



Definition of photosynthesis

History of the word *photosynthesis* and evolution of its definition

Howard Gest

Department of Biology and Department of History and Philosophy of Science, Indiana University, Bloomington IN 47405, USA (e-mail: hgest@bio.indiana.edu)

Received 24 October 2001; accepted in revised form 14 December 2001

Key words: Charles Barnes, definition of photosynthesis, Theodor Engelmann, Martin Kamen, Conway McMillan, Oxford English Dictionary

Abstract

In 1893, Charles Barnes (1858–1910) proposed that the biological process for ‘synthesis of complex carbon compounds out of carbonic acid, in the presence of chlorophyll, under the influence of light’ should be designated as either ‘photosyntax’ or ‘photosynthesis.’ He preferred the word ‘photosyntax,’ but ‘photosynthesis’ came into common usage as the term of choice. Later discovery of anoxygenic photosynthetic bacteria and photophosphorylation necessitated redefinition of the term. This essay examines the history of changes in the meaning of *photosynthesis*.

Charles Reid Barnes

Before 1893, the light-dependent process by which plants reduce CO₂ to organic matter was called *assimilation*. This word was also then used to describe the anabolic metabolism of animals. In 1893, Charles Barnes realized that use of the same term for plant and animal processes was ill-advised and confusing. Barnes addressed the problem in a paper he read before the Botanical Section of the American Association for the Advancement of Science at its meeting in Madison, Wisconsin, in August 1893. In his paper, published in the Botanical Gazette, Barnes proposed two new, alternative names for the green plant biosynthetic process, namely, *photosyntax* and *photosynthesis* (Barnes 1893).

Barnes (1893) noted that the plant process:

has been called ‘assimilation’, ‘assimilation proper’, and ‘assimilation of carbon’. I think that none of these terms is appropriate. Assimilation has long been used in animal physiology to designate the appropriation of digested food by the different tissues, and its conversion into the substances of those tissues. . . . For the process of formation of complex carbon compounds out of simple ones under the influence of light, I propose

that the term *photosyntax* be used. Photosyntax is the synthesis of complex carbon compounds out of carbonic acid, in the presence of chlorophyll, under the action of light. . . . I have carefully considered the etymology and adaptation, as well as the expressiveness, of the word proposed, and consider it preferable to *photosynthesis which naturally occurs as a substitute* (emphasis added).

The Botanical Gazette for 1894 (Volume 19) included a section (pp. 341–343) on ‘Current Literature’ which described a ‘Manual of Vegetable Physiology’, namely, an English translation of Oels’ ‘Pflanzenphysiologische Versuche’:

The translator has taken great liberties with the Roman-paged prelude to the text proper, but the body of the work has been rendered into English with fidelity, the only change of moment being the substitution of the word ‘photosynthesis’ for that of ‘assimilation’. This change follows from a suggestion by Dr Barnes made a year ago before the American Association at Madison, who clearly pointed out the need of a distinctive term for the synthetical process in plants, brought about by protoplasm in the presence of chlorophyll and light. He proposed the word ‘photosyntax’, which met with favor. In the discussion Professor Conway



Figure 1. Charles Reid Barnes (1858–1910). The above photograph was prepared and provided by Govindjee. Original source: Anonymous (1910).

MacMillan suggested [evidently what is meant here is 'suggested a preference for'] the word 'photosynthesis' [first proposed by Barnes in 1893] as etymologically more satisfactory and accurate, a claim which Dr Barnes showed could not be maintained. The suggestion of Dr Barnes not only received tacit acceptance by the botanists of the association, but was practically approved by the Madison Congress in the course of a discussion upon this point. In the interest of harmony, therefore, even if courtesy be ignored, the word substituted for assimilation, if any were to be inserted, should have been 'photosyntax' and not 'photosynthesis'.

It must be noted that, aside from Barnes (1893), there were no published discussions of the 1893 Madison meeting or Proceedings of the Congress that mention 'photosynthesis' or 'photosyntax.' An obituary of Barnes (Anonymous 1910; see Figure 1) describes his distinguished career and his many interests in plant biology.

Use of the new terms

It is a well-known phenomenon that the introduction of new scientific terms is frequently resisted. At a

botany meeting in 1896, Barnes (1896) made a brief comment in this connection:

...the word photosyntax, proposed in 1893 by the speaker, but objected to by Professor MacMillan as etymologically bad, has been resubmitted to three competent Greek scholars and pronounced by all to be linguistically unobjectionable and accurately expressive of the process of carbohydrate formation as now understood.

In 1898, Barnes felt obliged to bring up the terminology question again, this time in a paper entitled 'So-called "Assimilation",' published in the German journal *Botanisches Centralblatt* (Barnes 1898). Publication in this journal is of significance because one of the leading plant physiologists of the day, Wilhelm Pfeffer, was German.

In his 1898 paper, Barnes refers to his 1893 paper and says:

This term [i.e., photosyntax] I have since employed in lecturing and writing and it has come into use by a number of students in this country. At the same time Professor MacMillan of the University of Minnesota expressed his preference for the term photosynthesis, which in the same paper I indicated as an available word (emphasis added), but rejected as etymologically less accurate. The latter term has been taken up by Professor MacDougal of the University of Minnesota and used by him, both in his translation of Oels's *Pflanzenphysiologische Versuche* and also in his *Experimental Plant Physiology*. The propounding of the same term by Hansen (no initial given, in a paper published in 1898) is of value only as a tardy recognition of the fact that the term assimilation can no longer be correctly used. It is not important whether photosyntax or photosynthesis, or some other word, finally comes into general use to describe the manufacture of carbohydrates by green tissues under the action of light. It is high time, however, that we drop as promptly as possible, the use of assimilation for this or any similar process. The reasons for this I have set forth in the paper 'On the food of green plants' previously referred to.

Even though Barnes preferred the term 'photosyntax,' he was the first to publish the word 'photosynthesis' as an alternative. History has shown that, as time went on, an increasing number of investigators chose to use *photosynthesis*. Some authors, however, were laggard. For example, F.F. Blackman and his

associates continued to use the term ‘vegetable assimilation’ as late as 1905 (Blackman and Matthaei 1905).

Pfeffer’s failure to credit Barnes

Wilhelm Pfeffer (1845–1920) was a famous plant physiologist, a member of many learned societies and the recipient of many honors. In 1881, he published a monumental handbook on plant physiology: ‘Pflanzenphysiologie: ein Handbuch der Lehre vom Stoffwechsels und Kraftwechsels in der Pflanze’ [W. Engelmann, Leipzig]. Volume I of the second edition was published in 1897, Volume II in 1904. The author index for both volumes is contained in Volume II, but Barnes’s name is absent. The subject index for Volumes I and II is also in Volume II, and has the following two entries: ‘Photosynthese, Begriff I, p. 273; Photosynthetische Kohlensäureassimilation, I, pp. 284.’ Again, no mention of Barnes or of his 1893 paper. It is clear, however, that Pfeffer knew that the word photosynthesis was coined by Barnes. Several editions of Pfeffer’s famous handbook were translated into English and published by Alfred J. Ewart of the Botanical Department, University of Oxford. The English edition of 1900 (Ewart 1900) contains a Preface, in English, written by Pfeffer in 1897. In this particular edition, Ewart added several footnotes, one of which is particularly pertinent (p. 302):

The term ‘photosynthetic assimilation’ is a perfectly general one, and would include the assimilation of other compounds by the aid of light, should any such processes be discovered in the future [*In fact, H. Molisch discovered the photoheterotrophic growth mode of purple bacteria in 1907*]. The photosynthetic assimilation of carbonic acid may be termed carbon dioxide assimilation. ‘Carbon-assimilation’ is obviously incorrect, for in analogy with the term ‘nitrogen assimilation’ would indicate that carbon could be directly assimilated. The uncouth term ‘photosyntax’ is quite unnecessary, and moreover has been erroneously used to indicate all cases of carbon dioxide assimilation, although the occurrence of a power of chemosynthetic assimilation of carbonic acid in certain bacteria was already well known.

It is remarkable and regrettable that neither the footnote nor the book cites Barnes or his 1893 paper. Similarly, in his Volume II of 1904, Pfeffer used the term photosynthesis a few times without citing Barnes,

and continued to use the word ‘assimilation.’ In his 1898 paper, Barnes felt obliged to say: ‘I may here take occasion to criticize Pfeffer’s defence of the term assimilation.’ This statement is followed by carefully reasoned arguments for abandoning ‘assimilation’ to describe the plant process. We owe a debt of gratitude to Charles Barnes, who was courageous enough to criticize one of the ‘giants’ of plant physiology in his time.

Evolution of the definition of photosynthesis

The definition of photosynthesis proposed by Barnes in 1893 is given, essentially unchanged, in numerous dictionaries up to the present time (see Gest 2001). The Oxford English Dictionary (OED) is considered to be the most authoritative dictionary of the English language and its second edition (1989) defines biological photosynthesis as follows: ‘The process by which carbon dioxide is converted into organic matter in the presence of the chlorophyll of plants under the influence of light, which in all plants except some bacteria involves the production of oxygen from water.’ This clumsy definition contains the curious phrase ‘in all plants except some bacteria,’ which incorrectly implies that bacteria are plants. The OED is also incorrect in citing Barnes 1898 as the first use of ‘photosynthesis’; the correct reference is Barnes 1893.

The discovery of anoxygenic bacterial photosynthesis made the general definition of ‘photosynthesis’ in the OED and most other dictionaries incorrect, but this is still not widely recognized. Ten years before Barnes (1893) coined the term ‘photosynthesis,’ Theodor Engelmann (1883) reported novel experiments that revealed photosensory behavior of purple sulfur bacteria (see description in Gest 1995). These experiments suggested that the bacteria were photosynthetic organisms, but doubts were raised because Engelmann’s tests for O₂ production gave negative results. Later, in 1907, H. Molisch demonstrated convincingly that purple bacteria do not produce O₂, and that they have the capacity to use organic compounds as sole carbon sources for growth with energy provided by light (Molisch 1907). Thus, the metabolic/physiological pattern of the purple bacteria obviously did not satisfy the criteria for photosynthesis as originally defined for green plants, and as a consequence, for several decades the bacteria were not generally accepted as being photosynthetic. The original definition of photosynthesis as an oxygenic process led investigators to continue designing fu-

tile experiments to find evidence of O₂ production by purple bacteria for some time. The last definitive negative experiments were reported in 1954, 71 years after Engelmann's first report! (see discussion in Gest 1988).

The discovery of photophosphorylation in 1954 revealed a basic 'common denominator' of oxygenic and anoxygenic photosyntheses, and paved the way for redefinition of 'photosynthesis.' In 1963, Martin Kamen suggested a revised definition which would have the effect of including anoxygenic bacterial photosynthesis by (a) avoiding any specification of the carbon source for growth, and (b) not indicating O₂ as a photosynthetic product. Kamen's definition is: 'Photosynthesis is a series of processes in which electromagnetic energy is converted to chemical free energy which can be used for biosynthesis.' Kamen recognized that he had offered a 'rather noncommittal definition,' and in fact it does not convey the essential character of the anoxygenic phototrophic life mode.

Thirty years later, I concluded that Kamen's definition required further sharpening, and suggested the following general definition (Gest 1993):

Photosynthesis is a series of processes in which electromagnetic energy is converted to chemical energy used for biosynthesis of organic cell materials; a photosynthetic *organism* is one in which a major fraction of the energy required for cellular syntheses is supplied by light.

Molecular oxygen and CO₂ are not included in the 'common denominator definition' of photosynthesis because photosynthetic bacteria do not produce O₂, and CO₂ is not necessarily a required carbon source. A number of the bacterial species can grow with *either* CO₂ *or* simple organic compounds, such as acetate, as the sole carbon source for synthesis of all cell constituents using light as the source of energy.

Including the definition of a photosynthetic *organism* is important because of the recent discovery of a number of aerobic bacterial species which contain bacteriochlorophyll and carotenoids, but which are incapable of using light as the sole or major source of energy for growth. I have described such organisms as 'quasi-photosynthetic bacteria' (Gest 1993). J. Thomas Beatty suggests designating them as 'aerobic phototrophic bacteria' (see J.T. Beatty, this issue). 'Phototrophic' in this context is taken to mean that such organisms under certain conditions can use light as a supplemental energy supply, but not necessarily as a major source.

The importance of definitions

Antoine Lavoisier, who revolutionized the science of chemistry in the 18th century and replaced the mythical 'phlogiston' with the term (and concept) of *oxygen*, clearly understood the importance of accurate definitions. In his words: 'We cannot improve the language of any science without at the same time improving the science itself; nor can we, on the other hand, improve a science without improving the language or nomenclature' (Lavoisier 1790).

Acknowledgments

I am indebted to Roger Beckman, Head, Life Sciences Library, Indiana University, Bloomington, for skilful electronic searches of the literature. Research of the author on photosynthetic bacteria is supported by National Institutes of Health Grant GM 58050. This manuscript was edited by Govindjee.

References

- Anonymous (1910) Charles Reid Barnes. Bot Gaz 49: 321–324
- Barnes CR (1893) On the food of green plants. Bot Gaz 18: 403–411
- Barnes CR (1896) *Photosyntax vs photosynthesis*. Botanical papers at Buffalo. Bot Gaz 22: 248
- Barnes CR (1898) So-called 'Assimilation'. Botan Centralblatt 76: 257–259
- Blackman FF and Matthaei GLC (1905) Experimental researches in vegetable assimilation and respiration. IV. A quantitative study of carbon-dioxide assimilation and leaf-temperature in natural illumination. Proc R Soc London Ser B 76: 402–460
- Engelmann TW (1883) *Bacterium photometricum*. Ein Beitrag zur vergleichenden Physiologie des Licht- und Farbensinnes. Arch Physiol 30: 95–124
- Ewart AJ (1900) The Physiology of Plants. A Treatise upon the Metabolism and Sources of Energy in Plants. [English translation of the 'Handbuch' by W. Pfeffer]. Clarendon Press, Oxford
- Gest H (1988) Sun-beams, cucumbers, and purple bacteria. Photosynth Res 19: 287–308
- Gest H (1993) Photosynthetic and quasi-photosynthetic bacteria. FEMS Microbiol Lett 112: 1–6
- Gest H (1995) Phototaxis and other sensory phenomena in purple photosynthetic bacteria. FEMS Microbiol Rev 16: 287–294
- Gest H (2001) Evolution of knowledge encapsulated in scientific definitions. Persp Biol Med 44: 556–564
- Hansen XX (1898) Review of Pfeffer's Pflanzenphysiologie (revised edition, 1897). Botanische Zeitung 56:II (2: 22–24) [Note: the paper does not have the initials of the author; thus, XX has been added to indicate that fact.]
- Kamen MD (1963) Primary Processes in Photosynthesis. Academic Press, New York
- Lavoisier A (1790) Elements of Chemistry, trans. by R. Kerr. Creech, Edinburgh
- Molisch H (1907) Die Purpurbakterien nach neuen Untersuchungen. Gustav Fischer, Jena
- Oxford English Dictionary (1989) 2nd ed. Clarendon Press, Oxford