THE STATE OF WATER IN DUCTS AND TRACHEIDS

GEORGE J. PEIRCE

In preceding papers (3, 4, 5) I have discussed various aspects of the problem of the ascent of sap, of how water goes up a tree, and I wish in this paper to carry the discussion forward another step. First, however, I wish to express certain convictions, the fruits of observation, experiment, and reflection, under climatic conditions of considerable variety.

I. If one conceive the living body to be a continuous mass of water, then one will readily admit the undesirability of interrupting the mass by wound or amputation in any study of water movement, and the possibility that the evidence produced after or in connection with the injury may be misleading. Therefore in recent experiments I have avoided all mechanical injury, even to the extent of using undisturbed trees, etc., out of doors. Shocks from uprooting, transplanting; diminished absorption through injured roots; cells in phloem and xylem stimulated to unusual if not abnormal activity by cutting or pressure; change in exposure to light, air, etc., following transplanting, or the transfer of potted plants to other positions; all of these have been avoided, as previously described, by using trees in situ growing out of doors. STRASBURGER (7) in his famous experiments on trees in the Botanical Garden in Bonn used living trees, but he amputated them at the butt. I have in nowise disturbed my trees except by applications to limited and intact parts, and by the results of these applications in the parts beyond.

II. It is absurd that it should be necessary to point out that glass and cellulose, and the derivatives of cellulose found in the bodies of plants, bear very different relations to water; and to warn the student that the results of experiment with glass may be quite misleading as to what actually occurs in cellulose and cellulose derivatives. It is true that the adhesion between water and clean glass is considerable; but anyone knows that to dry glass in any form to a constant weight is a task easier and quicker than to dry any mass of cellulose, whether lumber or fabric. The relations of water and cellulose, furthermore, are not merely mass relations, as for the most part at least between water and glass; but they are molecular relations, and there is in every cellulose mass a certain amount of bound water. It was with realization of this that Woodhouse (8) tried to qualify and correct his experiments in the glass tubing which he used. But in my experiments I have avoided the use of glass and of all supposed imitations of plant structures.

III. I have lived for many years in a semi-arid climate, in which the temperatures at all seasons are moderate, in which there are regularly
alternating rainy and dry seasons during which atmospheric humidities are respectively high and low; and illumination is more intense and richer than in corresponding latitudes and altitudes with which I am acquainted elsewhere. Just as the sugar maple has a season in which it can be bled of its sweet sap, and another much longer season in which no sap will flow from it, so we have plants which exhibit similar phenomena, with little or no difference in the water maxima, but with water deficits more pronounced and even revealing themselves by wilting, by rainy season and dry season foliage, by leaf fall, and by complete disappearance from the landscape. I have seen *Pinus radiata* Don. wilt in sandy soil near the coast under high temperatures on dry sunny days. The tarweeds (*Hemisonia*, etc.) have dry season foliage made up of relatively few long, narrow, and glandular-hairy leaves borne on the slender woody flowering stem, which rises in late spring from a rosette of broad, rather fleshy and smooth leaves, which has formed on the surface of the damp soil during the rainy season. *Aesculus californica* Nutt., the California buckeye, is our first tree to put out leaves in the early spring (February or March or April) and the first to lose them in early summer (in June or July or August), according to the dryness of the soil in which it grows; and the Miners’ Lettuce, of the days of the “Gold Rush,” *Montia perfoliata* Howell, thriving in shade, commonly under oaks, and in orchards, during the rainy season, dries and dies at the beginning of the dry season. This last is as characteristically a rainy season plant as the hayfield tarweeds in bloom are characteristic of the dry season. Their vascular tissues correspond to their respective seasons of growth, their heights and their foliage (3).

Under these conditions the maintenance of solid columns or cylinders of water in ducts and tracheids would seem to be difficult and doubtful. This is recognized by MacDougall, Oertzon, and Smith (1) who give the name of the pneumatic system to those ducts and tracheids in the plants which they studied which do not contain liquid. That there are such elements in the vascular bundles cannot be questioned; but the relative numbers of hydrostatic and of pneumatic elements at one time is not necessarily the same at all times, as may be demonstrated by testing with starch suspension (6). The elements filled with water are obviously most numerous at times of water surplus, fewest at times of water deficit. The same set of ducts or tracheids will, therefore, be a part of the hydrostatic system at one time and of the pneumatic system at another. When they are full of water they may be made to bleed; when they cannot bleed, what do they contain?

This question is only partly answered in MacDougall’s later paper (2), for while the proportions of carbon dioxide, oxygen, and nitrogen are reported, there is no indication of the proportion of water vapor. Since it
is inconceivable that the contents of the pneumatic system form a mixture of dry gases, water vapor must be present, varying in proportion from time to time, as do the proportions of the pneumatic system itself.

† From the foregoing it is clear that in the mass of wet wood which constitutes a part of the vascular system of a living land plant, water may exist exclusively in liquid form, or part of it in liquid form, part of it as vapor. The liquid water may fill a duct or a tracheid, it may be "bound" in the walls, it may be more or less free on the surface of the walls as a thicker or thinner film, and it may fill as vapor the remainder of the space surrounded by the wet wall. If this reasoning and these inferences are correct, it is possible to prove them by proper experiment.

If one apply sufficient cold to the outside of an intact branch of a living plant, whatever water is in the part chilled will condense to liquid and will freeze. If the quantity of water be sufficient to form an ice plug in the vessel, movement of any sort through that part of the vessel will be prevented by the plug. If, on the other hand, the quantity of water be insufficient to close the vessel, motion through it will not be prevented. It is possible to blow through certain kinds of wood when they are dry, notably oak. Of course it is not possible to blow through the tracheids of the wood of the Conifere. Branches of California buckeye can be blown through as readily as oak branches or pieces of oak wood because of the large ducts in the xylem. One may blow through dry pieces of buckeye wood, demonstrating the results by bubbling through water or by moistening and soaping the end through which the gas exudes. If one use breath, bicycle tire-pump, or compressed air, the result is the same in kind—sooner or later bubbles come through. They come through immediately in the dry season, less and less promptly the earlier in the season the experiment is made; for the more water there is in the wood, the more must be blown out before bubbling can occur. But if the wood should be full of water and frozen by liquid air, as described in a previous paper (5), air could not be blown through as long as the water remained frozen. On the other hand, if the wood should contain little more liquid water than that bound in the walls of ducts and tracheids, freezing would not cause water plugs to form in the ducts, and air could be blown through.

The experimental record is as follows:

April 11, 1935, 3 P.M. Into a paper cup made as described previously (5) pour liquid air to the depth of 1 cm. (approximately) around a leafy branch of buckeye, near the laboratory.

3:15 P.M. After thorough freezing cut off the branch below the frozen zone, rush into the laboratory, carrying branch with butt in Dewar flask containing liquid air in the bottom; cut fresh surface, con-
nect with compressed air cock, open the cock and attempt to blow through, with the end under water: no bubbles.

But yesterday a similar branch, cut off but not previously frozen, frothed when tested with compressed air. This showed the presence of continuous open ducts for lengths of 15 cm. or more.

At these dates there had been a total rainfall of 16" for the season (since the preceding July 1), soil and vegetation were full of water, and there should at this time, if ever, be continuous columns of water in some or all ducts. Hence I expected the vascular system at this time to be full of water and therefore plugged with ice if I applied sufficient cold. This was the case as the observation showed.

April 12, 2 P.M. Put two paper cups on two erect foliage branches of buckeye, tying tight with adhesive tape at the bottom of the cups, and pour liquid air into the cups to freeze, not chill, a zone of 1 cm. on each branch. Air temperature 20° C., sunshine and clouds. Within 5 minutes, the foliage above the cups wilting.

10-15 minutes leaflets and tender shoots hanging limp.

April 17, 11 A.M. Air temperature 16.5° C. No recovery of foliage of frozen branches, leaves dead, dry, though much cloudy weather, 0.7 in. rain, high humidity and little full sunshine since preceding entry, and the rest of the foliage of the tree in fine condition.

May 2, 10:35 A.M. Liquid air treatment, amputation, and compressed air as above: no bubbling.

Air temp. 17.5° C., humidity high, soil moist from recent rain. Longitudinal halving of the branch showed that the water continued to move from above the frozen (plugged) part toward the foliage, and that the part of the vascular system just above the frozen zone, under these conditions, was dried by the withdrawal of its water by the parts above.

May 20, 3:40 P.M. Air temp. 32.4° C., top leaves of buckeyes half wilted, but no pronounced water deficit further down as shown by freezing and using compressed air on the green current year's branch, through which slight bubbling was noted. Same treatment of a last year's branch, bearing new growth and new foliage beyond, showed no bubbling. My work was interrupted and delayed soon after; but later in the season, and before the leaves had fallen, when, therefore, there should be the maximum draft upon the conducting tissues by reason of the low humidities, at least by day, the warmth and motion of the air, the drying of the soil because of the absence of rain from the onset of the dry season, freezing and compressed air showed the passage of air, as indicated by bubbles, through the branches tested. These internodes were 15-20 cm. long. By using internodes, anastomoses at the joints and at leaf bases were avoided.
It may be said that this compressed air treatment after freezing shows only that there are unfilled (unplugged) vessels in the vascular system of buckeye, that it does not show that there are no vessels filled with solid columns of water at normal temperatures. This is true; but it is also true that, with the change from a water surplus to a water deficit, the freezing-compressed air treatment shows a corresponding change from no passage of air, to the passage of small amounts to a water deficit, the freezing-compressed air treatment shows a corresponding change from no passage of air, to the passage of small amounts to air, through the vascular system. The proportions of hydrostatic to pneumatic tissues in the vascular system are not fixed, but vary from time to time according to the internal and external circumstances of a tree (3), there being very little if any pneumatic tissue at the time when bleeding is a natural or induced phenomenon, there being very little if any hydrostatic tissue containing water other than as vapor, film, and bound water at times of deficit, when bleeding is not possible.

This is confirmed by repeated observation that, in buckeye, castor bean, and other plants, the position of starch suspension (6) used to show the course of water movement varies according to the water relations of the plant upon which one experiments. At times of water abundance some, but not necessarily all, vessels may be filled with starch suspension. At times of less and less water, the starch suspension is confined more and more to the walls of the vessels, except in the region immediately affected by the injection following amputation of the branch under the surface of the starch suspension.

It was the repeated observation of this distribution of starch in the vascular system of the plants experimented upon by using the starch suspension method that led me to consider how to determine, without amputation, the condition and the position of the water in the vessels at different times, and to conclude that if instead of the water being at all times in a larger or smaller number of unbroken columns of liquid, it may be in unbroken liquid columns or in hollow liquid columns (films on the walls) filled with water vapor, and water bound in the cellulose and cellulose derivatives of the walls. As indicated above, the application of freezing cold to short zones of water-conducting intact branches confirms the conclusions suggested by the condition in amputated branches as shown by the starch suspension method.

I feel, therefore, that the idea as to the condition and movement of water, as set forth in my first paper (3) is correct as regards woody plants in arid and semi-arid areas, and in all vascular plants at times of water deficit in the vascular tissues, whatever may be the condition at times of water surplus in humid climates whether tropical or temperate. That there may be great force (suction force) exerted by the foliar parts above upon the conducting vascular tissues below is obvious; but that this force
is dependent upon micro-menisci in the walls of mesophyll cells does not seem necessary or indicated by the evidence. Evaporation, transpiration from the surfaces, wherever they may be, of the continuous mass of water of which each living organism consists, will set up in the mass forces, tensions, which will conform in place and power to the structure and composition of the system. The bound water of the walls of the vascular elements forms a water-seal which obviates and excludes drawing in air from the sides. Hence the traction is upward, not lateral; it is a lifting force pulling up the water as vapor or as liquid, according to position and condition in the vascular system. That this force is adequate has been shown repeatedly by others.

The maintenance of water as vapor, liquid film, and liquid mass in the vascular elements and their walls, in the hydrostatic-pneumatic system of woody plants, is possible only when living cells are duly associated with the vascular tissues. Death of these cells by poisons and by heat, immediately interfering with the moving mass of water only to a partial extent, disturbs the movement of sap far less than cold, which completely stops the movement of the water as well as the life of the cells in the zone of freezing. The living cells are indispensable, not for moving, but for conditioning the movement of the water.

LITERATURE CITED