1	4·2
243	1.3.12	5·4	1·9
421	4.5.14	3·4	5·9
423	5.5.14	1·1	8·9
429	16.5.14	2·4	6·8
432	23.5.14	4·5	12·4
435	29.5.14	3·9	4·0
438	2.6.14	7·0	5·6
444	8.6.14	9·8	13·4
447	6.7.14	11·5	17·1
449	10.7.14	2·3	8·8
450	15.7.14	24·6	13·2
451	22.7.14	6·5	3·5
452	24.7.14	27·2	13·9

* Transpiration estimated by weighing.

† The readings for S and T are, as a rule, taken just before the dark period. In Expt. 96 both curves fell before the dark period; if this fall is included, T = 4·2, S = 3·7.

‡ In the series 213–243 the fall in columns T and S was not produced by darkness but by removing the plants from a north window to the dull light in the middle of a large laboratory.

§ In Expt. 229, transpiration fell from 18·7 in light to 0 in darkness. This result should have been expressed in column T as infinity, which could not have been brought into the average of column T. I have therefore assumed that the transpiration fell to 1 in darkness, which introduces an error less serious than the omission of the whole experiment.

TABLE VIII.—Laurel. Giving for Laurel what Table VII gives for Ivy.

No.	Date.	T, Transpiration. Light/Dark.	S, √Porometer. Light/Dark.	No.	Date.	T, Transpiration. Light/Dark.	S, √Porometer. Light/Dark.
4	10.5.10	2·2	2·5	218	30.11.11	7·2	4·1
21	7.4.10	1·9	1·7	219	1.12.11	2·5	1·3
22	10.4.10	1·8	1·9	220	5.12.11	2·4	1·5
34*	4.7.10	3·7	2·6	226	16.1.12	1·2	1·3
35	6.7.10	2·2	1·6	227	17.1.12	1·7	1·6
75	10.10.10	8·0	4·2	381	11.12.13	1·4	1·7
76	14.10.10	5·9	6·4		12.12.13	2·6	4·3
90	25.1.11	1·3	1·4	382 A§	15.12.13	1·4	4·4
91	26.1.11	1·7	1·3	382 B	15.12.13	2·4	2·1
93	28.1.11	1·9	2·1	383 A	17.12.13	1·8	2·9
94	31.1.11	1·3	2·6	383 B	17.12.13	1·3	7·6‖
108	20.2.11	1·7	1·8	413	22.4.14	1·7	2·4
109	25.2.11	1·7	3·5	414	23.4.14	6·7	5·9
120†	15.3.13	1·1	1·4	415	24.4.14	1·6	1·8
121	16.3.13	1·3	3·1	416	27.4.14	3·1	5·5
122	17.3.13	4·1	18·2	417	28.4.14	3·0	1·9
124	20.2.13	1·7	4·4	420	30.4.14	1·4	2·0
128*	28.3.13	1·5	1·2	425	11.5.14	2·5	4·1
130	31.3.13	1·9	2·5	427	13.5.14	1·4	2·0
131	1.4.13	1·7	2·6	465	14.11.14	21·2	6·3
133	4.4.13	3·0	6·7	466	20.11.14	6·6	2·9
136*	10.4.13	3·4	2·9	468	24.11.14	2·9	4·7
166*	1.7.11	1·5	1·1	469 A	26.11.14	1·6	3·0
217‡	28.11.11	2·5	1·4	469 B	27.11.14	4·8	2·2

* In Expts. 34, 128, 136, 166 transpiration was estimated by weighing; in the remainder by means of a potometer.

† In the series 120–136 an attempt was made to avoid an error formerly referred to (see DARWIN and PERTZ (3), p. 140), namely that the porometer readings vary greatly from leaf to leaf on a given branch at a given hour. In Expts. 120–136 the twigs used had roughly half a dozen leaves each, and porometer readings were taken on from 3 to 7 leaves in most cases. In 133 and 136 such readings were taken on all the leaves. The figures in column S are obtained by taking the average of all the porometer readings on a given branch and dividing it by a similar average for darkness. It must be admitted the results remain unsatisfactory in spite of this treatment.

‡ In Expts. 217–227 the plants were "darkened" by being placed in the centre of a large room, *i.e.*, in dull light.

§ In Expt. 382 A the porometer was fixed to a different leaf to that used for 382 B; the same is true of 383 A and B. This shows once more how the stomata vary from leaf to leaf on a given branch.

‖ In Expt. 383 B the porometer readings were 7·6 in light, 0 in darkness. This means that the reading was so small as to be not recognisable. I have assumed the reading to be 1.

Tables VII and VIII are founded on observations in which no correction was made for cuticular transpiration or for the "direct effect" of light. But, since it has been shown in § 4 that these sources of error neutralise each other to some extent, we may consider the results as roughly trustworthy. I freely grant that great and inexplicable differences exist between many pairs of figures in columns S and T. These differences are so great that the obvious method of taking the averages* of the columns T and S is not allowable.

I have therefore expressed the results graphically in the subjoined diagrams.

Ivy.

The method employed is to divide each number in column T by the corresponding number in S. The result should be unity if the effect of darkness on transpiration were exactly the same as the corresponding effect on the stomatal aperture. If this were the case all the dots would be piled up on the line marked 1. The curve, however, culminates at the value 0·7, which is but a rough approach to unity. Since, however, each class differs from its neighbours by not more than 10 per cent., and as this is a small difference in relation to possible errors, it is allowable to transfer dots from any class to the next ones on either hand; in this way the free-hand curves in figs. 19 and 20 are drawn. I have omitted a single case in which $\frac{T}{S} = 5{\cdot}5$, which would unduly exaggerate the result.

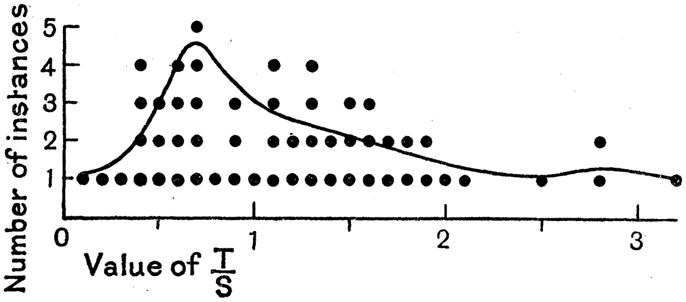

FIG. 19.

Laurel.

In the case of laurel the curve is smoother, and there is an obvious tendency for the values to group themselves round 0·9.

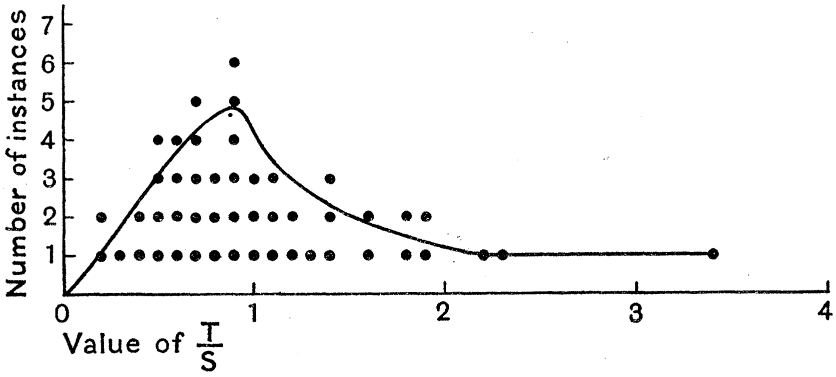

FIG. 20.

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* It happens that the averages of columns T and S for 103 experiments on ivy and laurel are very close to each other, differing only by 3 or 4 per cent. from the value 4·0.

Figs. 21 and 22 are of a different character; here the ordinates give the value of T from Tables VII and VIII, while the abscissæ are values of S. If the effect (T) of darkness on transpiration were equal to the same effect (S) on stomatal aperture, it is clear that the dots would make a line at 45°.

Ivy (fig. 21).

In fig. 21, taking the values from 0 to 6, there is, I think, a rough but undeniable tendency to group about the oblique line. The rest of the dots are irregular in position.

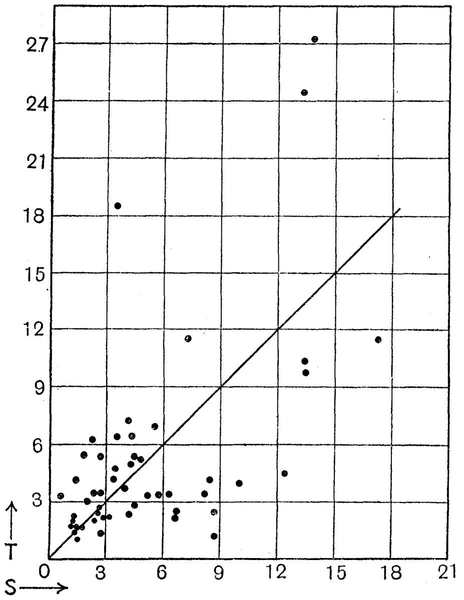

Fig. 21.

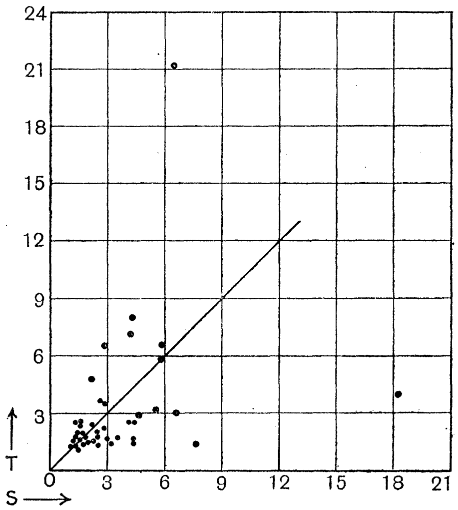

Fig. 22.

Laurel (fig. 22).

Here the dots between 0 and 3 are clearly grouped about the 45° line; those from 3 to 9 only make a rough approximation. Here, again, the outlying dots are far enough from the oblique line.

Conclusion.

The series of diagrams, figs. 1A to 18 (which might easily have been increased in number), supplies the most easily appreciable evidence for my thesis that transpiration is regulated by stomatal aperture. There are many irregularities, but on the whole there is a strong tendency to parallelism in the curves of transpiration and of stomatal condition.

It should be remembered that in nearly all cases stomatal aperture is taken from a single leaf, while transpiration is that of a number of leaves. Since stomatal aperture is known to vary widely from leaf to leaf, this is a clear source of error. It must be stated, however, that when (see p. 434) the stomatal aperture is taken from the average of several leaves on the same branch, some discordance between the values T and S still remains.

Tables VII and VIII summarise the experiments. They exhibit much irregularity, and for that reason have not been reduced to averages. They are graphically represented in figs. 19–22. These (in spite of much irregularity) show a grouping which points to a causal relation between transpiration and stomatal aperture.

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