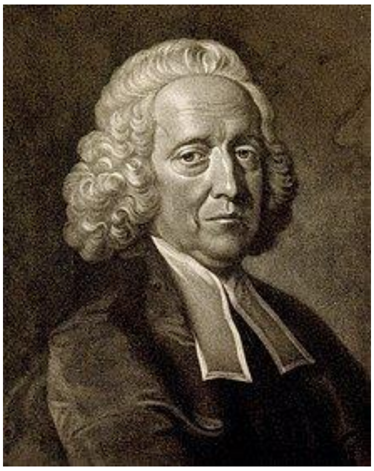
Stephen Hales and the foundations of experimental plant physiology

My PhD was largely about transport of nutrient ions, particularly Ca^{2+} in plants, through the water stream in the xylem tissue of the stem, showing how this acted as an ion exchange system, with the positive ions associating with negatively charged sites on the lignin walls of the xylem vessels. My postdoc, with my late friend and colleague David Clarkson at the Letcombe Laboratory in England, was on transport pathways of nutrient ions and molecules across roots, following intra- and intercellular pathways, and identifying the barriers and limits of the processes.



With all this, how could you not respond to an 18th century gentleman experimenter and clergyman who was one of the first to show how water moved in plants, the pathways of sap flow, and how water pressures and tensions, water potential in modern terms, developed, and who was one of the first to examine gas exchange in plants. He was also one of the first to devise practical experiments, make precise measurements, and to deal in numbers and quantities to make his conclusions, hence his book, '*Vegetable Staticks'*. 'Staticks' means the collecting and analysis of data.

The modern exclusivity of restricting study to either plants or animals was not an 18th century way of doing things, and Hales benefitted from his experimentation on both plants and animals. Let's cover off the animal physiology first. His main work on this was published in the second volume of a two-volume edition of *Vegetable Staticks* in 1733[1], although the first single volume edition of 1827 also had a chapter largely on animal experimentation. The work he describes contains observations and measurements from experiments which even he thought disagreeable, making measurements on live animals, but he made very original and significant discoveries on blood pressure, heart rate, blood flow, vascodilation and vasoconstriction, lung capacity and respiration.

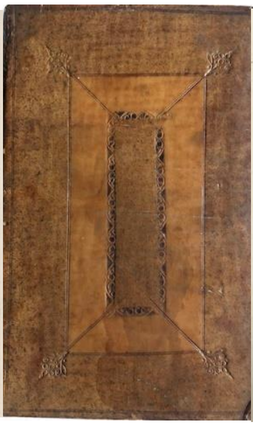
We can criticise Hales' animal experiments for their brutality, as many did at the time. Even a good friend, and dog lover, such as Alexander Pope is reported in 1718 as saying: '*He commits most of these barbarities with the thought of its being of use to man. But how do we know that we have a right to kill creatures that we are so little above as dogs, for our curiosity, or even for some use to us?*' And there he is in the words of Thomas Twining, of the Twining's tea merchant family, and a far lesser poet:

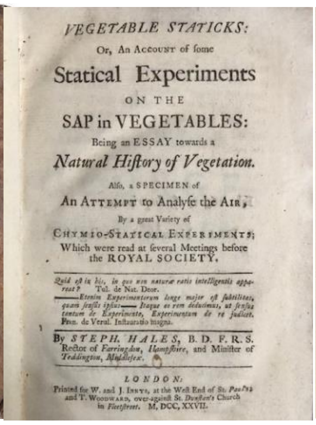
> *Green Teddington's serene retreat,*
> *For Philosophic studies meet,*
> *Where the good Pastor, Stephen Hales*
> *Weigh'd moisture in a pair of scales,*
> *To ling'ring death put mares and dogs,*
> *And stripp'd the skin from living frogs*
> *(Nature he loved, her works intent*
> *To search, and sometimes, to torment!)*[2]

This is from his poem, '*The Boat*', a lyrical work following the flow of a boat down the river Thames, in imitation of Catullus' '*Dedicatio Phaseli*'. In a footnote to these lines, Twining, either Thomas or his great-nephew editor Richard, states:

> *Dr H. was an ingenious man, and made some useful experiment; but those here alluded to are such as can be justified by anything scarce short of necessity, or, at least a strong probability of their leading to discoveries highly importing the good of mankind. Curiosity, or the vague expectation of discovering something or other, is not a sufficient excuse for putting any living creature to a painful death; but it is generally the real motive, though men are glad to conceal from themselves their cruelty by giving it a better name, and talking about the good of mankind. See Vol. II. of the Vegetable Statics, where several mares, not fewer than twenty dogs, and some other animals, were put to death in the most painful and lingering way; and he was particularly interested in flaying the skin off the bellies of live frogs, to see the motion of their blood and muscles. (Page 59.) And see the dedication to Vol. I, where he speaks of it as one great use of studying the works of Nature, that they 'convince us of the goodness and benevolence of their author'. One would not expect such an observation to be followed by such experiments.*

But let's move on, while remembering that sensitivities on animal experimentation are not exclusive to our present times. It's clear that Hales' thinking moved continuously across the boundaries of animals and plants, pursuing analogies between blood flow and sap flow, and of gas exchange. He applied his statical methods to plants, and his numerous experiments, their results and his conclusions, were published in *Vegetable Staticks*[3].



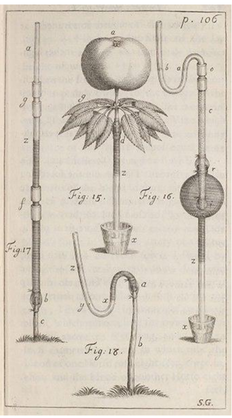


VEGETABLE STATICKS:
Or, An Account of ſome
Statical Experiments
ON THE
SAP in VEGETABLES:
Being an ESSAY towards a
Natural Hiſtory of Vegetation.
Alſo, a SPECIMEN of
An Attempt to Analyſe the Air,
By a great Variety of
Chymio-Statical Experiments;
Which were read at ſeveral Meetings before
the ROYAL SOCIETY.

Quid eſt in his, in quo non naturæ ratio intelligentis appareat? Tul. de Nat. Deor.
——*Etenim Experimentorum longe major eſt ſubtilitas, quam ſenſus ipſius*—— *Itaque eo rem deducimus, ut ſenſus tantum de Experimento, Experimentum de re judicet.* Fran. de Verul. Inſtauratio magna.

By *STEPH. HALES*, B. D. F. R. S.
Rector of *Farringdon*, *Hampſhire*, and Miniſter of
Teddington, *Middleſex*.

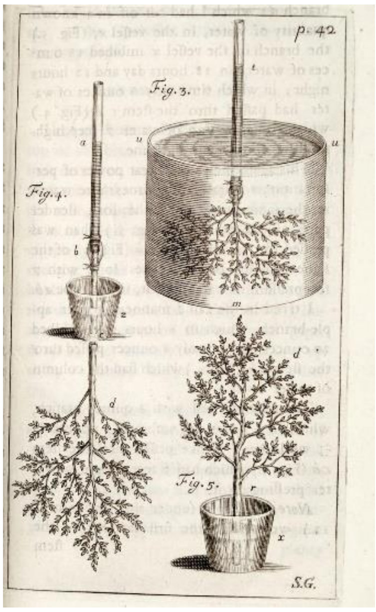
LONDON:
Printed for W. and J. Innys, at the Weſt End of St. *Paul's*
and T. Woodward, over-againſt St. *Dunſtan's* Church
in *Fleetſtreet*. M, DCC, XXVII.



The book bears the imprimatur of Isaac Newton as President of the Royal Society, and dated February 16, 172$\frac{6}{7}$. There is a dedication to George, Prince of Wales, who became George II in June 1727. An enthusiasm for plants already creeps into the dedication: '*And as Solomon, the greatest and wisest of men, deigned not to inquire into the nature of Plants, from the Cedar in Lebanon, to the Hyssop that springeth out of the wall: so it will not, I presume, be an unacceptable entertainment to your Royal Highness...*' in his preface he acknowledges '*Dr Grew and Malpighi*' the 17th century pioneers of plant anatomy and microscopy, for their anatomical studies on the structure of vessels in plants, and points out how much more they could have advanced knowledge if they had pursued the statical way, in other words, moving on from observation to experimentation, measurement and data collection. This is the core of his work.

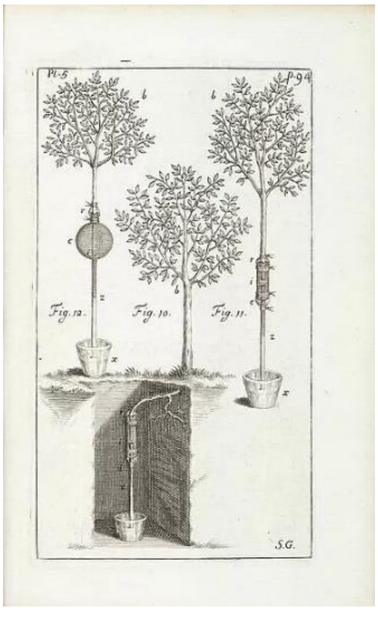
Chapter I. *Experiments, showing the quantities of moisture imbibed and perspired by Plants and Trees.*

Right from the start, the measurements begin. He seals a pot with a plant in it, weighs it at different times of the day and shows the water loss through the stem and leaves. Then he cuts off the leaves, measures the surface area using a grid, measures the length of the roots, and comes up with an estimate of the amount and rate of water loss. He attaches a siphon tube to a plants such as vines, apple and lemon trees, and herbaceous plants such as spearmint to measure and calculate water uptake. And here is the comparative physiologist. He compares plant water uptake and loss with the perspiration rates of a man, and calculates that the ratio of perspiration of a man to the sunflower is 140:100.



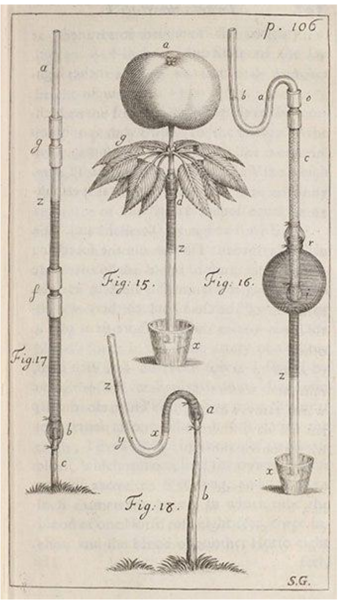
Hale continues through a number of ingenious experiments, making the important conclusion that water is drawn through the plant, not driven: ‘*The third day in the morning I took the branch out of the water; and hung it with the Tube affixed to it in the open air; it imbibed this day 27 inches in 12 hours. This Experiment shews the great power of perspiration; since when the branch was immersed in the vessel of water, the 7 feet column of water in the tube, above the surface of the water, could drive very little thro ' the leaves, till the branch was exposed to the open air. This also proves, that the perspiring matter of trees is rather actuated by warmth, and so exhaled, than protruded by the force of the sap upwards.’* He further concludes that there is very little sap pressure: ‘..*that tho ' the capillary sap vessels imbibe moisture plentifully; yet they have little power to protrude it farther, without the assistance of the perspiring leaves, which do greatly promote its progress*.’

Chapter II. *Experiments, whereby to find out the force with which Trees imbibe moisture*.



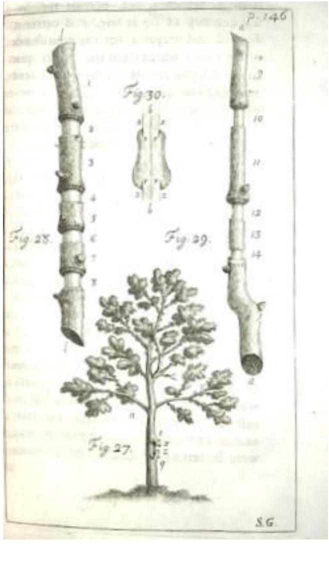
He is intrigued to know what force drives water flow, though he has largely worked this out in the first Chapter. He attached branches, and the whole trees to glass tubes, setting them in mercury and measuring the levels of mercury associated with water loss, and proves: ‘...*that branches will strongly imbibe from the small end immersed in water to the great end as well as from the great end immersed in water to the small end*,’ and by removing bark shows it has no effect on water movement. The passive nature of the xylem vessels and what we know as transpirational pull, emerges from the experiments. ‘*I tryed also the imbibing force of a great variety of trees, by fixing Aqueo - mercurial gages to branches of them cut off.’* And being the fruiting season (with a *Russet Pippin*): ‘*So a twig, with an apple and leaves raised the mercury 4 inches, one with leaves only 3 inches, one with an apple without leaves 1 inch*.’

Chapter III. *Experiments, shewing the force of the sap in the Vine in the bleeding season.*



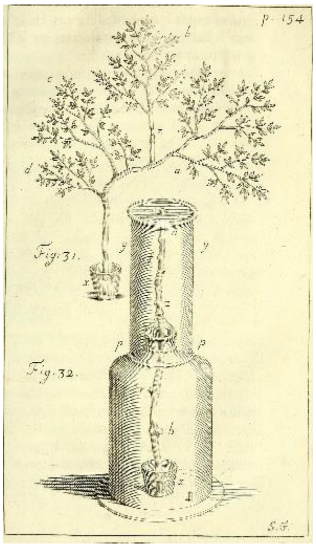
There follows a series of experiments on bleeding sap, which widely occurs in spring, where the xylem sap can become under pressure, from what we call root pressure, rather than tension, particularly in large-vesseled vines. He also observes capillary action: '*From these Experiments, I say, it seems evident, that the capillary sap vessels, out of the bleeding season, have little power to protrude sap in any plenty beyond their orifices; but as any sap is evaporated off, they can by their strong attraction (assisted by the genial warmth of the sun) supply the great quantities of sap drawn off by perspiration.*' He has, by this stage, largely elucidated the principles of sap flow, tension in the xylem, pressure with raising temperatures before leaves open, the passive nature of xylem vessels, the transpirational pull, with the power of water loss from leaves, and starts to understand (followed up in the next Chapter) the relationship between bark (the phloem transport system, carrying sugars and other solutes under pressure) from the xylem water flow: '*And as in the Vine, so is the case the same in all the bleeding trees, which cease bleeding as soon as the young leaves begin to expand enough, to perspire plentifully, and to draw off the redundant sap. Thus the bark of Oaks and many other trees most easily separates, while it is lubricated with plenty of sap: But as soon as the leaves expand - sufficiently to perspire off plenty of sap, the bark will then no longer run (as they term it) but adheres most firmly to the wood*.'

Chapter IV. *Experiments, shewing the ready lateral motion of the sap, and consequently the lateral communication of the sap vessels. The free passage of it from the small branches towards the stem, as well as from the stem to the branches. With an account of some Experiments, relating to the circulation or non circulation of the sap.*



By cutting out rings or segments of bark on different sides of cut or intact branches, he shows that sap can pass laterally across stems, bypassing the gaps. He is intrigued by the bark, and makes clear that just as the sun warms the leaves and thus increases water loss and flow, so warmth on the bark has the same effect, again suggesting lateral flow. He also shows, by inverting cut branches into vessels of water and sealing the cut end with a bladder, that water can still pass up an inverted stem, drawn by the leaves. His insight goes beyond just sap flow. Less sap goes to leaves which have the bark removed, and while he still is not clear about the differences between phloem sap and xylem water flow, he does recognise that the bark carries sap necessary for growth. And here we come to fruit: '*The same is the reason why Apples, Pears, and many other fruits, which have some of their great sap vessels eaten asunder by insects bred in them, are ripe many days before the rest of the fruit on the same trees; As also that fruit, which is gathered some time before it is ripe, will ripen* *sooner than if it had hung on the tree, tho ' it will not be so good; because in these cases the worm eaten fruit is deprived of part of its nourishment, and the green gathered fruit of all. And for the same reason some fruits are sooner ripe towards the tops of the trees, than the other fruit on the same tree; not only, because they are more exposed to the sun; but also, because being at a greater distance from the root, they have somewhat less nourishment*.' This is a demonstration of the effects of the age-old fruit-growing horticultural practise of girdling, and Hales is so close now to an understanding of phloem-based sugar transport, continuing to come back to the issues of circulation, as familiar in animals: ' *Upon the whole, I think we have, from these experiments and observations, sufficient ground to believe that there is no circulation of the sap in vegetables; notwithstanding many ingenious persons have been induced to think there was, from several curious observations and experiments, which evidently prove, that the sap does in some measure recede from the top towards the lower parts of plants, whence they were with good probability of reason induced to think that the sap circulated*.'

Chapter V. *Experiments, whereby to prove, that a considerable quantity of air is inspired by Plants.*



Hales uses branches attached to tubes again, but with air between the water in the reservoir and the end of the branch, showing that air is taken up by the stem, and passed through vessels with the water flow. He further shows that air will pass through bark into the stem, more easily in old bark than young.

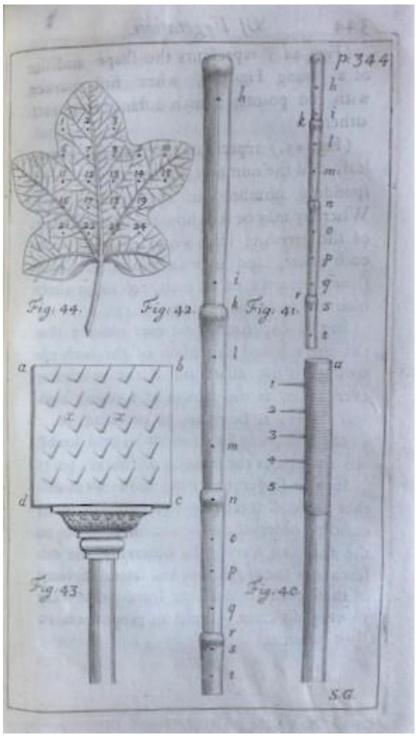
Chapter VI. *A specimen of an attempt to analyze the Air by a great variety of chymio - statical Experiments, which shew in how great a proportion Air is wrought into the composition of animal, vegetable, and mineral Substances, and withal how readily it resumes its former elastick state, when in the dissolution of those Substances it is disingaged from them.*

Hales moves on to enquire into the nature of the air: '*Having ..... produced many Experiments to prove that the Air is freely inspired by Vegetables, ... this put me upon making a more particular inquiry into the nature of a Fluid, which is so absolutely necessary for the support of the life and growth of Animals and Vegetables*.' He refers back to Boyle's measurements of air produced by plants, their respiration, and carries out some quite sophisticated studies with fermentation and heat on plant and animal substances to show the release of air from organic matter. He measures the air released from honey, camphor, sugar, beeswax, aniseed oil, working his way through a long list of materials, finding very little air in brandy, but more in well-water. What he is measuring is a great mixture of carbon dioxide, sulphurous gases and other volatiles, and not enough oxygen for a sparrow to survive in (he tested that). There is a diversion into looking into stones from gall and urinary bladders, which he published on separately, and then goes back to looking at gases produced from heating and fermenting mixtures: sal ammonia, sal tartar and spirits of wine together produced 26 cubic inches of air.

Time and again throughout the book, Hales refers back to Newton, here ruminating on the central issue of what state all this gas is in, in the whole body or organ. He considers the apple, and this is worth following through: ‘*To instance in the case of the pounded Apples which generated above 48 times their bulk of Air; this air, when in the Apples, must be compressed into less than a forty eighth part of the space it takes up, when freed from them, and it will consequently be 48 times more dense; and since the force of compressed air is proportional to its density, that force which compresses and confines this air in the Apples, must be equal to the weight of 48 of our atmospheres when the Mercury in the Barometer stands at fair, that is 30 inches high. Now a cubick inch of Mercury weighing 3580 grains, thirty cubick inches (which is equal to the weight of our atmosphere on an area of a cubick inch) will weigh 15 pounds, 5 ounces, 215 grains; and 48 of them will weigh above 736 pounds; which is therefore equal to the force with which an inch square of the surface of the Apple would compress the air, supposing there were no other substance but air in the Apple: And if we take the surface of an Apple at 16 square inches, then the whole force with which that surface would compress the included air, would be 11776 pounds. And since action and reaction are equal, this would be the force, with which the air in the Apple would endeavour to expand itself, if it were there in an elastick and strongly compressed state: But so great an expansive force in an Apple would certainly rend the substance of it with a strong explosion, especially when that force was increased, by the vigorous influence of the Sun's warmth.*’ And makes the obvious conclusion that while air is present as a gas in the plant, ‘*...many of these particles of air were in a fixt state, strongly adhering to and wrought into the substance of Apples.*’ As indeed they are, but chemically rather than physically, and apples don’t explode.

There follows many experiments on the elasticity of air, animal respiration and lung capacity, and unfortunately, many dead animals. But we are talking plants here, so we move to the next chapter.

Chapter VII. *Of Vegetation*



He sums up: ‘*We find by the chymical analysis of vegetables, that their substance is composed of sulphur, volatile salt, water and earth; which principles are all endued with mutually attracting powers, and also of a large portion of air, which has a wonderful property of strongly attracting in a fixt state, or of repelling in an elastick state, with a power which is superior to vast compressing forces; and it is by the infinite combinations, action and re - action of these principles, that all the operations in animal and vegetable bodies are effected*.’ Seeds have more oil, less cold-hardy plants have more salt and water, there is more salt and water in plants in the Spring, and he dwells on the nature of leaves and prefigures the understanding of photosynthesis: ‘*We may therefore reasonably conclude, that one great use of leaves is what has been long suspected by many, viz. to perform in some measure the same office for the support of the vegetable life, that the lungs of animals do, for the support of the animal life; Plants very probably drawing thro ' their leaves some part of their nourishment from the air*.’ He agrees with Sir Isaac Newton: ‘*And may not light also, by freely entering the expanded surfaces of leaves and flowers, contribute much to the ennobling the principles of vegetables.*’ Here we see light and carbon dioxide, together with water, the components of hotodynthesis and thus carbohydrate and energy production in plants[4].

The growth of shoots and leaves leads him to devise a means of measuring leaf expansion, using a grid with points which he paints and then showing with time that repositioning the grid results in a measurement of expansion: '*In this Experiment we may observe that the growth and expansion of the leaves is owing to the dilatation of the vesicles in every part, as the growth of a young shoot was shewn to be owing to the same cause in the foregoing Experiment 8; and doubtless the case is the same in all fruits. If these Experiments on leaves were further pursued, there might probably be many curious observations made in relation to the shape of leaves: By observing the difference of the progressive and lateral motions of these points in different leaves, that were of very different lengths in proportion to their breadths*.'

The Conclusion

Ever the practical man, he finishes by summarising his findings, and then shows how they help explain and indeed, should improve, gardening and agricultural practise. Much of what he has shown, is what gardeners and farmers have known for a long time, though without understanding the science.

> *We have from the foregoing Experiments many proofs of the very great and different quantities of moisture imbibed and perspired by different kinds of Trees, and also of the influence of the several states of the air, as to warm or cold, wet or dry, have on that perspiration. We see also what stores of moisture nature has provided in the Earth against a dry season, to answer this great expence of it in the production and support of vegetables; how far the dew can contribute to this supply, and how insufficient its small quantity is towards making good the great demands of perspiration: And that plants can plentifully imbibe moisture thro ' their stems and leaves as well as perspire it.*
> *We see with what degrees of warmth the sun, that kindly natural genius of vegetation, acts on the several parts of vegetables, from their tops down to their roots two feet underground.*
> *We have also many proofs of the great force with which plants and their several branches and leaves imbibe moisture, up their capillary sap vessels: The great influence the perspiring leaves have in this work, and the care nature has taken to place them in such order, and at such proper distances, as may render them most serviceable to this purpose, especially in bringing plenty of nourishment to the young growing shoots and fruit whose stem is usually surrounded with them near the fruit's insertion into the twig.*
> *We fee here too that the growth of shoots, leaves and fruit, consists in the extension of every part; for the effecting of which, nature has provided innumerable little vesicles, which being replete with dilating moisture, it does thereby powerfully extend, and draw out every ductile part.*
> *We have here also many instances of the great force of the ascending sap in the vine in the bleeding season; as also of the sap's freely either ascending or descending, as it shall happen to be drawn by the perspiring leaves; and also of its ready lateral motion thro ' the laterally communicating sap vessels; together with many proofs of the great plenty of air drawn in and mixed with the sap and incorporated into the substance of vegetables.*
> *If therefore these Experiments and observations give us any farther insight into the nature of plants, they will then doubtless be of some use in Agriculture and Gardening, either by serving to rectify some mistaken notions, or by helping farther to explain the reasons of many kinds of culture, which long repeated experience has found to be good, and perhaps by leading us to make some advances therein...*

There is quite a lot written on Hales and his achievements, easily accessible[5], and first editions of the works are still available. He wrote other papers and books, including an essay on *The Means of Dissolving the Stone in the Bladder, &c*, for which he was awarded the Royal Society Copley gold medal in 1737. In 1734 he published *Admonition to the Drinkers of Gin, Brandy, &c.*, and there was another work, published in 1739, which had some impact on voyagers concerned about life and health on the ship:

Philosophical experiments: containing Useful and Necessary Instructions for such as undertake Voyages at Sea. Shewing how Sea-Water may be made fresh and Wholesome: and how Fresh Water may be preserv'd Sweet. How Biscuit, Corn &c, may be secured from the Weevils, meggots and other Insects. And Flesh preserv'd in hot Climes, by salting Animals whole. To which is added and Account of several experiments and Observations on Chalybeate or Steel-Waters: with some Attempts to convey them to distant places, preserving their virtue to a greater Degree than has hitherto been done. Likewise a proposal for cleansing away mud, &c. out of Rivers, Harbours, and Reservoirs, with engraved plate of apparatus. W. Innys and R. Manby, M.DCC.XXIX [1739]

Hales died at the age of 84, still in Teddington, and is buried under the tower of the church where he had spent most of his life. He had married, but there were no children.

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[1] **Hales, Stephen,** Vegetable staticks; or, an account of some statical experiment on the sap in vegetables: Being an essay towards a natural history of vegetation. Also, a specimen of an attempt to analyse the air, by a great variety of chymio-statical experiments. (offered with) Statical essays: Containing haemastaticks, or, an account of some hydraulick and hydrostatical experiments made on the blood and blood vessels of animals. Also an account of some experiments on stones in the kidneys and bladder. . . London, W. and J. Innys, 1733.

[2] **[Twining, Thomas.],** Recreations and Studies of a Country Clergyman of the Eighteenth Century: being Selections from the Correspondence of the Rev. Thomas Twining. John Murray. 1882. Edited by his great-nephew, Richard Twining. p. 243.

[3] **Hales** (Stephen) Vegetable Staticks: or an account of some statical experiments on the sap of vegetables: being an essay towards a natural history of vegetation. Also a specimen of an attempt to analyse the air, by a great variety of chymio-statical experiments; which were read before several meetings of the Royal Society. London: W. and J. Innys, M,DCC,XXVII [1727].

[4] Carbon dioxide was not discovered until about 1755, and nitrogen gas in the 1770s.

[5] https://www.encyclopedia.com/people/science-and-technology/biology-biographies/stephen-hales; http://scihi.org/stephan-hales-blood-pressure/; https://royalsocietypublishing.org/doi/pdf/10.1098/rsnr.1940.0005; https://medicalphysiologyonline.files.wordpress.com/2011/10/brown-simcock_hales_mpo-028-2011p.pdf; https://hekint.org/2017/01/29/stephen-hales-the-priest-who-pioneered-clinical-physiology/
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