Jour Pl Sci Res **38 (1)** 1-7 2022

Letter to the Editor

Frederick Robert (Bob) Whatley (1924-2020): Co-discoverer of photophosphorylation in chloroplasts and much more

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I present here a personal reminiscence of the life and research of Frederick Robert (Bob) Whatley (January 26, 1924–November 14, 2020). He was responsible for showing that chloroplasts are complete units for oxygenic photosynthesis and that 'photophosphorylation' is what is common between anoxygenic and oxygenic photosynthesis. He had an innovative nature and exploited many biophysical and biochemical techniques to understand, in depth, the regulatory nature of photosynthesis. Bob Whatley was a self-sufficient, thorough, quiet, and confident scientist, but he was 'self-effacing' and never ever "blew his own horn". My presentation is mingled a bit, at places, with my own thoughts – to give it a 'personal' touch.

Keywords: Daniel Arnon, Mary Bell Allen, University of California at Berkeley, Oxford University, Photophosphorylation, Mitochondria, Chloroplasts, $NADP^+$, Ferredoxin, Vitamin K.

PROLOG AND INTRODUCTION

Frederick Robert (Bob) Whatley, born on January 26, 1924 in Wilton, Wiltshire, UK, was the son of Frederick Norman and Maud Louise (née Hare) Whatley. He was educated at Bishop boys school, a Church of England private school in Salisbury, Wiltshire. Bob was a bright student and at 19-years old gained entry to Cambridge University and Selwyn College to study Agriculture. He graduated in 1945 with a First-Class Honors degree in Biochemistry.

I knew Bob Whatley only by his name and his work except once when we gave our talks at the same conference (see Govindjee, 1963; Whatley, 1963). He was known as a true gentleman, and one with a very high sense of fair play. I read his work, published in the early 1950s, when I was a student at the University of Allahabad, India (1952-1954), under Shri Ranjan (b.1899-d.1969; see Laloraya, 1970), who had been a student of Frederick Frost Blackman of Cambridge, UK (b.1866-d.1947; see Briggs, 1948), and then at the University of Illinois at Urbana-Champaign, USA (1956-1960), when I was studying under Robert Emerson (b. 1903- d.1959; Govindjee and Govindjee, 2021) and Eugene Rabinowitch (b.1901d. 1973; Govindjee et al., 2019).

I have known for a long time that Bob Whatley gained his PhD in 1948 at the University of Cambridge, UK (the year I had finished my 10th grade at Colonelganj High School in Allahabad, India). Further, I had a keen interest in the topic of Whatley's PhD thesis "*Enzyme Systems in the Green Leaf*", which he had finished under the supervision of Robert (Robin) Hill (b.1899-d.1991; see Bendall, 1994). It was later that I learnt that during this time Bob Whatley had met Daniel (Dan) I. Arnon (b.1910-d.1994; see Buchanan, 2001), who was then visiting David Keilin (b.1887-d.1963; see Slater, 2003) in Cambridge, UK. Arnon invited Whatley to work at UC Berkeley. After his PhD, Whatley did post doctoral research with Arnon for about a year. On the personal side, it was at the International House at UC Berkeley that Bob met his future wife Jean Bowie; he and Jean went to Sydney (Australia) and they were married there. Bob served as a lecturer at the University of Sydney, teaching plant biology (physiology) for four years (1950-1953). At Sydney he did research on ATP synthesis in mitochondria in leaves. Bob returned to Dan Arnon's

DOI:-https://doi.org/10.32381/JPSR.2021.38.1.1

lab and stayed there for several years, where he overlapped with Mary Belle Allen (b.1922-d.1973; see Provasoli and Hutner, 1974).

Figure 1 shows a photograph of Bob Whatley from that time. What I have presented below in this *Reminiscence* is basically his research from that period.

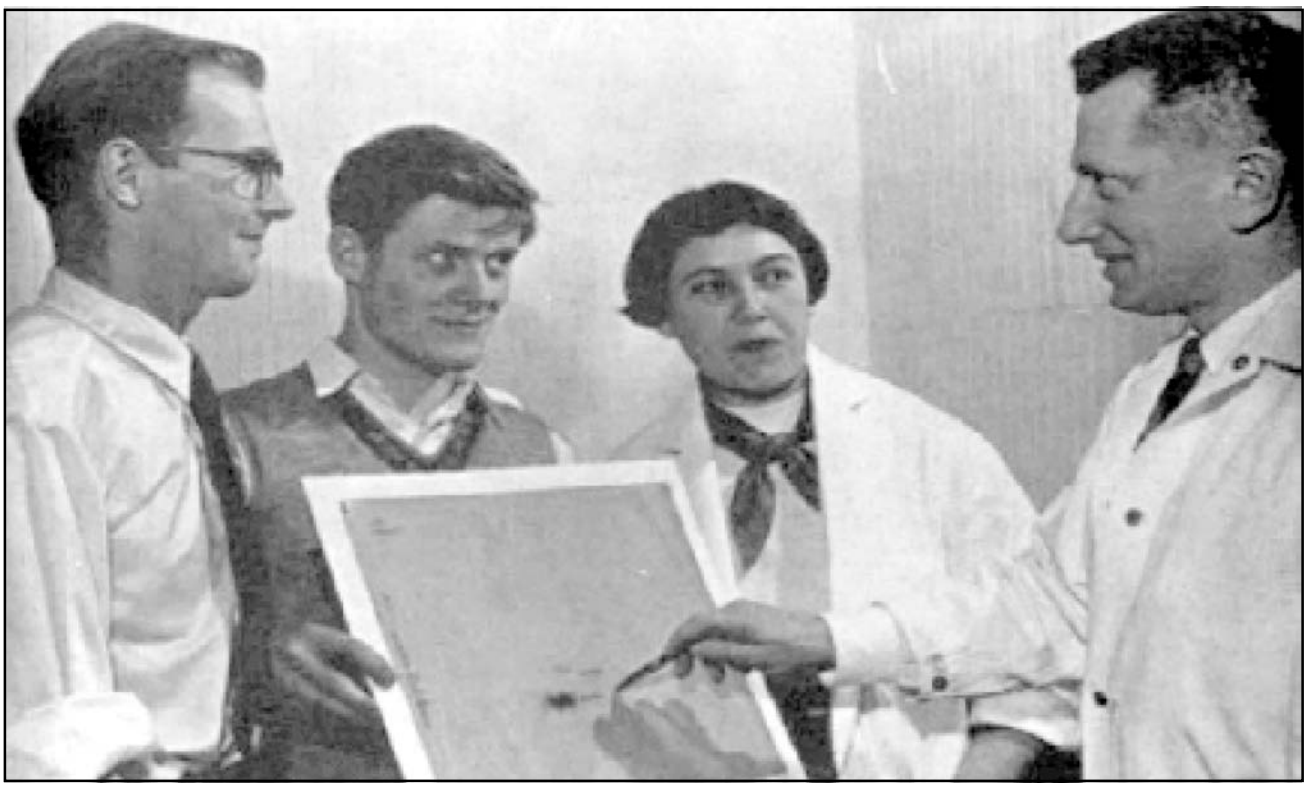

Figure 1. Left to right: Frederick Robert (Bob) Whatley, J.B. Capindale, Mary Bell Allen, and Daniel Israel Arnon, 1955, University of California Berkeley. Reformatted from the original Figure 3 (top) in Buchanan and Carlson (1995).

Bob Whatley was a self-sufficient, thorough, quiet, and confident scientist, but he was 'self-effacing' and never ever "blew his own horn"; this was in contrast to Dan Arnon, who I remember vividly from many meetings and from my personal visit to his office at UC Berkeley. Below, I briefly expand on Whatley's early work in Arnon's Lab. In brief, and to me – rather important – Whatley showed that"*Chloroplasts are complete units for photosynthesis from oxygen evolution to carbon fixation, and that the real common feature between oxygenic and anoxygenic photosynthesis is that both do 'photophosphorylation', i.e., produce ATP*". See below for further information, and an in-depth personal description by Whatley (1995) himself.

RESEARCH CONTRIBUTIONS OF F. ROBERT (BOB) WHATLEY

A. My recollection of Bob Whatley's early work includes his discoveries, in photosynthesis, of the following:

(1) Discovery of methaemoglobin reducing factor (Davenport, Hill and Whatley, 1952), later shown to be "ferredoxin" (Fd), which is a key electron carrier at the end of Photosystem I (PSI). Ten years later, Whatley, Tagawa, and Arnon (1963) established the stoichiometry of electron transport for Fd; then, Gibson et al. (1966) established its electron acceptor side activity, and Hall, Gibson, and Whatley (1966) established its Electron Spin Resonance (ESR) spectra. For a

discussion of the role of ferredoxin in the origin of life and evolution, see Hall et al. (1971), where Whatley was thanked for discussions.

(2) Chloroplasts are the sites of complete photosynthesis (see e.g., Allen et al., 1955).

(3) A common feature of oxygenic and anoxygenic photosynthesis is the presence of cyclic photophosphorylation in both systems (see e.g., Whatley, 1965).

B. Together with Mary Belle Allen, and Dan Arnon, Whatley played a key role in establishing the following:

(a) Isolated chloroplasts do complete photosynthesis all the way from water oxidation to carbon fixation (see Arnon, Allen and Whatley, 1954a; Allen et al., 1955; Arnon et al., 1956; and, Allen, Whatley and Arnon, 1958); this research also provided quantitative information on the rates of these reactions in photosynthesis. All of the above was possible because of the way Bob Whatley had isolated highly active chloroplasts (Arnon and Whatley, 1949).

(b) A common feature between the oxygenic and the anoxygenic photosynthesis is that both are engaged in photophosphorylation, i.e., production of ATP in the light (Arnon, Whatley and Allen, 1954b). The latter conclusion was soon followed by Bob Whatley establishing that photophosphorylation was indeed an anoxygenic process, i.e., it was not dependent on oxygen evolution (Whatley, Allen and Arnon, 1955). About that time, Whatley, Allen, Rosenberg, Capindale, and Arnon (1956) thoroughly examined the relationship of photophosphorylation and carbon fixation in broken chloroplasts.

C. Other contributions of Whatley, while he was still in Arnon's Lab, included the following:

(i) The establishment of $NADP^+$ (nicotinamide adenine dinucleotide phosphate), then called TPN (triphosphonucleotide), serving as an electron transport carrier on what we now call Photosystem I (see Arnon, Whatley and Allen, 1957), something that we now take for granted. I note that the existence of the Emerson Enhancement, and, thus, the two light reactions for TPN ($NADP^+$) reduction was shown, 5 years later, by Rajni Govindjee and myself, working with George Hoch: see R. Govindjee, G. Govindjee and G. Hoch, 1962, 1964; this finding was not recognized even later by Dan Arnon–and, unfortunately, for us at the University of Illinois at Urbana- Champaign (UIUC), Whatley followed this "trend" – perhaps, because of Arnon!

(ii) A comprehensive description of the entire photosynthetic system: production of the overall "assimilatory power" by chloroplasts was provided by Arnon, Whatley and Allen (1958); also see Arnon, Whatley and Allen (1959), where the emphasis was on its relationship to photophosphorylation. Also, see Arnon, Losada, Whatley, Tsujimoto, Hall, and Horton (1961), where the emphasis was on the relationship of the latter to the oxidation of water to oxygen. (For information on David Hall (b.1935-d.1999), see Rao, 1999.) Whatley's contribution to "cyclic photophosphorylation" and its relationship to other factors involved has been very thorough and deep, as has been discussed by Grant and Whatley (1967).

(iii) We associate with Bob Whatley the establishment of two other components in the electron transport chain of photosynthesis: (**a**) Vitamin K in Photosystem (PS) I (Whatley, Allen, and Arnon, 1959), and (**b**) Chloride on the water oxidation side of Photosystem II (Bove, J.M., Bove, C., Whatley, and Arnon, 1963); the latter finding is a reminder of our own later research and ideas (see a review on the role of chloride in PSII by Coleman and Govindjee, 1987).

(iv) Another important contribution of Bob that has been of interest to me is the work of Losada, Whatley and Arnon (1961), where the existence, in chloroplasts, of the two light reactions in photosynthesis was discussed (cf. the two-light effect work of R. Govindjee et al., 1960, on the Hill reaction, which was recognized by Losada

et al., 1961; for work on the two-light effect in photosynthesis of Chlorella cells, see G. Govindjee and Rabinowitch, 1960). All this was placed on firm biochemical footing by the work of Losada et al. (1961), just mentioned.

(**v**) Bob Whatley was quite intrigued by the role of oxygen (or the absence of it) on photophosphorylation of isolated chloroplasts; he summarized it, and then explained the differences in results in different systems, and in different labs (see Whatley, 1963). I vividly remember this presentation of Bob Whatley, as well as by others, all personally known to me (see Notes*, and Govindjee, 1963).

In 1964, Bob was appointed Professor of Botany at King's College in London. In 1971, he became Sherardian Professor and Head of Botany at Oxford University and a Fellow of Magdalen College (see https://en.wikipedia.org/wiki/Sherardian_Professor_of_Botany). In addition, Bob Whatley became the "Keeper of the Botanic Garden" at Oxford University - a job, I am told, he really enjoyed. In 1975, Bob was elected as a Fellow of the Royal Society (UK), a highly prestigious honor.

I end this part of Bob's contributions by mentioning that his own contributions and his research life, during the period I have covered, is wonderfully described by Whatley (1995) himself. Now, I provide below just a glimpse of a few things Bob did later while he was back in UK.

D. A glimpse of part of Whatley's collaborative research while he was affiliated with the University of Oxford.

During 1980s-2000s, several scientists had worked with Bob on various areas of plant biology. Among them were John Allen, James Burnell, Hugh Dunstan, S. English, W. Greenaway, Philip John, Jeviana May, Luciana Rosa, T. Scarisbrook, Antoni Slabas; and his wife the Late Jean M. Whatley. A major point from my perspective was his innovative nature of exploiting and using many biophysical and biochemical techniques such as gas chromatography, mass spectrometry, biochemical analysis of phenolics, and the use of C-13 compounds.

Bob Whatley published more than 100 high quality research papers during his affiliation at the University of Oxford, but I mention here only a few that are of direct interest to me: **(1)** On the function of ATPase (Ferguson et al., 1976); **(2)** On the catalase activity of chloroplasts (Allen and Whatley, 1978); **(3)** On the relation of mitochondria and chloroplasts and on their evolution (J.M. Whatley et al., 1979; F.R. Whatley, 1981; J.M. Whatley, 1981; Whatley and Whatley, 1980, 1984); **(4)** On the relation of light and the evolution of plant life (Woodward et al., 1981); **(5)** On the regulation of various photosynthetic reactions, especially of phosphorylation, by light (Rosa and Whatley, 1981; Powles et al., 1982; Searcy and Whatley, 1982; Allen and Whatley, 1983); and **(6)** On the structure of Rubisco (Ribulose bisphosphate carboxylase oxygenase), the key enzyme for carbon fixation (Bárcena et al., 1983).

CONCLUDING REMARK

It was in 1991 that both Bob and Jean retired from Oxford University, but continued research there as well as travels, mainly to Australia. On November 14, 2020, Bob Whatley died at the age of 96, in Buckinghamshire, UK. We all miss this wonderful human being. For me, Frederick Robert (Bob) Whatley was a legend.

ACKNOWLEDGMENT

I thank Robert Blankenship (USA), John Allen (UK) and Keith Boardman (Australia) for reading this personal reminiscence of F. R. Whatley and for editing it before its submission for publication. I am also grateful to Philip John (UK) for reading it, approving it, and for providing me with an obituary of Bob Whatley, written by Janice Coates, daughter of Bob Whatley, for the Magdalen College in UK. I also thank P.V. (Raj) Sane (India) for reading and approving the final text before its publication.

***Notes:**

H.E. Davenport, Richard Dilley. Sakae Katoh; Paul Levine, Shigetoh Miyachi, and William Ogren, as well as the following who are deceased:

Mary Belle Allen (1922-1973); *Daniel (Dan) I. Arnon* (1910-1994); *William (Bill) Arnold* (1904–

2001); *Mordechei (Mordhay)*Avron (1931-1991); *James A. Bassham* (1922–2012); *Andrew (Andy) A. Benson* (1917–2015); *Lawrence (Larry) R. Blinks* (1900-1989); *Lawrence (Larry) Bogorad* (1921–2003); *Warren L. Butler* (1925–1984); *Britton (Brit) Chance* (1913–2010); *Louis (Lou) Nico Marie Duysens* (1921–2015); *James Franck* (1882–1964; 1925 Nobel Prize in Physics); *Charles Stacy French* (1907-1995); *Giorgio Forti* (1931–2021); *Hans Gaffron* (1902-1979); *Martin Gibbs* (1922–2006); *André Jagendorf* (1926-2017); *Bessel Kok* (1918–1979); *David (Dave) Krogmann* (1934–2016); *Gleb Paul Krotkov* (1901–1968); *William Menke* (1910–2007); *Jack Myers* (1913-2006); *Lester (Les) Packer* (1929–2018); *Eugene I. Rabinowitch* (1898–1973); *Anthony (Tony) Gordon San Pietro* (1922–2008); *Achim Trebst* (1929–2017); *Leo Preston Vernon* (1925–2010); *Wolf Vishniac* (1922–1973); *Charles Percival Whittingham* (1923–2011); and *Horst Tobias Witt* (1922–2007).

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Received:

Accepted: