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THE GROWTH OF OUR KNOWLEDGE OF PHOTOSYNTHESIS

by Robert Hill

There is not as much green shade now as in former days. Before I attempt to take you back with the green thoughts let us look at these two diagrams of a great country (figs. 1, 2). There is an interval of ninety-five years. We use enormous quantities of wood-pulp now. All this is only one reason why the study of photosynthesis is important.

Photosynthesis is the word used to describe a process fundamental to plant nutrition. This word came into being relatively recently. Absent in the 1880 edition of Pfeffer's great *Plant physiology*, it appeared in the 1897 edition as 'photosynthetische assimilation'. It was translated by Ewart as 'photosynthetic assimilation' (Pfeffer, 1900–1906). Between these two editions, Barnes in America (1893) had proposed the word 'photosyntax' and had rejected 'photosynthesis' on etymological grounds; one of his colleagues, Macdougal, preferred photosynthesis and he used this form in his textbook on practical plant physiology. The true origin of the word does not seem to be stated in any of the numerous textbooks that we have. Judging from the literature there seems to have been a polemic about who had actually invented it.

At that time, during the second half of the nineteenth century, the process of photosynthesis was formulated as:

Carbon dioxide + water + light =
Carbohydrate + oxygen + chemical energy.

This was essentially the reverse of the process of respiration. The green plants are called autotrophic or self-feeding because they require to take in no organic food for the increase of their substance. Because animals, including human beings, are

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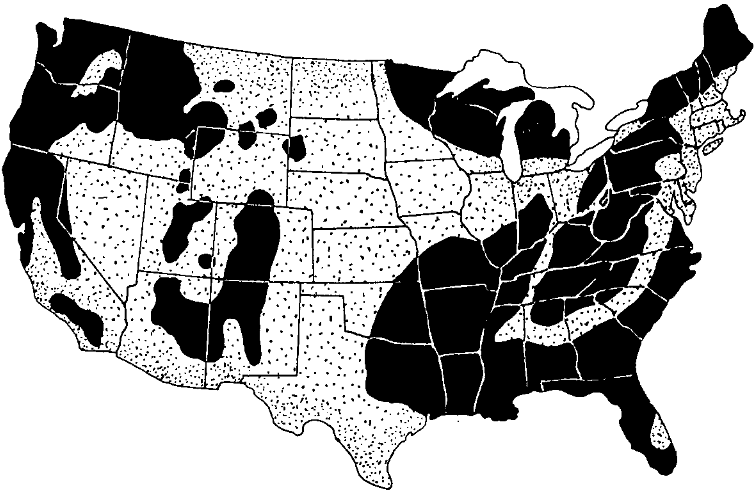

Fig. 1. Virgin forests in 1850

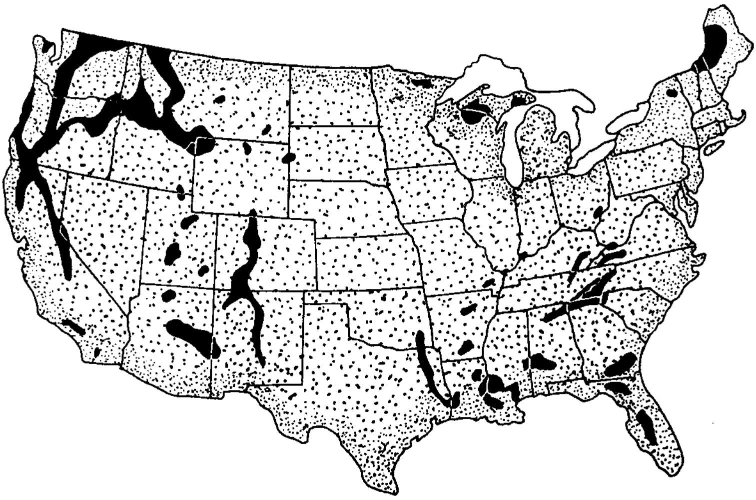

Fig. 2. Virgin forests in 1945

(Both figs 1 and 2 from R. A. H. Thompson, 'What's happening to the timber' *Harper's Magazine*, August 1945, p. 125. Reproduced in H. Gaffron 'Photosynthesis and the production of organic matter on Earth' in *Currents in biochemical research*, ed. D. E. Green, New York, Interscience, 1946) absolutely dependent on their coexistence with plants our thoughts go back to the very dim past. E. J. H. Corner (1964) once stated that the subject of botany is essentially the relation between man and plants—botany is a very old subject indeed.

EARLY GREEK CONCEPTS

In prehistoric times, in places where agriculture was developed, it would be clear that water and soil were both essential requirements for the living plants. It would have also become obvious that plants could be burnt, for, when the use of fire had been established, wood was used as fuel.

In considering the study of plant nutrition, I can attempt to take you back to the beginning of the Greek era. The essay in this is inevitably distorted because, as you no doubt will allow, we are so conditioned with scientific jargon and later conceptions. But you could see that the Greeks would grasp a relation between the plant and one at least of the items in our equation. That is the *water*. Nowadays, we could feel that there was some dim connexion between a prehistoric conception of fire and perhaps what we now call energy. But energy in the precise scientific sense is a very recent conception; Partington gives 1850 as the date, virtually the last item to be placed correctly in the nineteenth-century formulation.

At any time when people simply think about things, what is variously held to be right and true shows wide discrepancies. So it was that quite independent and mutually conflicting views about the nature of things have come down to us from the Greeks. These influences, sometimes quite amazingly, are still to be recognized in current thought. In science we assume that the thought is tempered by results of experiments and by the experimental methods. It would be fine to have a thought that would explain everything.

Thales of Miletus (*c.* 640–546 B.C.) gave us the thought 'all things are water' (*πάντα ὕδωρ ἐστί*)

$$\text{Water} = \text{Plant}.$$

It seems now that when this thought took over there would have been a subjective sense of ultimate reality. Could it not somehow resemble in effect the equation of Einstein relating energy and mass? Perhaps in this way we could follow Parmenides of Elea (b. *c.* 539 B.C.) who considered the 'one' (which *is*) and the 'not one' or the 'many' (which *is not*) as being separate for investigation. He was considered by Plato (427–347 B.C.) to be not an idealist but a precursor for idealism. But Plato had maintained that to study separately the 'one' and the 'many' was sterile. An approximation to this as we might see it now, being precocupied with science, would be: the 'one' is a joy and a stimulus, the 'many' is a toiling and a moiling.

A different type of theory which was associated with Democritus, *c.* 360 B.C., was that everything was composed of characteristic atoms. These atoms would confer the characteristic to each plant. Here the atoms composing an olive tree would generally be supposed to be different from those composing the grape vine, that is Atoms (*a*) = Plant (*a*), and Atoms (*b*) = Plant (*b*). This was an important idea in relation to a Greek conception of plant mutations which persisted through the middle ages. The plants took their nourishment from the earth. Each plant took the atoms appropriate to its kind. Thus the plants, unlike animals, produced no excreta. But for animals the conception was that the food, after intake, was absorbed in part by an intelligent agent and the inappropriate parts were rejected. For the plant, by contrast, the intelligent agent would have to be in the earth or soil. Thus a plant would have seemed to resemble a foetus drawing its nourishment from the Mother-Earth, where the appropriate atoms were elaborated in the soil. We might note how the botanist F. O. Bower (1855–1948) in his book *Botany of the living plant* described a growing plant as showing continuous embryology. Again, do not some of the still current non-scientific ideas about humus and plant growth seem to be derived from this Greek idea of plant nutrition?

$$\text{Earth} = \text{Plant.}$$

The other conception of the plant being derived from water also persisted. This involved a transmutation theory even though most living plants like animals consist of 50–90 per cent. of water. These two representations of nutrition of plants had a significant influence extending in to the era of direct scientific experiment in the sixteenth to eigthteenth centuries. In fact they tended to be reconciled by a widely held belief that water would change into earth.

Water = Earth.

Bringing us back to Thales of Miletus again.

Then there is the theory of the four elements (see fig. 3) which seems to have been brought in to greatest development

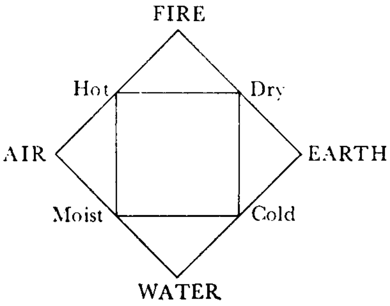

Fig. 3. Aristotle's theory of the four elements

(From J. R. Partington (1957) *A short history of chemistry*, 3rd ed. London: Macmillan)

by Aristotle. This is sometimes considered to have been a somewhat negative influence on scientific development, on account of the fire principle being considered a material substance. Be that as it may, the influence was powerful—it happens that just as of old, some of us are more interested in people than in things. The magnificent effort towards perfection in all things was especially accentuated in Plato who was interested in the individual and the society. Concepts of reality in this way were relevant to men's relations with each other but less useful in men's relation with the earth or 'Nature'.

The four elements were defined by Aristotle in much the same way as originally were the chemical elements of the present day. The differences in what we now understand as a mixture from that of a single compound was appreciated. Mercury metal was called silver-water; the different kinds of matter were described in terms of intermediate or combined qualities. It is in this question of matter and quality of attributes where the difficulties for scientific progress came in. Nowadays we should tend to think that the four elements would symbolize a manifestation of energy as fire, and the three states of matter, solid, liquid and gas. In any case the idea of transmutation became dominant in the alchemical middle ages. In evaporation something changed into air and, in liquifacture of a solid, part of the earth had to be changed into water. With the original atomic ideas there was no need, I think, for the atoms to change into each other. The conservation of material seems to have been taken as axiomatic. The changes of state were readily appreciated by Heron of Alexandria in the first century A.D. In fact from what is known about his writing, as also from the *De rerum natura* of Lucretius, the modern theory of gases was anticipated. Yet, it was many hundreds of years later that an experimental knowledge of gases was developed.

Quite apart from this theoretical aspect very much practical experience on both agriculture and in chemical matters existed in early times. This can be gathered from the writings of Pliny the elder especially as regards soils and fertilizers. Again it was long known that it was often dangerous to go in to the bottoms of wine vats. If, on testing with a lamp, the lamp did not go out, this showed that it was safe. A famous experiment of a candle burning in a closed space over water was carried out by Philon of Byzantium (third century B.C.). After the candle became extinguished a contraction was observed. But experiments and material practice were usually subsequent to theory and often diverged from it.

The growth of our knowledge of photosynthesis

THE BEGINNINGS OF MODERN EXPERIMENT

Just as the Greek philosophers had sought for perfection in the individual and society so the early alchemists sought for perfection in material. Now we often think of the pursuit of alchemy as being the effort to transmute dross into gold. On the other hand the search for the philosopher's stone can be viewed as an effort to find an imagined 'one way' to control material processes. The gap which had so long appeared to exist between practical men and the philosophers gradually disappeared. The study of natural philosophy came to be directed by the results of experiments, rather than by systematic description and cataloguing. In *The legacy of Greece* D'Arcy Thompson (1921) in his account of Aristotle discussed the reasons for the absence of contact between trade and scholasticism. Even up to the time of Robert Boyle (1627–91) chemistry does not seem to have been regarded as a 'proper' study, being too closely associated with a menial task.

The experimental method for the study of plant nutrition is generally considered to begin with van Helmont. He not only invented the word gas, *c.* 1630, but also contributed much to the beginnings of chemistry, as distinct from alchemy, and again, indeed, in view of his conception of a 'ferment', to the beginnings of biochemistry. Van Helmont decided to test the theory:

Water = Plant.

His famous experiment, which was so carefully carried out, nearly completely satisfied the theory when judged by the knowledge at the time. The permanent value of the experiment lies in the fact that it showed how little of the actual matter composing the plant can be derived from the soil.*

> I took an Earthen Vessel, in which I put 200 pounds of Earth that had been dried in a Furnace, which I moystened with Rain-water, and I implanted therein the Trunk or Stem of a Willow Tree, weighing five pounds; and at length, five years being finished, the Tree sprung from thence, did weigh 169 pounds, and about three

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* The quotation is taken from Partington (1957), *A short history of chemistry*, pp. 51–2.

ounces: But I moystened the Earthen Vessel with Rain-water, or distilled water (alwayes when there was need) and it was large and implanted into the Earth, and least the dust that flew about should be co-mingled with the Earth, I covered the lip or mouth of the Vessel, with an Iron-Plate covered with Tin, and easily passable with many holes. I computed not the weight of the leaves that fell off in the four Autumnes. At length, I again dried the Earth of the Vessel, and there were found the same 200 pounds, wanting about two ounces. Therefore 164 pounds of Wood, Barks, and Roots, arose out of water onely.

Now the contemporary interpretation of this experiment, I think, could really involve the conflicting notions of conservation of the soil (earth) element and the transformation of the water element. Both the conservation and transmutation ideas had come from the Greek philosophy. Then again there was the idea of each plant requiring to take its specific kind of atoms from the soil. The different kinds of plants, especially those used in agriculture and in medicine, have been recognized, depicted and described from very early times. In fact, the purely descriptive side of botany has dominated in the study of plants on more than one occasion in the history of this science.

It was simply this description of plant species and not any direct experiment that was used by Edme Mariotte (*c.* 1620–84) to test a Greek view of the earth nutrition of plants. He argued thus. I can take a definite amount of soil say 7–8 lb. In this soil I can grow a plant which will weigh say ¼ lb.—but it matters little out of 3,000–4,000 different kinds of plant which one I choose to grow. Thus if each plant has to take atoms or elements for its characteristic kind from the soil (and a small amount of rain water with its salts) there certainly could not be enough kinds of atoms to produce the material of 3,000 different plants.

THE DISCOVERY OF PHOTOSYNTHESIS

As was indicated previously, from the time of Robert Boyle (1627–91) and the foundation of the Royal Society in England (1645–62) the pursuit of experimental science came to be considered quite respectable. Eugene Rabinowitch in volume 1 of his classical book on photosynthesis (1945–58) has given a splendid historical account of the discovery of photosynthesis starting from the work of Stephen Hales (1677–1761) up to the time of the famous plant physiologist Julius von Sachs (1832–97). Rabinowitch gives to Stephen Hales the credit for showing that air must be an important constituent of all organic matter. He quotes from *Vegetable staticks* (1727) where Hales wrote 'Plants very probably draw through their leaves some part of their nourishment from the air, may not light also by freely entering surfaces of leaves and flowers contribute much to ennobling the principles of vegetables'.

This is especially interesting because in previous descriptions of plants the requirement for light, apart from its affect on ripening fruit, seems hardly ever to have been mentioned. The necessity for light must have been obvious in very early days but perhaps only apparent to people working in horticultural practice.

It now seems that we should consider the work of van Helmont as providing much of the experimental basis for the development towards modern chemistry and biochemistry. He was not only able to distinguish the properties of different kinds of gas but also distinguished them by different methods of producing them. He burnt charcoal and called the product 'gas carbonum', which also he called 'gas silvestre' in circumstances where it comes from fermenting wine. This was the 'fixed air' later described by Joseph Black (1728–99) which he obtained from the action of acid on limestone. The word air continued to be used to designate the different gases for a considerable time after van Helmont.

It was never possible to contain a gas in an open vessel and in some experiments a closed vessel would burst. The development of the study of the nutrition of plants, and indeed the development of chemistry itself largely depended on the experimental procedures which involved gases.

The postulate of conservation of material substance seems to have been the basis of both the atomic and transmutational theories in antiquity. This perhaps accounted for the tendency to regard all the four elements as substances. It could long have been observed that flame was burning smoke; this was stated by Aristotle and by van Helmont. Thus fire came to be represented by a flame (φλογιστον) principle which had to be an actual material component of all combustible materials. We may perhaps see how this came about because heat itself was generally considered to be a fluid contained in materials. Count Rumford's experiment (1798) on the heat produced in boring cannons revived and proved the alternative theory, very long accepted by a minority, that heat was motion. The word 'caloric' dating from 1787 in France and the German 'warmstoff' may still be found in (not so old) dictionaries. The postulation of a material flame principle led to the 'phlogiston' theory, which is associated with J. J. Becher, 1635–1682 and with G. E. Stahl, 1660–1734. On this theory, when the candle, being very rich in phlogiston, was burnt in a closed space the air became 'phlogistigated' and then it was incapable of supporting combustion. This strange scientific jargon actually persisted among a few scientists until the beginning of the nineteenth century.

The real beginning of the experimental study of photosynthesis was due to Joseph Priestley (1733–1804). He was skilful in carrying out experiments with gases—air as they were called even then in spite of van Helmont (see fig. 4). The great discovery was when Priestley found that the 'phlogistigated' air, which no longer could support combustion and the respiration of a mouse, could be restored by a green plant. The green plant could 'dephlogistigate' the 'phlogistigated air'. The gas which Priestley called 'dephlogistigated air' we should now, following Lavoisier, call oxygen. In this discovery Priestley first showed the complementary relationship existing between vegetation and animals. Priestley was especially amazed by the vigorous combustion of a candle in his dephlogistigated air when he prepared it from oxide of mercury. He realized that the common air was less pure. Partington (1957) quotes him: 'the air which Nature has provided for us is as good as we deserve'. Later, Priestley showed, by using his 'nitrous air' (nitric oxide), how to determine the amount of pure dephlogistigated air in the atmosphere. He found one-fifth of a volume present; this was an accurate result.