Thomas Brotherton, Robert Hooke, and Some Neglected Experiments in Plant Physiology During the Late Seventeenth Century

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Botanical historians (Sachs, 1906; Darwin, 1913; Green, 1914; Reed, 1942) consider experimental plant physiology to have become established with the quantitative studies of Stephen Hales (1727) upon movement of sap, the role of leaves in transpiration, root pressure, etc. However, isolated experiments had been made upon plants in the 17th century, notably by van Helmont in the early part of the century and by Woodward toward its end (Sachs, 1906, Bk. 3, Chap. 2; Green, 1914, Chap. 14; Ritterbush, 1964, pp. 70-88). This article discusses some neglected but important experiments by Thomas Brotherton, communicated in 1687 to the Royal Society of London and commented upon by Robert Hooke, author of the *Micrographia,* wherein cells were first described in 1665.

In 1671, Brotherton removed a 4-inch ring of bark from a crabapple tree and found that growth above the ring continued for 2 years before death supervened. In another experiment he removed a 3-inch ring of bark from a 3-year seedling of "Scotch-Firr" (*Pinus silvestris*), its age determined by the number of whorls of branches. This seedling also grew in height and showed unexpectedly great increase in stem thickness above the girdled zone, but none just beneath. Again the tree died in its third year. On another "Scotch-Firr" seedling opposite branches were examined, one branch being girdled and the other left as a control. The girdled limb grew twice or thrice as much as the control, and the bark healed downward for more than half an inch. Then narrow helical swaths were cut from the bark of young trees, but no differences in growth above and below the cuts were seen, although the bark healing downward increased in thickness while that healing upward did not. Within the year the wounds healed over. In yet another girdling experiment, rings of bark were cut from a 3-year "Scotch-Firr" stem at the midpoints between whorls of branches. The branches grew, but no stem thickening was observed between each ring and the branches below, while a good deal occurred between each ring and the branches above. In another kind of experiment, longitudinal incisions were made in a young hazel sapling so as to free a narrow vertical strip of wood from the trunk, except at its two ends. By a horizontal cut across the middle, two strips of wood plus bark were separated and were then wedged out free from the trunk and from one another. The top strip, joined to the trunk at its upper end, grew well; the bottom strip, attached at its lower end, did not grow. The rest of the tree grew normally. An incomplete experiment, in which a leafy branch was left on a similar bottom strip, was made in anticipation that this would enable growth there, though not a normal amount.

A third sort of experiment involved four poplars chosen as closely similar in size and habitat. One had the canopy removed; on another, only a small head was left at the top; on yet another, the lower half of the canopy was removed. The fourth tree served as a control. Growth was proportionate to amount of canopy, and in about 10 years the control tree had grown more than four times as large as the one whose canopy was completely removed. Severe pruning increased frost sensitivity in poplars during the harsh winter of 1684, while girdling the stems had no ill effect.

A final observation showed greatest terminal growth in top branches, whose shoots might extend 2 feet, and least growth in lower branches, whose shoots did not exceed 4 inches.

Brotherton concluded that sap ascends mainly in the vessels of the wood of trees and not in the bark or between wood and bark. He also pointed out that growth in thickness of trees is due to descent of sap throughout the summer. His ringing experiments demonstrated a clear functional distinction between the wood and bark of trees as regards movement of sap and plant nutrition and were published four decades before those of Hales. Indeed, it is likely that Hales's ringing experiments were stimulated by Brotherton's work, since Hales mentioned having read of it in the abridged Philosophical Transactions of the Royal Society (*Vegetable Staticks 1738,* 3rd ed., p. 148). Unfortunately, the sources of Brotherton's inspiration are unknown, though Hooke's communication implied that he had some familiarity with the then current theories of sap movement.

In communicating Brotherton's work to the Royal Society, Hooke drew a further and most interesting conclusion, that plant bodies "are nourished and increased by a double food; the one an impregnated water, and the other an impregnated air." These "do mutually mix and coalesce, and parts of the air convert to water, and parts of water convert to air." Hooke also remarked that plants have "a twofold kind of roots, one that branches and spreads into the earth, and another that spreads and shoots into the air, both kinds of roots serve to receive and carry their proper nourishment to the body of the plant, and both serve also to convey and carry off the useless recrements."

These statements provide a clearer and more concise description of the aerial contribution to plant nutrition than any other 17th-century writings known to the present author.

This brief account shows that a purely experimental approach to plant physiology was being attempted at about the same time that predominantly anatomical studies by Malpighi and Grew were providing clues to plant function.

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