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THE EVAPORATION OF WATER FROM *HELIX ASPERSA*

II. MEASUREMENT OF AIR FLOW AND THE DIFFUSION OF WATER VAPOUR

BY JOHN MACHIN

*Department of Zoology, Queen Mary College, University of London**

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INTRODUCTION

It has been shown in the previous paper (Machin, 1964*a*) that the vapour pressure at the surface of a snail is identical for practical purposes to that of a free water surface. It is appropriate now to consider the removal of water vapour from the evaporating surface by diffusion and how this is affected by air flow.

When air moves over a smooth stationary surface, two types of flow are distinguished. In the thin 'boundary layer' close to the surface flow is parallel or laminar, whereas the layers of 'free' air above this are irregularly mixed by turbulence. It is known that above certain critical wind speeds (Sutton, 1953) laminar flow in the boundary layer becomes unstable and gives rise to turbulent flow. However, the very low wind speeds relevant to the evaporation problems of terrestrial snails are far below this value. When laminar air flow occurs above a freely evaporating surface, a vapour pressure gradient is set up. In the boundary layer, where there is no mixing normal to the surface, the outward movement of water vapour occurs only by molecular diffusion. Since this is relatively slow, the vapour pressure gradient across the boundary layer is very steep and almost linear. Once the diffusing vapour reaches 'free' air, the vapour pressure gradient becomes much less steep and non-linear, due to rapid mixing in turbulent air. Fig. 1 adapted from Leighly (1937) illustrates this point.

In practice evaporation from a free water surface is given by the following equation:

$$E = \frac{k(p_0 - p_d)}{D}, \tag{1}$$

where E is the rate of evaporation per unit area of evaporating surface; k is the coefficient of diffusion of water vapour in air expressed in appropriate units; p_0 is the vapour pressure at the evaporating surface; p_d is the vapour pressure of 'free' air; and D is the boundary-layer thickness. Since k can be calculated, and p_0 and p_d measured, the solution of the evaporation equation would depend on obtaining some measurement of D, boundary-layer thickness.

Since the transition from zero wind speed at the surface to the maximum speed of 'free' air takes place across the boundary layer, it was thought the boundary layer could be detected in this way. Experiments described in the first part of this paper indicate how some mean value for boundary-layer thickness was obtained for the

* Present address: Department of Zoology, University of Toronto, Toronto 5, Canada.

complex three-dimensional form of a snail. These measurements are compared with effective values for D, calculated from direct measurements of evaporation rate. Boundary-layer thickness directly determined from wind-speed measurements will be referred to as $D_{aero.}$, and those indirectly determined from evaporation measurements as $D_{evap.}$.

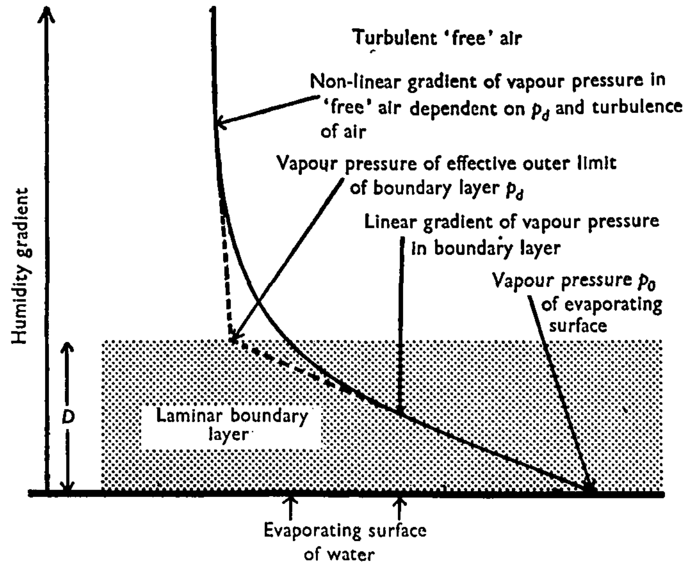

Fig. 1. The water-vapour pressure gradient in the boundary layer and in the adjacent 'free' air over an evaporating surface. (After Leighly.)

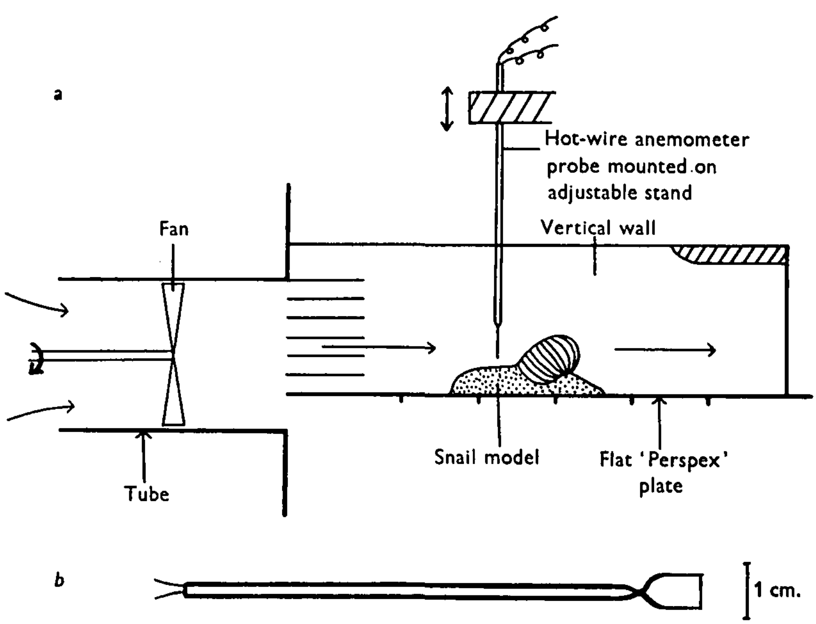

Fig. 2. *a*, Diagram of the apparatus used for the measurement of boundary-layer distributio over the snail model and for evaporation measurements in room conditions. *b*, Hot-wii anemometer probe.

MEASUREMENT OF BOUNDARY-LAYER THICKNESS

The apparatus used for measurement of boundary-layer distribution is shown in Fig. 2*a*. It consisted of a 4 in. wide parallel-sided corridor constructed from 'Perspex' plate. At one end a four-inch fan, mounted within a close-fitting tube, was driven by a variable-speed electric motor. A 3 in. deep section of honeycombing was placed across the tube opening. The top of the corridor was left open to allow a hot-wire anemometer probe easy access to the experimental area.

Wind-speed profiles were plotted from wind-speed measurements taken at vertical intervals of 1 mm. above the various surfaces used in the experiments. Boundary-layer thickness (to the nearest millimetre) was taken as the minimum distance at which maximum wind speed was reached.

A hot-wire anemometer is suitable for this type of measurement because of its high sensitivity, even at very low wind speeds. Very little interference in air flow could be expected, since the sensitive part of the instrument, the hot wire, consisted of about 5 mm. of 0·002 in. diameter nickel resistance wire soldered between the prongs of a long thin probe (see Fig .2*b*). Wind-speed measurements were made by the constant resistance method described by Ower (1949), where the hot wire formed one arm of a Wheatstone bridge. The voltage necessary to maintain the wire at a set resistance was measured at different wind speeds. This voltage was calibrated against known wind speeds by mounting the anemometer probe on a revolving arm inside an enclosed chamber. By adjusting the original voltage applied across the wire the sensitivity of the instrument could be increased until wind speeds down to 1 cm./sec. could be accurately measured. Largely as a result of inadequate methods of measurement, previous workers (Ramsay, 1935, *inter alia*) have been restricted to the use of the higher range of wind speeds, often in excess of those normally experienced by the animal.

As it was feared that hot-wire anemometer measurements might be disturbed by the effects of evaporation, a 'plasticine' model of the same proportions as those of an active snail was used instead of an actual animal. The model was moulded into an empty *Helix aspersa* shell. The snail model was placed with its leading edge 15 cm. from the down-wind edge of the honeycombing. Wind-speed profiles were then plotted at strategic points over the model's surface at each of three different positions relative to a constant 'free' air flow of 26 cm./sec. These different positions were with the snail facing directly into, away from and at right angles to, the direction of air flow.

ASSESSMENT OF EVAPORATION RATE

Experimental material

Evaporation rates were measured for a number of whole snails in the three different positions described previously. Freshly drowned specimens of *Helix aspersa* were used, because it was important that the snail did not move and remained fully extended throughout the experiment. Drowned specimens not fully extended or misshapen due to excessive intake of water were discarded. The specimen was shaken to remove superficial water and any excessive amounts of mucus. Water, when necessary, was removed with a pipette from the lung cavity. Specimens were handled only by way of a small rectangle of waxed paper on which they were placed. The animals used in the following experiments were between 5 and 6 cm. in overall length and between 1 and 1·8 cm. maximum foot width.

Measurement of water loss

Water loss from specimens of *Helix aspersa* was estimated by weighing before and after an experimental period in the apparatus shown in Fig. 2*a*. With the doors and windows of the room kept shut, air temperature did not vary more than $\pm 1 \cdot 0^\circ$ C. during experimental periods of 20–30 min., there being presumably corresponding fluctuation in humidity. Since the amount of water-loss involved was relatively great, it seemed possible that reasonably reliable measurements of water loss could be made in room conditions. Measurements of temperature and humidity were made at 5 min. intervals throughout the experiments, using a thermometer reading to $0 \cdot 1^\circ$ C. and an 'Edney' paper hygrometer suitably calibrated and equilibrated. These readings were averaged for purposes of calculation.

Estimation of surface area

An estimation of the surface area used for the calculation of evaporation rate per unit area was obtained by dividing the body into a number of component geometrical shapes whose areas could be calculated from appropriate dimensions of the animal. Assessment of the surface area of the tentacles was not made as they were always collapsed or withdrawn in the drowned specimens. Appropriate deductions were made for the non-evaporating areas of the animals, the shell and the sole of the foot. However, no correction for the irregular nature of the skin surface was made.

RESULTS

Distribution of boundary layer

Figure 3 shows a representative series of wind-speed profiles measured 15 cm. downwind from the honeycomb above a smooth flat surface at a number of different ambient wind speeds. Wind-speed measurement is sufficiently sensitive to distinguish between the different 'free' air wind speeds used and also provides some means of measuring boundary-layer thickness. In Fig. 4 the outer limit of the boundary layer has been plotted over various typical profiles of the snail model in the three different positions. It can be seen that the boundary layer varies over the surface of the model, being relatively thin over its leading surfaces and very much thicker over its trailing surfaces. Air flow over a three-dimensional object is complex and the boundary layer which is established varies all over the surface. It is, however, necessary to calculate a mean value for the boundary-layer thickness which would be relevant to evaporation from the animal as a whole. This was done in the following way. Large-scale drawings of the snail model and the boundary layer were used to calculate a number of areas, each covered by the same boundary-layer thickness. Each thickness was then added together in proportion to the surface area covered by each value. The mean thickness was then obtained by dividing by the total surface area. The area important in this calculation is that section of the animal's surface which would contribute most to evaporation losses, namely the dorsal region of the body. The lower margin of the animal, within the substratum boundary layer, was not included since its thickness measured perpendicular to the animal's surface would be great. It was concluded that evaporation from this area would be negligible. An example of this calculation is as follows:

(*a*) area of body (less shell and sole of foot) = 12·1 sq.cm.,

(*b*) area influenced by boundary layer of substratum = 3·7 sq.cm.,

main area of evaporation $(a-b)$ = 8·4 sq.cm.

	Leading area		Central area		Trailing area	Total
Mean boundary-layer thickness (mm.)	1·0		2·5		35·0	—
Surface area (sq.cm.)	1·0		6·8		0·6	8·4
Ratio of surface areas	5	:	34	:	3	42

$$\text{Mean boundary-layer thickness} = \frac{(1{\cdot}0\times 5)(2{\cdot}5\times 34)(35{\cdot}0\times 3)}{42},$$

$$= 4{\cdot}64 \text{ mm.}$$

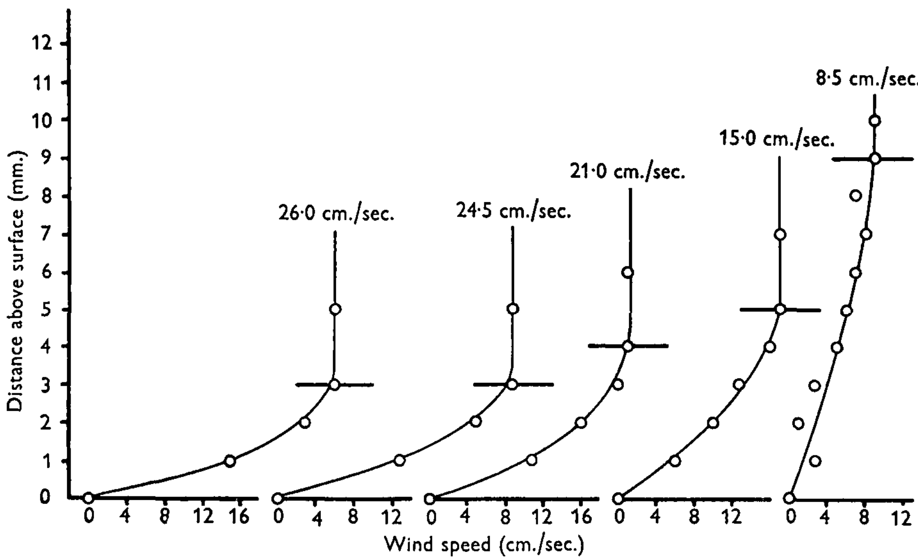

Fig. 3. Wind-speed profiles plotted from hot-wire anemometer measurements made above a smooth flat surface. The upper limit of the aerodynamic boundary layer is indicated in each case by a thick horizontal line. The ambient or 'free' air wind speeds are also given.

Table 1. *Measured mean boundary-layer thickness* ($D_{aero.}$) *over the snail model compared with values of* $D_{evap.}$ *calculated from evaporation data of freshly drowned* Helix aspersa

Position of snail	Mean $D_{aero.}$ (mm.)	Mean $D_{evap.}$ (6 values) (mm.)	$D_{aero.}/D_{evap.}$
Facing into wind	4·64	1·49	3·1
At right angles to wind	5·75	1·82	3·2
Facing away from wind	13·6	2·27	6·0

In Table 1 estimates of mean aerodynamic boundary-layer thickness ($D_{aero.}$), calculated in this way, are given in column 1. These are compared with $D_{evap.}$ (column 2), calculated from evaporation data of freshly drowned snails with equation (1). It will be seen that $D_{aero.}$ is considerably greater than the corresponding $D_{evap.}$. Measurements were also made using a flat surface, where $D_{aero.}$ could be more easily measured. This surface, which consisted of a rectangle of filter-paper

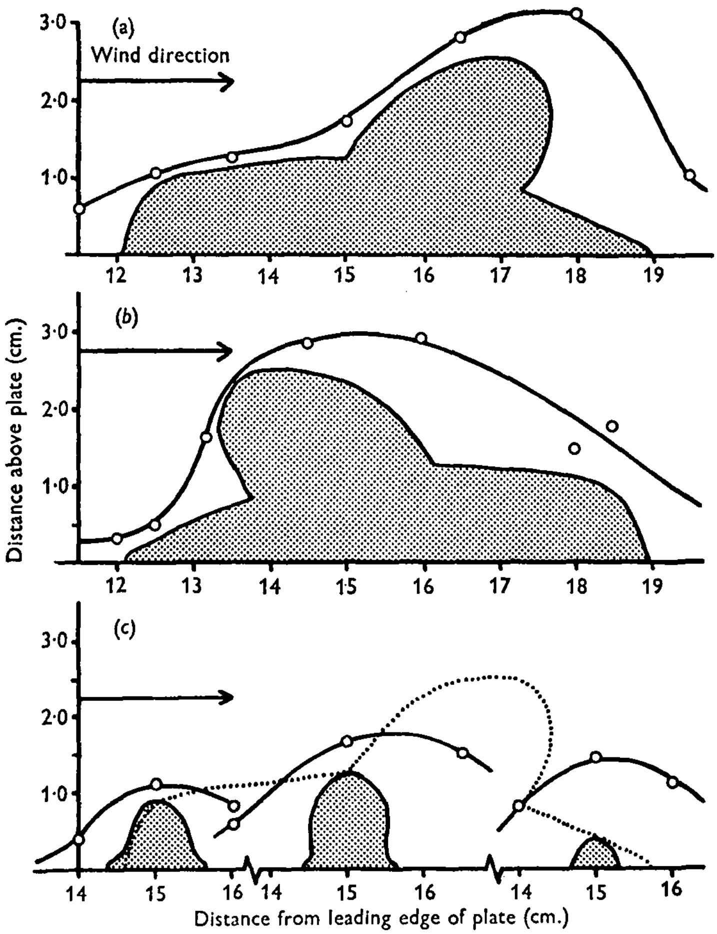

Fig. 4. The distribution of boundary layer over various typical profiles of the snail model, at a 'free' air wind speed of 26 cm./sec. *a*, Model facing into the wind; *b*, model facing downwind; *c*, model at right angles to wind. The dotted outline indicates the relative position of each profile.

Table 2. *Measured boundary-layer thickness* ($D_{aero.}$) *compared with corresponding values of* $D_{evap.}$ *calculated from evaporation data obtained from rectangle of filter-paper,* 4 × 1·5 *cm.*

(Temperature 18°C.; R.H. 60%.)

Wind speed (cm./sec.)	Calculated $D_{evap.}$ (mm.)	Observed $D_{aero.}$ (mm.)	$\frac{D_{aero.}}{D_{evap.}}$
26	1·29	3·5	2·7
23	1·36	4·0	2·9
21	1·52	4·0	2·6
14	2·02	4·0	2·0
11	2·50	5·0	2·0
8·5	2·75	5·0	1·8

soaked in distilled water, was the same size as the main evaporation area of an average specimen of *Helix aspersa*, 4 by 1·5 cm. The values of $D_{\text{aero.}}$ in Table 2 were measured at the centre of the rectangle, with its length parallel to the direction of the wind.

Table 2 (column 4) shows that $D_{\text{aero.}}$ is about twice $D_{\text{evap.}}$ which is therefore in general agreement with the results obtained with the snail.

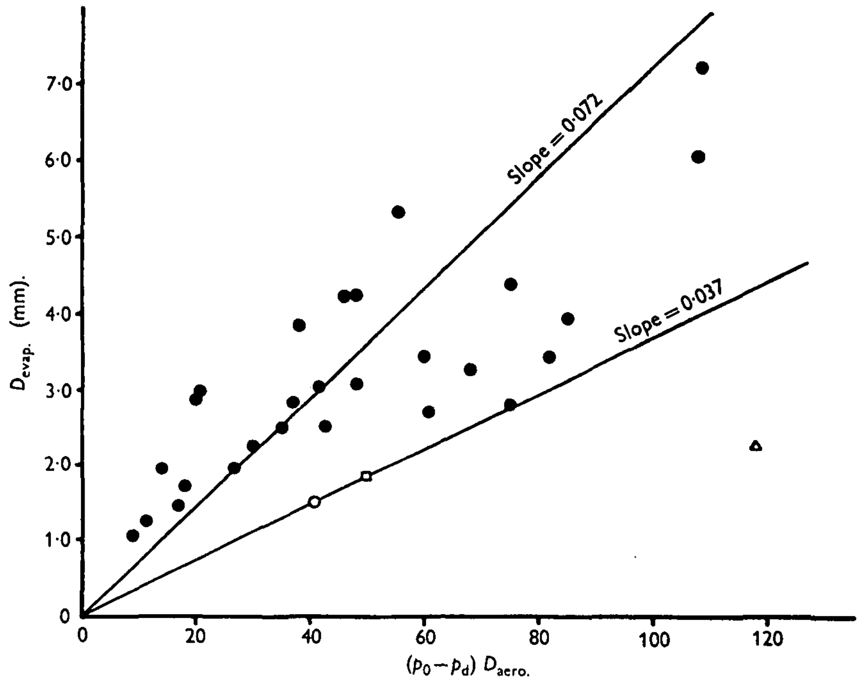

Fig. 5. Graph showing that $D_{\text{evap.}}$ is directly proportional to $(p_0-p_d)D_{\text{aero.}}$. Points relating to the rectangle of filter-paper are indicated thus: (●). Those of the snail are (○), facing into the wind; (□), at right angles to the wind; and (△), facing downwind.

Empirical determination of relationship between $D_{\text{evap.}}$ *and* $D_{\text{aero.}}$

It is known from aerodynamic theory (Schlichting, 1955) that boundary-layer thickness varies directly with the surface length and inversely with the wind speed. Similarly, vapour boundary-layer thickness must depend on these two factors, but also on (p_0-p_d). If the dimensions of the evaporating surface remain constant it is possible to obtain a combined relationship for both boundary layers, given by the formula:

$$D_{\text{evap.}} = c(p_0-p_d)D_{\text{aero.}},$$

where c is the slope of $D_{\text{evap.}}$ plotted against $(p_0-p_d)D_{\text{aero.}}$ Accordingly, the data obtained from the flat rectangle of filter-paper (●) have been used to construct the straight line of slope 0·072 in Fig. 5, which is the mean of the slopes drawn through each point and the graph origin. Since measurements using freshly drowned *Helix aspersa* were limited to a single wind speed, one point only for each of the three different positions of the snail is available.

It can be seen that a straight line of slope 0·035 passes through the graph origin and the points corresponding to the snail facing into the wind (○) and at right angles to the wind (□). This indicates that in these two positions the relationship between $D_{evap.}$ and $D_{aero.}$ is the same. The same relationship does not hold for the snail facing downwind since the point corresponding to this position (△) falls below the line. However, not too much importance should be placed on this; reasons for supposing that measurement in this position is subject to error will be presented in the discussion.

Substituting for $D_{evap.}$ (or D) in equation (1), the formulae for the two types of evaporating surfaces become:

flat rectangle (4 × 1·5 cm.),

$$E = \frac{k}{0{\cdot}072\, D_{aero.}}; \qquad (2)$$

Helix aspersa (facing into and at right angles to the wind),

$$E = \frac{k}{0{\cdot}035\, D_{aero.}}. \qquad (3)$$

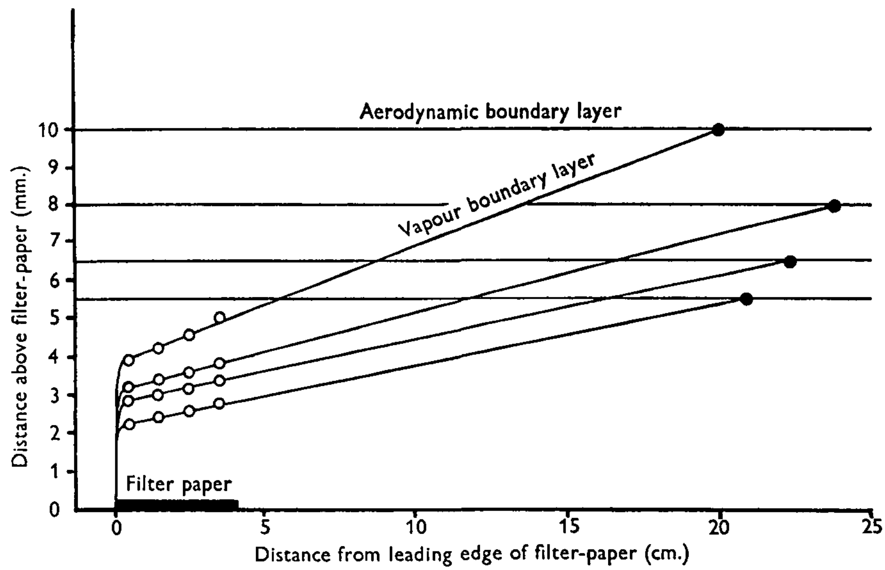

Fig. 6. Extrapolated vapour boundary-layer profiles obtained from a rectangle of filter-paper soaked in distilled water, at ambient wind speeds of 16·5, 13·0, 6·0 and 3·5 cm./sec. The aerodynamic boundary-layer profile for the different wind speeds is also given. The point at which the two meet is indicated thus: (●).

Calculation of the point at which $D_{aero.}$ and $D_{evap.}$ coincide

It has been shown that the vapour boundary layer of small evaporating surfaces of the same order of size as a snail is such that it falls short of the aerodynamically defined boundary layer. It follows, however, that diffusing water vapour would eventually reach the outer limit of the aerodynamic boundary layer at some point along an evaporator of longer dimensions. Unfortunately limits imposed by the apparatus did not permit the use of greatly elongated evaporators. One further approach, however, was possible. The local evaporation rate at four different points along a 4 cm. rectangle of wet filter-paper was calculated by dividing the evaporation rate of the whole area in proportion to the surface-temperature depression, measured at these points by a series of thermocouples. A vapour boundary-layer profile was then plotted along the evaporator by means of the $D_{evap.}$ values calculated from each local evaporation rate. Since a more accurate control of atmospheric conditions was required, these measurements were made in the wind-tunnel apparatus described in Machin (1964*b*).

In Fig. 6 the vapour boundary-layer profiles have been extrapolated back until they meet the previously measured aerodynamic boundary layer. $D_{evap.}$ and $D_{aero.}$ coincided at an average distance for four different wind speeds of 21·9 cm. from the leading edge of the evaporating surface.

DISCUSSION

Detailed studies of air flow over the surface of animals and its effect on evaporation have never been previously made. Although Ramsay, Butler & Sang (1938) introduced a promising new technique, in which the distribution of water vapour over the surface of a transpiring leaf was measured, they failed to draw any conclusions from their experiments. Largely as a result of sensitive techniques borrowed from aerodynamics, a new approach to the evaporation problem is now possible. It has been suggested that the main resistance to evaporative water loss from animals with moist skins occurs in the surrounding air. The emphasis of this type of study is therefore on 'the permeability of the air' rather than the permeability of the animal's skin. In this context the useful concept of boundary-layer thickness has been introduced.

It has been shown that evaporative water loss takes place far more rapidly than direct measurements of aerodynamic boundary-layer distribution suggest. This discrepancy is attributed to the fact that the water-vapour gradient above the snail never reaches its theoretical limit, the outer edge of the aerodynamic boundary layer. An attempt has been made to estimate the point at which diffusing water vapour would eventually meet the outer limit of the aerodynamic boundary layer. An average distance of 21·9 cm. from the leading edge of the evaporator was determined. In spite of the probable error due to a straight line extrapolation instead of a more likely curve, the value of 22 cm. indicates approximately the minimum distance necessary for $D_{evap.}$ and $D_{aero.}$ to coincide. Since 22 cm. is considerably greater than the dimensions of most moist-skinned animals, terrestrial snails included, values of $D_{evap.}$ appropriate to biological problems would have to be derived indirectly from $D_{aero.}$ measurements.

On the other hand, when the dimensions of the evaporating surface are much greater than 22 cm., diffusing water vapour would have sufficient time to reach the aerodynamic boundary layer limit and thus $D_{aero.}$ would provide a direct measurement of $D_{evap.}$ This type of approach could perhaps be used to advantage in studies similar to those of Rohwer (1931) and Penman (1948) where evaporation from ponds, lakes and areas of soil are considered.

A formula which relates aerodynamic boundary-layer thickness, $D_{aero.}$, with vapour boundary-layer thickness, $D_{evap.}$, has been derived, as follows:

$$D_{evap.} = c(p_0 - p_d) D_{aero.}.$$

Evidence that evaporation from the three-dimensional form of a snail does not correspond exactly to that of a two-dimensional evaporator of similar dimensions, is provided by the fact that constant *c*, in the formula, is different in the two cases. It must be emphasized, however, that these values are empirical, and do not necessarily express a fundamental relationship applicable to all types of evaporators of different size and form.

It has been shown (see Tables 1 and 2), that the ratios of corresponding values of $D_{aero.}$ and $D_{evap.}$ for both types of evaporator are fairly constant. However, in one case, when the snail is facing downwind, the calculated average value for $D_{aero.}$ is too high in relation to the observed evaporation measurements. Furthermore, the point corresponding to this position in Fig. 5 does not fall on the straight line drawn through the points relating to the snail facing into the wind and at right angles to it. It is suggested that direct boundary-layer measurement may be subject to error whenever air has to pass over the shell before the main evaporating surface of the snail is reached. This may be due to eddies and other irregularities of air flow being set up within the thickened boundary layer in this region, which are not detected by the present method of boundary-layer measurement. This is the first time an approach of this type has been made. No doubt the use of the formula described above, or a simple derivation of it, would be more readily applicable to animals whose forms could be conveniently regarded as similar to a flat or streamlined surface. Better agreement might, for example, have been obtained using a slug or even a terrestrial isopod.

The work presented here suggests the importance of a number of hitherto unsuspected phenomena. When a moist-skinned animal such as a snail is orientated differently in relation to the wind direction, differences occur in the distribution of aerodynamic boundary layer. It has been shown that parallel differences occur in the evaporation rate measured in each position. The same snail, at right angles to the wind, for example, loses only 83 % of the amount lost facing into the wind. When the snail is facing downwind, the corresponding loss is only 68 %. Although the linear dimensions, parallel to the wind, when the snail is facing into and away from it are identical, there is a 32 % difference in the observed evaporation rate. It must be emphasized, therefore, that the form of terrestrial snails, including the shell, which is not itself an evaporating surface, plays an important part in determining the amount of evaporative water loss from the animal.

SUMMARY

1. Air flow and the water-vapour gradient over a freely evaporating surface is described, and the concept of boundary-layer thickness which expresses such a gradient is introduced.

2. A direct method of estimating boundary-layer thickness by means of a hot-wire anemometer is described.

3. Comparison of observed and effective boundary-layer thickness, calculated from evaporation data, have suggested that the gradient of water vapour is steeper than aerodynamic measurements indicate.

4. An empirical relationship between aerodynamic and vapour boundary layers has been obtained for a two-dimensional evaporator and for the snail, *Helix aspersa*, and a new evaporation formula derived.

5. Evidence for supposing that aerodynamic and vapour boundary layers do not coincide unless the evaporating surface is greater than 22 cm. in length is presented.

6. Possible errors in the estimation of boundary-layer thickness when air flow is interrupted by the snail's shell are considered.

7. The importance of differences in air flow produced by placing the animal in different positions relative to the wind is discussed.

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