# THE HUMIDITY GRADIENT AT THE SURFACE OF A TRANSPIRING LEAF

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(With Seven Text-figures)

## INTRODUCTION

Such observations as those of Leeson & Mellanby (1933) have drawn attention to the importance of the study of microclimates in insect ecology. It is becoming more generally realized that meteorological readings from a Stevenson screen do not necessarily give a true picture of the actual conditions under which the insect is living. Any attempt to establish a relation between the insect and the environment can only be successful if the environmental conditions in the immediate neighbourhood of the insect can be measured.

In the conclusion to his review, Buxton (1932) points out that one of the chief needs of an entomologist is an apparatus which is capable of measuring the humidity of a thin layer of air, such as that which exists over the surface of a leaf. That a humidity gradient must exist over the surface of a transpiring leaf is mathematically certain; the problem is not to demonstrate the existence of a gradient but to measure its extent. Mellanby (1933), using a paper hygrometer, found that in an atmosphere of 33% relative humidity at 39° C., the relative humidity near the upper surface of a cabbage leaf was 52% and near the lower surface 53%. The investigations in the present paper were prompted by the fact that one of us (C. G. B.) encountered this problem in the course of a study of the biology of the cabbage whitefly, *Aleurodes brassicae*. Certain apparatus has been constructed which enables some progress to be made in this direction, and it is the purpose of this paper merely to describe the apparatus with some of the results obtained using leaves known to transpire rapidly.

## DESCRIPTION OF APPARATUS

In the investigation of this problem it was decided to make all measurements under conditions of moving air, partly because such conditions normally prevail in nature and partly because of the difficulty of maintaining conditions of still air except on a very small scale. On the other hand, a rapid stream of air would undoubtedly tend to restrict the gradient very closely to the evaporating surface and make it more difficult to detect. The slow air stream used was thus a compromise between conditions tending to stability and conditions tending to allow a gradient of reasonable extent to develop.

The examination of the conditions above the evaporating surface may be approached in two different ways. First, one may endeavour to measure separately all three factors which contribute to the evaporative power of the air, namely temperature, humidity and wind velocity, or secondly, one may, by using an evaporimeter, measure their combined effects without attempting to evaluate the relative importance of each.

### (a) *The hygrometer*

In the first case we are measuring three related factors, to each of which an absolute value can be given. It is important, therefore, that the measuring instruments should disturb the conditions over the leaf surface as little as possible. In this respect Mellanby's method (1933) is not altogether suitable, since so large an object as the square centimetre of paper near or upon the leaf surface must very considerably affect the air flow over it. For the same reason any apparatus involving considerable changes of temperature in its use, e.g. dew-point apparatus, hot wires, etc., is to be avoided, since the convection currents set up may appreciably affect the air movement in the slow stream used. The temperature gradient can be measured by means of a fine wire thermocouple, without any more disturbance than that due to the thickness of the wire, and the wind velocity gradient may for practical purposes be taken as the same as that over a similar dry surface of the same dimensions and orientation. In order to measure the humidity a special hygrometer, involving only a single human hair about 1 cm. long, was constructed. This apparatus is shown in Fig. 1. The hair *h* was stretched between a fixed brass rod *r* and a movable lever *l* which was made out of a piece of watch hair-spring bent at right angles. The lever was free to move about the axis *s* which was a piece of oiled silk thread stretched between two springs *t*. The weight *w* maintained a slight tension upon the hair. Changes in length of the hair were recorded optically by means of a beam of light falling on the mirror *a* and reflected on to a scale; the zero on the scale was given by the reflexion from the mirror *b* which was fixed to the frame. Moving the whole apparatus up and down did not affect the reading which was given by the distance between the two spots of light on the scale.

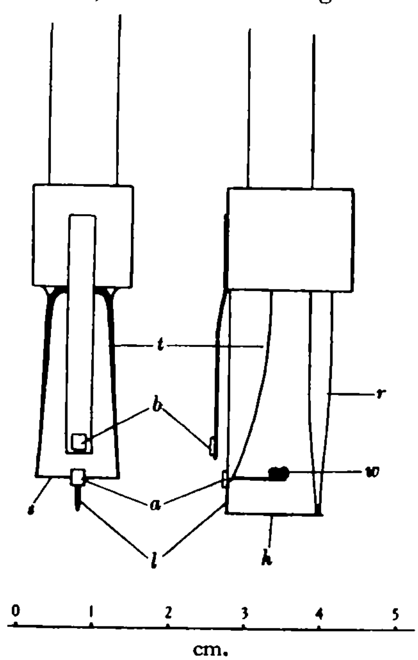


Fig. 1. The hygrometer. *a*, *b*, mirrors; *h*, hair; *l*, lever; *r*, brass rod; *s*, silk thread; *t*, spring; *w*, weight.

The apparatus was capable of being read to ± 1% relative humidity, but owing to hysteresis the readings cannot be taken as more accurate than ± 2·5%. It was found that in moist air, e.g. 90% relative humidity, the time taken for equilibrium to be reached was about 15 min., but in dry air, e.g. 10% relative humidity, the time was 1 hr. or more; consequently this apparatus was used only under conditions in which the oncoming air was fairly moist.

### (*b*) *The evaporimeter*

In the second case we are measuring the evaporative power of the air which is not an absolute value but one which can only be expressed relative to some known body from which water evaporates. It may seem strange that in the first case precautions are taken to avoid disturbing effects and in the second an evaporating body is introduced into the actual region under investigation. Apart from the fact, as stated above, that we are measuring different things in the two cases, it may further be pointed out that this paper is concerned with the study of the environment of animals and in so far as these lose water by evaporation they are more comparable to evaporimeters than to hygrometers. It is not proposed to enter here into a detailed discussion of the use of evaporimeters in animal ecology; but if there are three factors, temperature, humidity and wind velocity, which contribute to the evaporative power of the air, and if a true measure of the evaporative power with respect to the animal can be obtained from a single instrument instead of from three, that is an obvious advantage. For such a measure to be a true one under all conditions, it is necessary: (1) that the effect of each of the three factors upon the evaporimeter and upon the animal must be the same, (2) that the evaporimeter must be of approximately the same size and shape as the animal, and (3) that the absolute rate at which water evaporates from the evaporimeter must be of the same order as the rate of evaporation from the animal; this is particularly important in confined spaces. In the present case the evaporimeter is not referred to any particular animal and the results obtained from it have not therefore any particular significance. The justification for its use in the present experiments lies in the fact that it can be used to give an indication of the diffusion of water vapour away from a wet surface, and that since many more readings can be taken in a given time than with the hygrometer, a greater extent of the surface can be investigated.

It is necessary, however, to consider carefully what happens when one evaporating body is brought close to another. Fig. 2 represents the conditions when a small evaporimeter *A* is used to measure the evaporative power over the area *B* of a large wet surface in a current of air. The dots in the diagram are intended to indicate the presence and concentration of water vapour in the air above the surface. In position (1) the evaporimeter is outside the influence of the evaporating surface; it measures the evaporative power of the oncoming air. In position (2) the evaporimeter is within the influence of the water vapour coming from the wet surface, and to some extent the water vapour coming from the evaporimeter will affect the rate of evaporation from the wet surface, but only some distance down wind from *B*; the evaporimeter in this position gives a true measure of the evaporative power of the air.

But in position (3) the water vapour coming from the evaporimeter affects the region *B*, just as the water vapour from the region *B* affects the evaporimeter. The conditions in the air just above *B* are now different from what they were when the evaporimeter was in position (2). There must be a critical height below which this interference sets in.[1] This critical height is a function of the size of the evaporimeter,

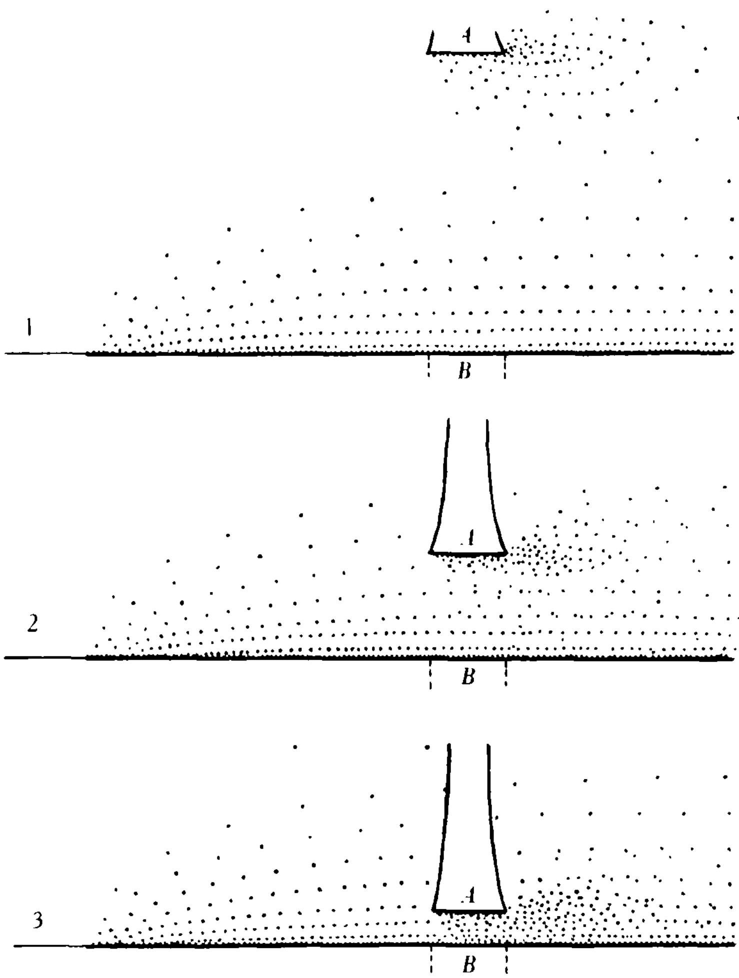


Fig. 2. For explanation see text.

being less when the size is less. Above the critical height the oncoming air (with respect to the evaporimeter) is conditioned by the large wet surface only; below the critical height it is conditioned partly by the evaporimeter itself.

The evaporimeter used in these experiments was made of a disc of cigarette paper, 2 mm. in diameter, placed on the end of a capillary tube filled with distilled

[1] This height is "critical" only in relation to the accuracy of measurements. In theory, the evaporimeter reading approaches a true measure only as the height approaches infinity.

water. The rate of evaporation was measured by observing the movement of the meniscus in the capillary tube by means of a microscope with a micrometer eye-piece. The form of the apparatus is shown in Fig. 3. There were in fact two capillaries, cemented into a brass tube containing a screw plunger by means of which the meniscus could be forced back after it had passed the field of vision of the

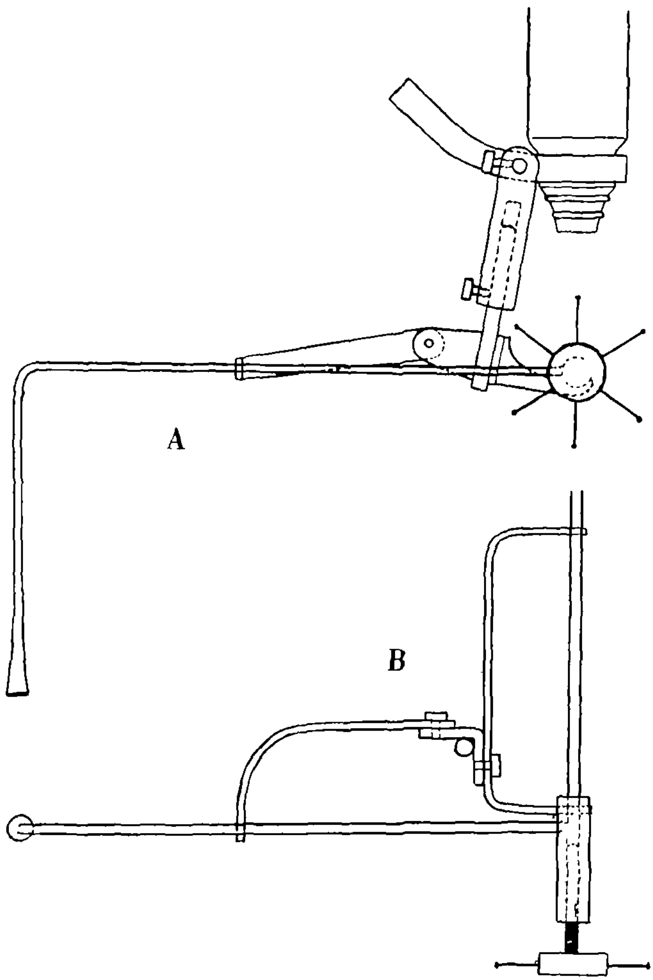


Fig. 3. The evaporimeter. A, from side; B, from above.

microscope. The whole apparatus was firmly fixed to the tube of the microscope so that it was permanently in focus, and the coarse adjustment was used to raise and lower it above the evaporating surface under investigation.

In order to discover the critical height an experiment was undertaken in which two similar evaporimeters were opposed, the one above the other, and moved nearer until the rate of evaporation from one of them began to fall off. From this it was found that with a wind speed of 1·6 ft. per min. (at which most of the experiments were carried out) the interference was first noticeable at a height of 2·5 mm., and the falling off in the rate of evaporation reached a value of 10% at a height of 1·9 mm. For heights of less than 2 mm. the evaporimeter readings must be accepted with caution, although the regularity of results within this range (as shown in Fig. 6) suggest that, with surfaces which lose water at a slower rate, the critical height is less.

### (c) *The wind-tunnel*

The experiments were carried out in a wind-tunnel which is shown in Fig. 4. It was constructed mainly from seasoned oak.

In order to obtain an even flow of air along the tunnel the air was led in by a funnel *F*, the mouth of which was covered with fine copper gauze, and directed against the back of the distribution chamber *G*. The air then passed forward through a fine wire gauze screen *W* and straws *S* into the tunnel proper. In one side and on the top of the tunnel, glass observation windows were let in. The inside

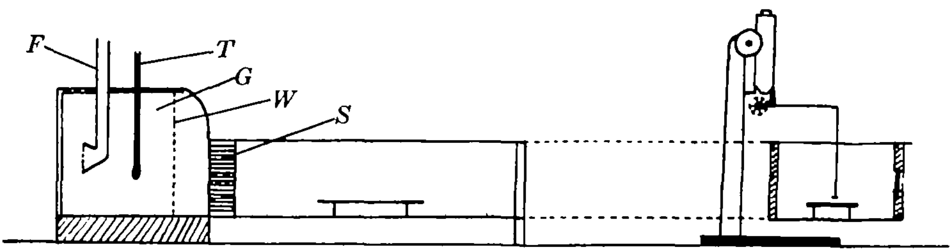


Fig. 4. The wind-tunnel with evaporimeter in position. *F*, funnel; *G*, distribution chamber; *S*, straws; *T*, thermostat control; *W*, wire gauze.

of the distribution chamber and the tunnel were covered with paraffin wax in order to prevent the loss or uptake of water by the wood. The leaf under examination was placed (underside uppermost) on a small table, 1¼ in. high, in the tunnel; the leaf received constant illumination from a 40 W. frosted electric-light bulb placed 3 ft. away. The water uptake of the leaf was measured by means of a potometer, so that it was possible to see whether the leaf were transpiring at a more or less even rate throughout the course of an experiment.

The air supply to the tunnel (see Fig. 5) was taken from the compressed air supply via a simple constant head device *E* and a manometer system *P*, the latter being calibrated for a wide range of wind velocity against a gas-meter, temporarily inserted into the air system. The temperature of the oncoming air was maintained to within 0·1° C. by means of two large composition-tubing coils $N_1$ and $N_2$ placed in an electrically heated water-bath *Z* controlled by means of a thermostat control *T* (Fig. 4) situated in the distribution chamber *G*. The humidity of the oncoming air could be maintained within 1% relative humidity over a range of humidity from 10 to 95%. This was achieved by dividing the air coming from the reducing valve into two streams by means of a Y-tube, the volume of air passing along either limb of the Y being controlled by taps $M_1$ and $M_2$; one limb of the Y led the air coming from the supply (this air always being relatively dry) straight through a heating coil $N_1$ in the water-bath; the other limb led through another heating coil by way of a large wash-bottle *O* filled with distilled water and glass chips, thus rendering the air moist. The wet and dry air streams were reunited by means of another Y-piece immediately before the manometer system *P* and thus passed into the tunnel. The humidity of the air was controlled by varying the mixture of wet and dry air, and was measured by means of a dew-point apparatus; a very thin chromium-plated brass thimble was used in place of a silver one, since it is both cheaper and very much easier to read, as it maintains a good polish and is less liable to oxidation. The whole apparatus was kept in a constant temperature room

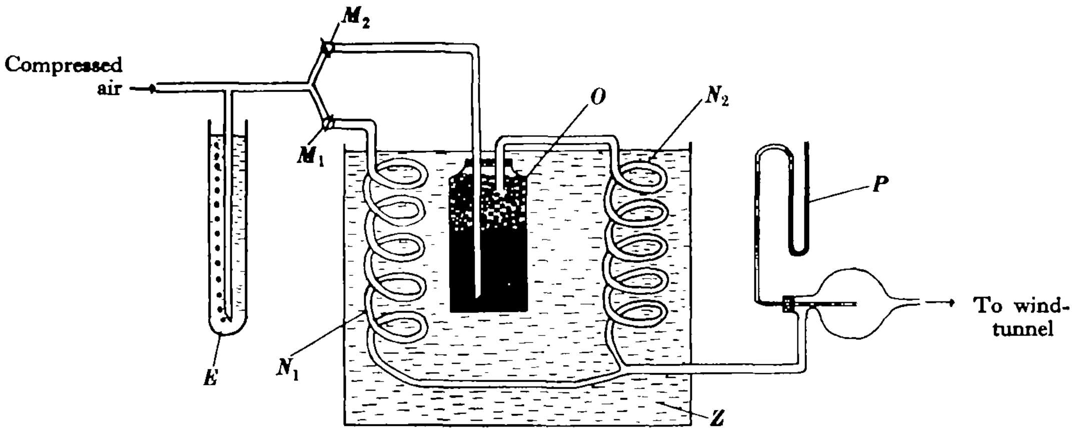


Fig. 5. *E*, constant head device; $M_1$, $M_2$, taps; $N_1$, $N_2$, heating coils; *O*, wash-bottle; *P*, oil manometer; *Z*, water-bath.

and it was possible to vary the temperature, wind velocity and humidity of the oncoming air at will.

The hygrometer, which could be raised or lowered by a simple screw device, was mounted on a narrow brass plate forming part of the roof of the tunnel. The evaporimeter and its microscope tube were carried upon a special stand which rested upon the bench; the capillary tube bearing the evaporimeter itself was introduced through a small hole in the brass plate.

## METHODS AND RESULTS

In the first series of experiments the hair hygrometer was used to measure the humidity gradient upon the surface of a hot-house tulip leaf, *Tulipa gasneriana*, which was chosen on account of its moderately rapid rate of transpiration. The leaf had a potometer fixed to its stem and was fixed, lower surface uppermost, by small pieces of plasticine to the table in the wind-tunnel. Great care was taken to get the leaf as flat as possible and to have its front edge at the leading edge of the table. The hair hygrometer was arranged so that it could be raised or lowered over a portion of the leaf some 5 cm. from the leading edge. The hair was then lowered until it was within 0·5 mm. from the leaf surface. At the end of half an hour a reading was taken, and readings were taken at 10 min. intervals until they reached a constant figure. The hygrometer was then raised to a height of 15 mm. above the leaf surface, in which position the humidity was found to be uninfluenced by the leaf and to be that of the oncoming air. A reading was taken in this position, the hygrometer lowered to within 1 mm. of the leaf surface again and another series of readings taken after half an hour. In this way the whole series of readings was taken, the hygrometer being raised to a point 15 mm. above the leaf surface and allowed to come into equilibrium with the moisture of the oncoming air before taking the readings at the different heights. The hygrometer was thus brought from drier to moister air for each reading near the leaf surface, and in this way the errors due to hysteresis were minimized. Before and after each experiment the hygrometer was calibrated against the dew-point apparatus, but no variation of its characteristics during the course of an experiment was detected.

In the experiments made with the evaporimeter the leaf was placed as flat as possible upon the table as before, the evaporimeter lowered to within 0·5 mm. of the leaf surface, the distance of this point from the forward edge of the leaf being noted. Five consecutive readings were taken at this point; the evaporimeter was then moved progressively higher above the surface, five readings being taken at each point, until a height was reached at which the rate of evaporation became independent of height. The readings for the points 0·5 and 1 mm. above the leaf surface were then repeated. Finally the leaf was replaced by a piece of white cardboard of the same shape and dimensions, and the gradient of evaporating power due to the gradient of wind velocity over a dry surface was measured. In this way the gradient of humidity over the undersurface of the leaf of the dock, *Rumex hydrolapathum*, which was found to transpire at very much the same rate as a tulip leaf, was measured, as were the gradients over a piece of wet filter paper and over the leaf of the cherry laurel, *Prunus laurocerasus*. In the latter case only a very small gradient was observed, falling almost within the limits of experimental error, owing to the very slow rate of transpiration of this evergreen plant.

From the readings taken with the evaporimeter it is theoretically possible to calculate the relative humidity at the various points above the leaf surface, provided the temperature and humidity of the oncoming air are known. It was found impracticable, however, to make corrections for the temperature gradient, but this was negligible in all cases except that of the wet filter paper. The calculations were made as follows:

Let $E$ = rate of evaporation (in mass/time), $x$ = time taken for the meniscus in the capillary tube of the evaporimeter to move a given distance. Then

$$E \propto 1/x.$$

$E$ also varies with $v$ = wind velocity, $a$ = humidity, $T$ = absolute temperature. If we assume that $T$ is constant throughout the system and that at any given height above the surface (e.g. 1 mm.) $v$ is constant, then:

$$E = K\,(100 - a),$$

where $a$ = relative humidity and $K$ is a constant depending on $T$ and $v$, or

$$1/x = K\,(100 - a).$$

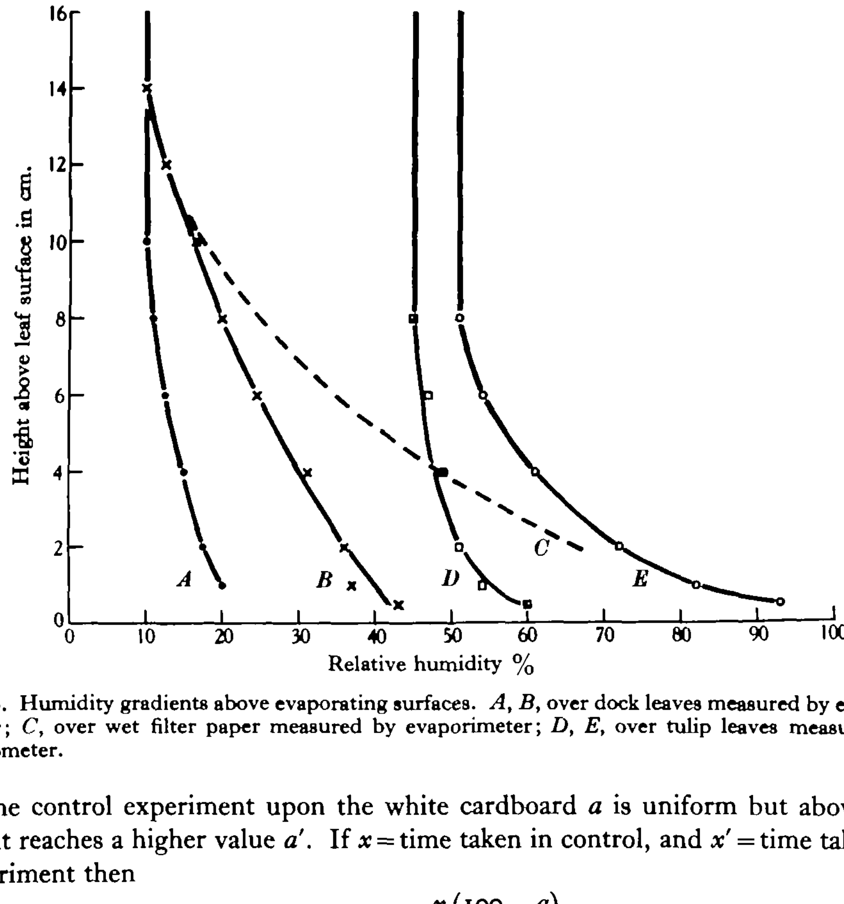


Fig. 6. Humidity gradients above evaporating surfaces. *A*, *B*, over dock leaves measured by evaporimeter; *C*, over wet filter paper measured by evaporimeter; *D*, *E*, over tulip leaves measured by hygrometer.

In the control experiment upon the white cardboard $a$ is uniform but above the leaf it reaches a higher value $a'$. If $x$ = time taken in control, and $x'$ = time taken in experiment then

$$a' = 100 - \frac{x\,(100 - a)}{x'}.$$

Examples of the results of these experiments made with the hygrometer upon tulip leaves, and with the evaporimeter upon dock leaves and wet filter paper, are shown graphically in Fig. 6. The protocol of curve *A* is given in Table I. In a further series of experiments made with the evaporimeter upon dock leaves and wet filter paper, the gradients of humidity at various distances from the front edge of the leaf (or wet filter paper) were determined. The results of two of these experiments are shown graphically in the form of lines of constant humidity in Fig. 7.

Table I

$T = 23{\cdot}8^\circ$ C. $a = 10\%$ R.H. Distance from leading edge = 4 cm. $x$, $x'$ average of five readings.

| Height above leaf in mm. | 0·5 | 1·0 | 2·0 | 4·0 | 6·0 | 8·0 | 10·0 | 12·0 | 14·0 |
|---|---|---|---|---|---|---|---|---|---|
| $x'$ (experiment) in sec. | 27·8 | 20·0 | 16·8 | 14·0 | 12·5 | 11·8 | 11·3 | 10·8 | 10·5 |
| $x$ (control) in sec. | 18·0 | 14·0 | 12·0 | 10·7 | 10·5 | 10·5 | 10·5 | 10·5 | 10·5 |
| $100 - \frac{x(100-a)}{x'}$ in R.H. | 43·0 | 37·0 | 36·0 | 31·0 | 24·5 | 20·0 | 16·5 | 12·5 | 10·0 |

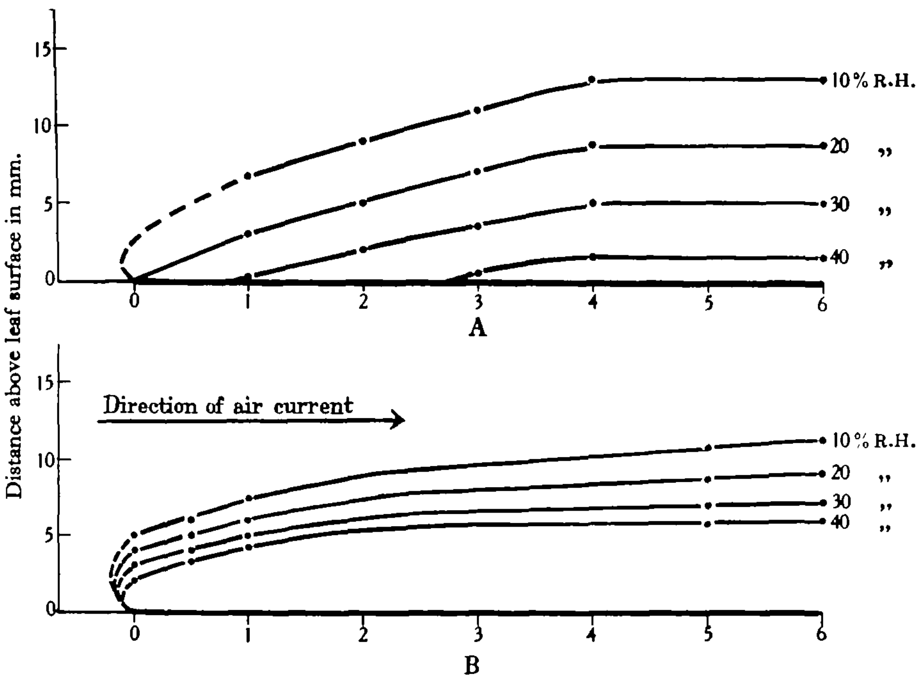


Fig. 7. The distribution of water vapour over A, wet filter paper, and B, a dock leaf, measured by the evaporimeter in a current of air of 10% R.H.

## DISCUSSION

The results of this investigation require little discussion. No attempt has been made to estimate the range of variation from one plant to another in respect of the humidity gradient above the leaf. This would be indeed a large undertaking in view of the range of variation within a single species, for the transpiration rate varies from time to time and from one leaf to another as the results given in Fig. 6 show. Nor has any attempt been made to account for the form of the gradient on a purely physical basis. We have been content to have shown that, under certain conditions which might normally be met with in the field, the humidity above the leaf surface may be affected up to a height of over 1 cm. by the water vapour coming from the leaf, and to have found methods which enable humidity gradients to be studied on a small scale.

Attempts to reduce the size of the hygrometer were not successful; a length of hair less than 1 cm. did not give readings of sufficient accuracy. On the other hand, there seems no reason why a considerable reduction in the size of the evaporimeter should not be possible. This instrument is easy to construct and to use, and its form could readily be modified for particular requirements. There is no reason why it should not be used for studying microclimates in the field.

It cannot be too strongly emphasized that no general applicability is claimed for the *results* given in this paper. They were obtained under conditions expressly designed to favour the development of an extensive humidity gradient. Even so, in the case of the cherry-laurel leaf it was not possible to do more than to detect a slightly increased humidity at a height of 0·5 mm. With more rapid currents of air, e.g. 1 m. per sec. (=2·75 m.p.h.), the gradient might well be equally restricted even in the case of rapidly transpiring leaves. But it is hoped that these methods may be applicable to the particular problems of other workers.

## SUMMARY

1. An hygrometer and an evaporimeter, capable of investigating atmospheric conditions over small areas close to the surface of a leaf, are described.

2. In the case of rapidly transpiring leaves in a slow air stream a humidity gradient has been detected up to a height of 1·2 cm.

## ACKNOWLEDGEMENTS

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