MOVEMENT OF WATER IN PLANTS AS AFFECTED BY A
MUTUAL RELATION BETWEEN THE HYDROSTATIC
AND PNEUMATIC SYSTEMS

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(WITH FIVE FIGURES)

When one considers the vast accumulation of literature dealing with
the problem of water movement in plants, the paths of its conduction, the
nature of the structural elements involved, the possible sources of energy
required, and the mechanics of its application, it seems rather late to offer
another suggestion. Yet the purpose of this paper is to call attention to a
certain phenomenon of water movement in plants, and to suggest an
explanation of it.

Recently during a series of studies on the paths of conduction, or rather,
of least resistance, between different parts of apple branches by means of
dye solutions, the following situation was repeatedly observed. Whenever
suction is applied to one cut-off branch and a dye solution to another, even
though the latter is located at considerable distance from the former, the
dye enters the main stem and then streams, not only through the conducing
elements toward the source of suction pull, but also rapidly and directly
away from it. There were certain variations in the path taken by the dye
solutions, depending on whether or not the suction was applied "above"
or "below" the source of the dye solution, or on the relative ages of the two
branches under observation. These details will be considered later, but the
interesting thing always evident was this, that there seemed to be some
force acting definitely and in somewhat the same strength, both toward
and away from the source of suction.

This opposite-acting force was at first assumed to be saturation deficit,
but the idea was discarded when it was found to require hours for dye solu-
tions without suction to traverse distances which could be accomplished in
2 to 15 minutes with suction.

It was then thought possible, since the suction connections had always
covered the bark of the cut-off branches, that the negative pneumatic ten-
sion had been propagated more rapidly through the cortex than through the
xylem to points beyond the branch receiving the dye solution, and that the
negative tension at such points had in some manner been translated radially
to the xylem, thereby causing the dye solution to be drawn away from the
suction force. Again, this idea had to be abandoned when it was found
that if the bark were completely removed, the same phenomenon persisted.

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It now became necessary to face the conception of a hydrostatic-pneumatic system in the xylem, a conception which has been so well brought forward through the extensive and critical researches of MacDougall (1, 2) and recently and, more particularly, by MacDougall, Overton and Smith (3). In the latter work it was shown that there is not only a definite water conducting portion in each annual ring, but also a gas-containing one. These portions of an annual ring were designated, early spring, spring and late summer wood, and the function of each as regards water conduction or gas-containing seemed to be more or less fixed for each species. This work, therefore, presents definite information as to the relative location of the hydrostatic and pneumatic systems of certain plants. Overton (4) has just announced that the relative areas occupied by these two systems in a given plant vary with the season.

The results of a particular series of experiments of MacDougall, Overton and Smith (3) bear directly upon the present question. These investigators fixed several air-connected manometers into a tree at varying distances apart and then applied suction. The manometers located directly above and below the point of suction responded quickly to the negative tension, but those on the opposite side of the tree trunk responded very slowly or not at all. The authors, however, observed no consistent response in the hydrostatic system to variations of tension in the pneumatic.

But in order to explain the results to be reported in the present paper, it seems necessary to assume a definite interaction between the hydrostatic and pneumatic systems, and that the pneumatic system can, under certain conditions, become a factor in aiding water movement in plants.

To illustrate this supposed interaction between the two systems, a few typical experiments will be described.

I. The quickest and simplest type of experiments for showing an interaction between hydrostatic and pneumatic units2 in plants is as follows:

An apple branch,3 say two to four years old, is connected with a source of suction at the basal end. Now cut off a small side-branch leaving a stub at least 4–6 cm. in length. Insert this stub into a beaker of dye

2 By the term hydrostatic or pneumatic "unit" is meant that definite portion of xylem tissue which is directly connected with, and in the main normally supplies, any given side-branch, so that such a "unit" may be either relatively large or small depending upon the size of the branch under consideration.

3 All branches or parts of branches used were freshly cut, within a few minutes before each experiment, from much larger branches which had been brought from the orchard, usually within 24 hours.

Such large branches were left out-of-doors where conditions were as in the orchard, that is to say, moist, and temperature low, but not below 0°C. All material was in the state of winter dormancy.
solution and start the suction. Sometimes within a few seconds, usually within five minutes, the dye will have been drawn to the main stem, and moved from the point of juncture, "downward" toward the source of suction, but at the same time a part of the stream of dye solution will have moved approximately an equal distance "upward"; that is to say, directly away from the source of suction. This experiment may be performed with or without removal of the bark. However, if the bark is previously removed, the movement of the dye can be followed readily; but if the bark is left intact during the experiment, it should be removed afterwards in order to observe results more easily. Fig. 1 shows the results of two such tests. Branch A was 4 years old and B was 3. The side branches (b–b) to which the dye solutions were connected were each one year old. The duration of the experiment was 5 minutes and the negative tension was equivalent to nearly 700 mm. of Hg. Under these conditions the dye solution was drawn entirely to the base (a–a) of each, or 14 cm. In A the dye solution also
streamed along a line directly upward from \( b \) to a distance of 27 cm. In B, there was a corresponding upward streaming of the dye from \( b \), but it reached a point only 17 cm. above \( b \) on account of having been largely deflected by branch \( c \), one side of which the stream of dye entered and moved upward for about 10 cm. In such experiments as these the dye never leaves the hydrostatic unit of the side branch through which it is introduced. But if there is another side branch having a portion of its hydrostatic unit in common with the first, then the dye will freely enter the other through, and only through, the common unit and will remain within it.

This behavior of dye solutions in small apple branches is also characteristic for many other plants. The same behavior was noted for the Italian prune, pear, sweet cherry, sour cherry, *Amelanchier alnifolia*, *Crataegus douglasii*, *Rosa 2 spp.*, red raspberry (var. Cuthbert), Loganberry, Evergreen blackberry (*R. laciniatus*), *Juglans cinerea*, *J. regia*, *Corylus avellana*, *Castanea dentata*, *Quercus garryana*, *Acer macrophyllum*, and *Salix spp.* Only two species tried have failed to respond in a manner as described above. These were *Fraxinus oregana* and the black raspberry (var. Plum Farmer).

II. A second type of experiment was tried where the procedure was exactly the reverse of the preceding, that is, the suction was applied to a side branch and the cut-off base was placed in the dye solution. The results, however, were the same as before, for when branches, which had been treated by this method were compared with specimens such as shown in fig. 1, it was difficult to distinguish them. The dye was drawn up from the base through the hydrostatic unit of the side branch in question, a portion of the dye passed into the branch, but the rest streamed up the stem beyond the side branch apparently against the suction force.

III. Experiments of type II above were modified to the extent that instead of placing the basal end into the dye solution, the stem was cut off above the suction attachment and that end placed in the solution. The resulting picture was somewhat different, although it still gave evidence of an interaction between the hydrostatic and pneumatic units. The characteristic results of this procedure are shown in B of fig. 2. Here the suction was applied at \( b \), with the dye solution entering at \( a \). The dye moved freely toward \( b \) in a rather wide stream, the middle part of which entered branch \( b \), but mostly through its adaxial side. The outside portions of the stream passed around the base of \( b \) and moved rapidly in two parallel bands down the main branch for 24 cm. The right hand band (see fig. 3 B) was itself divided by the presence of another side branch at \( c \). The dye did not enter that part of the hydrostatic unit which supplied the outside face of \( b \). The situation is relative, however, for if suction is prolonged, the dye will cross over into the remaining part of \( b \) fairly completely. The duration of this particular experiment was 6 minutes only.
IV. While the foregoing experiments seem to indicate an interaction within a single hydrostatic-pneumatic unit, and that this interaction causes definite water movement, they have not furnished evidence as to whether or not there is an interaction between separate hydrostatic-pneumatic units. It has been assumed so far, that the water movements recorded, especially those away from the source of energy, were caused by a more rapid propagation of negative tension through the pneumatic units, so that this tension quickly passed around the greater resistance in the hydrostatic unit. In such situation it was then capable of applying itself to all points along the latter. Whenever the tension was transmitted in this manner to somewhat distant points, it caused water movements which appeared paradoxical.

In all experiments described, the dye solution and suction force were applied to the same hydrostatic-pneumatic unit. But the following experiments were designed to yield information concerning a possible interaction between relatively distant hydrostatic-pneumatic units.

The results of a typical experiment of this sort are shown in fig. 3. The material used was an apple branch, the main stem of which was 7 years old, and, near the bottom of the photograph, 5.8 cm. in diameter. Suction
was applied at branch $a$. A dye solution was connected to the small side branch $b$ which was situated $135^\circ$ around the stem from branch $a$, and about 35 cm. above it. Suction was allowed to act for 40 minutes. The bark was then removed as shown. It was observed that the dye solution had entered the main branch and traveled 19 cm. upwards and about 40 cm. downwards. It is here admitted that there are forces, e.g., saturation deficits, within such a branch capable of causing the dye solutions to be drawn in without suction, and afterwards the dye may be distributed in practically the same manner as in all cases described. There is this difference, however, namely: with suction the distribution of the dye may take place in a few minutes while without it, many hours are usually required to produce a corresponding effect.

In the results of this type of experiment, there are some points of especial interest. First, it was apparent that there was a cross transference of negative tension between separate pneumatic units, but practically no cross-transference between corresponding hydrostatic units. Note C
and B in fig. 3. These are photographs of cross-sections made just above and below b to show how strictly the dye solution is confined to the hydrostatic unit of b. At no point below did it show any tendency to leave this unit in order to move toward the source of suction at a. This result is interesting because it indicates that the pneumatic units of a stem, being relatively more in communication than the corresponding hydrostatic units, can transmit a negative tension from one hydrostatic-pneumatic unit to another, and as a consequence cause work to be performed in other, perhaps distant, hydrostatic units.

Experiments of the above type were carried out with a number of different combinations of "hook-ups," some of which yielded surprising results. An interesting, though simple one, is shown at A in fig. 2. The main stem was 7 years old and about 5 cm. in diameter. Branch b was 6 years old, branch a, 5 years and the stub c 2 years old. (The entire branch was cut back after the experiment while observing results). Suction was applied at a; the entire cut surface of b was placed in a solution of light green dye; and c was connected with a solution of trypan blue. After suction had acted for 35 minutes, the experiment was stopped and the bark removed. It was found that the light green dye had entered at b and passed over into a, but only in the hydrostatic unit which branches a and b shared in common. However, in addition, the green dye had streamed down the main stem for 44 cm. from the junction of the two branches. The cross-section of the main stem (now at the bottom of the photograph) showed the green color as a semi-circular band outlining the hydrostatic unit supplying the adaxial faces of b and a. The trypan blue entered at c, but since this shoot was a relatively recent addition to this branch system, it possessed only a thin hydrostatic-pneumatic unit which had little or no hydrostatic connection with a or b. As a result the dye did not enter branch a but streamed down the main stem in its own tortuous (at the beginning) and shallow hydrostatic unit for 35 cm. running directly away from the source of negative tension.

Another experiment of the same general type as the above will be described. The general situation at the end of the experiment is shown as fig 4. It was carried out with an apple branch 8 years old and over three meters in length. Suction was applied at a, a branch 5 years old. Five mercury manometers, air-connected, to record pneumatic tension, were fixed in the main stem as follows: No. 1, directly below a at 27 cm.; no. 2, also directly below at 89 cm.; no. 3, directly above a at 21 cm.; no. 4, also directly above at 73 cm.; and no. 5, directly opposite from a and at a distance of 110 cm. Then an eosin solution was connected to the three year old branch b, situated about 90° around the trunk from a; trypan blue solutions were attached to the two-year old branches c and d situated
FIG. 4. Showing the arrangement and final result of the last specimen described under section IV.
at 130° and 143° around the trunk respectively; and finally, light green solution was attached to the two-year old branch e, situated approximately at 180° around from a.

Suction was started and in less than 10 seconds the Hg in manometer no. 3 was drawn into the boring, the negative tension having had to exceed 18 cm. of Hg to produce this effect. Manometer no. 2 quickly registered 14 cm. and no. 1, after a few minutes showed a negative tension of 8 mm. At the same time, no. 4 showed a tension of 12 mm. One-half hour later no. 5 indicated a trace of negative tension, possibly 2 mm. In the meantime the entrance of the dye solutions was being observed. This was done by stripping off bark above and below connection points. It was noted especially, how, in spite of the fact that manometer no. 5 had not yet recorded any negative tension, the dye solution had entered at e, located only 17 cm. below this latter manometer, and had moved both upward and downward 3.5 cm. and 4.5 cm. respectively in 15 minutes. The experiment was stopped in one hour and thirty minutes. The extent of the movement of the dye solution was as follows: From b the eosin moved upward 37 cm. and downward 18 cm.; from c the trypan blue moved upward 85 cm. and downward 12 cm.; from d the same dye moved upward 48 cm. and downward 16 cm.; and from e the light green had gone upward 32 cm. (but had been almost completely blocked by the boring for manometer no. 5), and downward 68 cm.

The results of this experiment indicate how water movements can be induced in a number of hydrostatic-pneumatic units simultaneously, by a negative tension originating in one of them, and being transmitted to the others through the several pneumatic units.

The responses of the pneumatic manometers in this experiment agree, in the main, with the more extensive results recorded by MacDougall, Overton and Smith (3). But it is interesting that water movement is initiated in a hydrostatic unit in response to a negative-tension originating in a relatively distant one, even though that tension is not strongly indicated by means of a pneumatically connected manometer in the vicinity of the former.

It should be mentioned in passing, that the relative location of the hydrostatic and pneumatic systems in each annual ring of the apple tree, during December is this: the hydrostatic system occupies the "early spring" and "spring" woods, and the pneumatic system the "late summer" wood only. Whether or not the pneumatic system encroaches upon the other during the summer months has not been determined, but considering Overton's (4) findings, it would seem likely.

V. A model was constructed to illustrate the possible mechanism by which a hydrostatic and a pneumatic unit in the plant interact. A model
of the sort is shown in fig. 5. It is extremely simple and can be assembled in any laboratory within a few minutes. The glass tubing used has an outside diameter of about 7 mm. That portion of the model indicated by cross-hatching is tightly filled with white sand of 20–40 mesh, and kept in place by cotton plugs. Tube A is connected to an aspirator for suction, D is connected to a short glass tube having a right angle bend so that it can be transferred at will from a beaker of distilled water to one of dye solution or \textit{vice versa}, and E is connected with a distilled water supply. To make the demonstrations, close clamp no. 2, open clamps nos. 1 and 3. After E and D are connected to their water supplies, start aspirator. When section B has thoroughly filled with water, it represents an hydrostatic unit of a branch and a cut-off side branch, through which a dye solution is to be drawn. C of course represents the corresponding pneumatic unit, but at the first stage of the demonstration it is prohibited from act-
ing by the closure of clamp no. 2. Now with aspirator still on, close clamp no. 3 and place D in a dye solution. When clamp no. 3 is reopened the dye solution will now enter into the "main branch," and will, if the negative pressure is kept constant, stream toward A only. Next open clamp no. 2, thus bringing the pneumatic unit into action. At once the dye solution will commence to stream "upward" through B also and will continue until it reaches the end of the tube. The behavior of the dye solution in the model resembles so much what one sees while performing the type of experiment recorded in section I, that it is difficult to refrain from judging the two mechanisms essentially the same. However, within a plant, the negative tension would be transferred from the pneumatic to the hydrostatic unit at numerous points, if not almost continuously, along the path. It may be also suggested that if a number of such models, or mechanical hydrostatic-pneumatic units, should be connected through their "pneumatic systems," each one would perform the same work when a negative tension is applied to any one of them. The interaction of this multiple system might be compared to what goes on in the several hydrostatic-pneumatic units of a stem. Yet the comparison is not entirely fair, on account of the obviously greater resistance between pneumatic units in a stem, and the loss of tension from air entering through lenticels.

In this paper there has been enough "discussion" in the introductory paragraphs and during the description of experiments, to leave little more desirable. It remains to say, however, that the significance, if any, of the results reported herewith, lies in the possibility of a functional relation between the hydrostatic and pneumatic systems in plants affecting water movements. How important the function really is under natural conditions, while transpiration is active, this paper offers no evidence. Nevertheless, the seeming fact that there is a mechanism which permits a negative tension in one hydrostatic-pneumatic unit of a stem to be propagated relatively quickly to other units, and in them to cause work to be done (i.e., movement of water), is worthy of consideration. Whenever calculations are made as to the total energy required to move a given quantity of water through a given length of stem in a given time, the recognized high hydrostatic resistance of the xylem is always taken into account. The resulting figures are frequently very large. Is it not possible that a more facile transmission of energy through the pneumatic units, and the consequent application of this energy all along the hydrostatic path, might lower the value of the previously calculated total energy requirements for the rise of the transpiration stream?

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4 To clean apparatus close clamp no. 2, open clamp no. 3, and transfer D back to the water supply, leaving suction on.
LITERATURE CITED


