STREAMLINE FLOW AND THE MOVEMENT OF SOLUTES
IN THE TRANSPIRATION STREAM

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Introduction

The classic experiment of Askenasy (1, 2), illustrating the pull exercised by an evaporating water surface, consists, as is well known, of a thistle funnel closed at the wide end by a plug of plaster of paris, made airtight, if necessary, by ringing with gold-size. The funnel is filled with well boiled distilled water, and inverted into a vessel of mercury. As the water evaporates from the upper surface of the plaster plug the mercury rises pari passu at the lower end of the tube, and might be expected to reach eventually barometric height, less the vapor pressure at the prevailing temperature. Actually the surface tension and the molecular cohesion of the water draw the mercury to much greater heights. Askenasy observed a rise of 89 cm. at a barometric pressure of 73.5 cm. Ursprung, in a series of papers (7, 8, 9, 10, 11), made more extensive observations and obtained a rise of 135 cm. above barometric height, in glass tubes, and of double barometric height in liane stems used as tubes. In all cases, bubbles are formed eventually and the cohesion breaks down.

The rate at which the mercury rises depends, of course, primarily on the rate of evaporation and secondarily on the ratio between the area of the evaporating disc and the cross section of the tube. The rate, however, is not exactly equivalent to the rate of removal of the water. Nordhausen (3) has shown that an evaporating surface can raise water from a vacuum, i.e., develops beneath it a negative pressure of at least one atmosphere. Our own experimental comparisons of the weight/volume ratio during the rise of the mercury column showed a diminution in the density of the water of as much as 10 per cent., so that as the experiment proceeds an increasing negative pressure develops in the water, long before barometric height is reached, which tends to withdraw the water menisci from the pores of the evaporating surface and thus check the rate of flow.

The existence of this negative pressure can readily be shown by using a thistle funnel with plaster plug, the stem of which dips into mercury in a closed filter flask. The flask is partly evacuated and time is then allowed for a negative pressure to establish itself and for the mercury to rise a short distance in the stem of the funnel. On admitting air to the flask the mercury rises with a sudden bound upward, often to twice its previous height, in replacement of the contracted water column.
Procedure

If, during the course of the Askensy experiment, a small amount of a strongly colored solution is introduced at the bottom of the tube by means of a curved pipette, so that the solution floats above the mercury, it will be observed that the upper surface of the colored layer does not rise as a level surface, but is drawn up in a delicate axial thread of color which advances at a surprising speed and reaches the top of the tube in a few minutes, even at low rates of evaporation. An array of dyes was tested in this way and it was found that the rate of rise was independent of the molecular weight of the dye used, and is therefore not a simple diffusion phenomenon. Moreover, the characteristic movement is absent in tubes sealed at the top.

For our experiments the original arrangement of the apparatus was modified only by the addition of an adiathermic shield, formed of a wide glass sleeve filled with a saturated solution of nickel sulphate. As each funnel has its own characteristics, compared tests were always made with the same funnel.

Observations

The apex of the column is sharply defined and usually obtuse. The latter point is striking. The appearance is different from that which one sees on applying a hydrostatic suction to the upper end of the water column when the color is drawn up axially in fine vanishing point. In this latter case, neutral red introduced over a 2-inch column of mercury forms a dense layer, with no streaming, until gentle suction is applied by opening a capillary siphon attached to the top of the tube. As soon as flow starts the color is immediately drawn out along the median line, forming a narrow cone with straight sides, which lengthens out so long as flow continues. When the siphon is closed the flow stops and the color sinks slowly back by gravitation into a uniform diffusion gradient. Left thus undisturbed the color took two weeks to reach the top of a 2-foot tube.

The rates of rise observed for the axial column of color are given in table I.

The rates of flow are linear until the top of the tube is reached, irrespective of the dye used.

The air temperature of the laboratory varied throughout the experiments, but the mean deviation of the averages for each group of tests from the average for the whole series was only 1.0° C., so that temperature changes cannot account for the observed differences.

Although experiments with sealed tubes and siphons, referred to above, show that the phenomenon is not one of diffusion pure and simple, there is a general relation between the diffusibility of the dyes and the rate of
TABLE I
RISE OF DYES IN ASKENASY TUBES*
(AVERAGES OF THREE OBSERVATIONS IN EACH CASE)

<table>
<thead>
<tr>
<th>Dye used</th>
<th>Molecular weight</th>
<th>Average time to rise 10 inches (half length of tube)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thionin</td>
<td>263</td>
<td>24 minutes 31 seconds</td>
</tr>
<tr>
<td>Neutral red chloride</td>
<td>288</td>
<td>12 minutes 53 seconds</td>
</tr>
<tr>
<td>Methylene blue</td>
<td>319</td>
<td>10 minutes 47 seconds</td>
</tr>
<tr>
<td>Safranin</td>
<td>350</td>
<td>6 minutes 25 seconds</td>
</tr>
<tr>
<td>Bismarck brown</td>
<td>418</td>
<td>3 hours to 6 inches only</td>
</tr>
<tr>
<td>Janus green B</td>
<td>422</td>
<td>20 minutes 39 seconds</td>
</tr>
<tr>
<td>Methyl violet 6B</td>
<td>482</td>
<td>14 minutes 45 seconds</td>
</tr>
<tr>
<td>Benzo-purpurin</td>
<td>628</td>
<td>No rise</td>
</tr>
<tr>
<td>Congo red</td>
<td>696</td>
<td>42 minutes to 4 inches only</td>
</tr>
<tr>
<td>Trypan red</td>
<td>766</td>
<td>60 minutes 0 seconds</td>
</tr>
<tr>
<td>Trypan blue</td>
<td>966</td>
<td>No rise</td>
</tr>
</tbody>
</table>

* Height of mercury in each case before introduction of dye, 1.4 inches.
Height of mercury after introduction of dye, 1 inch.
Quantity of dye (0.5 per cent. solution) introduced, 0.3 cc.
Mean air temperature, 18.4°C.

rise. Some of the dyes used are colloidal or semi-colloidal, and their solution aggregates are apparently too heavy to be raised in the flow lines of these tubes. Such are benzo-purpurin, congo red, and trypan blue, as table II shows.

Theoretical considerations
The comparative rate of rise, however, is only of secondary importance in consideration of the remarkably rapid movement of practically all the

TABLE II
COMPARISON OF RATE OF RISE AND DIFFUSIBILITY

<table>
<thead>
<tr>
<th>Dyes in order of rate of rise</th>
<th>Order of diffusibility into 10 per cent. gelatin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Safranin</td>
<td>1</td>
</tr>
<tr>
<td>2. Methylene blue</td>
<td>2</td>
</tr>
<tr>
<td>3. Neutral red chloride</td>
<td>4</td>
</tr>
<tr>
<td>4. Methyl violet</td>
<td>6</td>
</tr>
<tr>
<td>5. Janus green</td>
<td>5</td>
</tr>
<tr>
<td>6. Thionin</td>
<td>3</td>
</tr>
<tr>
<td>7. Trypan red</td>
<td>8</td>
</tr>
<tr>
<td>8. Bismarck brown</td>
<td>7</td>
</tr>
<tr>
<td>9. Congo red</td>
<td>10</td>
</tr>
<tr>
<td>10. Trypan blue</td>
<td>9</td>
</tr>
<tr>
<td>11. Benzo-purpurin</td>
<td>11</td>
</tr>
</tbody>
</table>
dyes, in the axial line. This appears to be due to the actual vertical flow of the water column and finds its explanation in the classic researches of REYNOLDS (5) on water flow in parallel-walled channels.

In REYNOLDS' experiments the colored fluid was introduced into the water current from a fine jet near the inlet end of the flow tube. At low speeds the color was drawn out into a fine axial thread, but as the rate of water flow increased the thread showed disturbance, due to eddies, near the outlet. This turbulent flow gradually approached nearer to the inlet end, until at a given speed the whole flow became turbulent. If the rate of flow was again reduced, it was found that the turbulent flow again gave place to linear flow at a fairly definite velocity, called the "critical velocity."

No sign of turbulent flow was observed in our experiments. This was according to expectation, for the flow due to evaporation is extremely slow and well below the critical velocity.

We may conclude that the flow of water in xylem vessels, in common with that in the experimental tubes, is purely of streamline type. The following considerations will make this clear.

In streamline flow, the inertia forces are small compared with the tangential frictional forces between neighboring layers of fluid. Calculations of the rate of flow, based purely on viscosity, agree so well with experimental observation that the reverse calculation is used as a standard method for measuring viscosity. When a fluid is moving over a smooth plane surface, the layer actually in contact with the surface is at rest, and each successive layer outward moves with greater velocity, i.e., there is a velocity gradient normal to the surface. If v is the velocity parallel to the surface at any distance, y, measured perpendicular to the surface, then the velocity gradient at the surface is given by \( \frac{dv}{dy} \).

Applying this to flow in pipes, REYNOLDS found that the critical velocity, \( v_c \), occurs under all conditions at a constant value of the ratio \( \frac{v_c \mu}{\delta p} \), where \( \delta \) = the diameter of the pipe, \( \rho \) = the density of the fluid, and \( \mu \) = the viscosity coefficient. This ratio has come to be known as the REYNOLDS number. It is valid for all conditions of flow and with all fluids, and its average value is 2000. As a ratio it is non-dimensional.

The mean critical velocity for water is therefore \( 2000 \times \frac{\mu}{\delta p} = \frac{26}{\delta} \) at 15° C., where \( \delta \) is the diameter of the pipe in centimeters. The critical velocity is therefore inversely related to the diameter of the tube. Assuming a diameter of 1.0 mm. for a xylem vessel, as an extreme case, the average critical velocity for water at 15° C. in such a tube would be 2.6 meters per second, which is well above physiological limits.
If, therefore, we are entitled to assume a condition of streamline flow as existing normally in xylem channels, then the difference between the axial and the average velocities in the moving columns of water in the vessels becomes a matter of considerable physiological importance.

Ower (4), discussing Reynolds' work, points out the conditions for the determination of this difference. Consider any cylindrical element of radius \( r \), assumed to lie in the axis of the pipe, the upstream end being denoted by \( A \) and the downstream end by \( B \), the distance between them being \( dl \). The pressure on \( A = p \) and on \( B = p - dp \). The case is the same whether a positive pressure be applied to \( A \) or a negative pressure to \( B \). The pressure difference maintaining the motion of \( AB \) is then \( \pi r^2 dp \). This quantity must equal the retarding force of fluid viscosity acting on the exterior of the cylinder, that is to say \( 2\pi r dl \frac{dv}{dr} \), when \( v \) = the velocity of flow at radius \( r \).

Therefore

\[ \pi r^2 dp = -2\pi r dl \frac{dv}{dr} \]  \hspace{1cm} (1)

and

\[ \frac{dp}{dl} = -2\frac{\mu}{r} \frac{dv}{dr} \]  \hspace{1cm} (2)

As the pressure does not vary across the section of the cylinder, \( \frac{dp}{dl} \) is constant for given conditions, and as velocity in streamline flow varies only with \( r \), then \( 2\frac{\mu}{r} \frac{dv}{dr} \) is a function of \( r \) only.

Now \( \frac{dp}{dl} \) may be written as equal to \( \frac{p_1 - p_2}{l} \) where \( p_1 \) and \( p_2 \) are the respective pressures at each end of \( l \).

Therefore \( \frac{p_1 - p_2}{l} \cdot r dr = -2\mu dv \) \hspace{1cm} (3)

Integrated from \( r = 0 \) to \( r = R \) the full radius of the tube, \( \frac{p_1 - p_2}{l} \cdot \frac{2}{R^2} = -2\mu (V_R - V_a) \), when \( V_a \) = the velocity at the axis, and, as the velocity at the wall of the tube is zero, \( V_R = 0 \) and

\[ \frac{p_1 - p_2}{l} = \frac{4\mu V_a}{R^2} \]  \hspace{1cm} (4)

Thus

\[ V_r = \frac{p_1 - p_2}{4\mu l} \left( R^2 - r^2 \right) \]  \hspace{1cm} (5)

which shows that the distribution of velocity according to radius is parabolic across the tube section.

Also, from equation (4) we have
From the classic formula for absolute viscosity: Volume flowing in unit time $= \frac{\pi R^4(p_1 - p_2)}{8 \mu_1}$ and volume flowing in unit time also $= \pi R^2 V_m$ where $V_m$ is the mean velocity of flow.

Therefore the mean velocity, $V_m = \frac{p_2 - p_1}{8 \mu_1} R^2$ ........................................ (7)

so that the axial velocity (equation 6) is twice the mean velocity.

Even where the absolute amount of flow is slight, there will be a relatively rapid movement of the axial column of liquid, as is evidenced by the rapid ascent of the dye solution in our experiments. Comparison of observations, made with the same apparatus, of the halfway rise of neutral red chloride at varying rates of evaporation, as measured by the number of minutes taken by the mercury to rise from zero to 1 inch, show, however, that the relationship is not so simple as the preceding reasoning suggests. According to equation (6) the relationship of axial velocity to pressure in the water column is directly linear. When the times of rise are plotted against rates of evaporation, however, the points show, although with considerable scatter, a convex distribution with a mode near the 1000-minute line, under the conditions of the experiment. On either side of this line the rate of dye ascent increases, with the paradoxical result that increasing the rate of evaporation from say 2000 to 1000 minutes per inch of mercury may have the effect of decreasing the rate of dye ascent, and vice versa. Any movement toward the mode, from either direction, is a move toward slower rates of ascent.

It is also found that extreme reduction in the rate of evaporation, short of absolute stoppage, has comparatively little effect on the rate of dye ascent, although it reduces the amount of dye raised. Thus, in one case where the mercury took 8 days (11,150 minutes) to rise from 0 to 1 inch, neutral red, when introduced at the end of this period, rose 10 inches in 10 minutes and 30 seconds.

In the other direction, the rate of ascent increases rapidly as the evaporation increases, until a point is reached, not very exactly defined but in the region of the 200-minute rate, where the phenomenon appears to cease altogether, although the rate of water movement is still considerably below the critical velocity. This result, at first sight surprising, may be deduced from the consideration of equations (5) and (6).

From equation (5) it will be seen that as $p_1 - p_2$ increases $V_r$ will increase toward the limiting case, determined by the Reynolds number, where streamline flow ceases. At this point $v_r = v_a$ and the radial gradient of velocity disappears. As this condition is approached $r^2$ diminishes and $r$
therefore becomes vanishingly small some time before the limit is reached; that is to say, the axial movement is restricted to a line of water too tenuous to draw up any observable amount of dye. The surface of the dye layer will therefore appear to remain undisturbed until true turbulent flow sets in. This corresponds presumably to the region of instability found by STANTON and PANNELL (6).

Conversely it may be seen that as \( p_1 - p_2 \) diminishes, with lower rates of evaporation, the consequent diminution of \( v \), may be compensated by the diminution of \( r^2 \). Reference to equation (1) shows that \( r \) is a more important factor in the equilibrium of force against viscosity than \( v \), the velocity, and that equilibrium will be more economically maintained by changes of \( r \) than of \( v \). With diminishing \( r \) one might therefore expect \( v \) to be maintained down to low values of \( p_1 - p_2 \).

A point of particular interest is that, in the evaporating system of the ASKENASY tube, there may be a movement of material against a concentration gradient. If a small quantity of dye be introduced at the base of the tube the axial current will shortly draw it all to the top of the tube, where it accumulates, so that the latter fractions of the dye material are moving toward a region of concentration.

**Discussion**

The application of these ideas to the conditions of water flow in the xylem looks, in the first place, to the cases where, under conditions of very low transpiration, such as obtain in very humid and sometimes also in very dry situations, there is little or no negative pressure and the cell elements are full of water. In any such case, short of complete hydrostasis, solutes will travel up the axes of the water channels at speeds considerably greater than the total measured water flow would suggest.

Even where air bubbles are present in the vessels, the free water-air surface will still travel at a rate at least twice the mean rate of flow, which will itself be locally accelerated in such conditions by the restriction of the available channel.

Observations at reduced rates of evaporation suggest that under such circumstances a tension may develop which leads to axial rates in excess of twice the mean velocity. In the case just mentioned, for example, where mercury took 8 days to rise 1 inch, the dye rose 10 inches in \( 10 \frac{1}{2} \) minutes. Observations made under constant conditions of evaporation, but starting with the mercury at varying heights in the tube, also show a consistent increase of velocity of axial flow as the mercury level rises.

The rate of flow is also slightly greater, under all conditions, in the upper part of the tube, but most markedly so when evaporation is reduced, that is to say under those circumstances where local tension is most likely to develop. The state of tension, most accentuated at the axis, reduces the
density and hence the viscosity, to which the velocity of flow is inversely related.

**Summary**

The problem of the diffusion of solutes in plants with very low rates of transpiration may be explained by consideration of the radial velocity gradient due to streamline flow in tubes.

With low rates of flow, there is a parabolic velocity gradient normal to the walls of the tube, and an axial current of at least twice the mean velocity of flow. Experiment shows that these conditions are maintained, and even exaggerated at very low rates of water movement, and only disappear, in one direction at complete hydrostasis and in the other direction at a velocity some way short of the beginning of true turbulent flow, which latter cannot, however, normally occur in the transpiration channels. Movement of the solute under these conditions may take place toward a region of concentration.

**LITERATURE CITED**