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HISTORY & BIOGRAPHY

Professor Charles Percival Whittingham (1922–2011)

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Professor Charles Percival Whittingham (1922–2011) (Fig. 1) lived a full life as a botanist and a plant physiologist *par excellence*. On the personal side, he was married, in 1946, to Alison Phillips, and they had two wonderful daughters Christine and Lucy. Whittingham was (and is) respected not only for his research on plants but for educating students, internationally, through his excellent books on the chemistry of plant processes (Whittingham 1964a), photosynthesis (Hill and Whittingham 1955, 1957), and the mechanism of photosynthesis (Whittingham 1974). One of us (Govindjee) vividly remembers Whittingham's excellent 1955 book on photosynthesis since he read it and used it to give his lectures on photosynthesis in the plant physiology course he taught at Allahabad University during 1955–1956.

Whittingham was educated at Owen's School in London and then St. John's College, Cambridge, where he obtained First-Class Honours in the Natural Sciences Tripos (Botany) in 1943 (see *News and Views, Nature*, 1964). During 1939–1945, he did research on the physiology of crop plants at Imperial College, London, and at the Department of Agriculture at Oxford University. During his visits to the USA in the 1950s, Whittingham worked with (1) Robert Emerson (1903–1959) at the University of Illinois at Urbana-Champaign on the maximum quantum yield of photosynthesis (see Nishimura *et al.* 1951); (2) Cornelius van Niel (1897–1985) at the Hopkins Marine Station at Pacific Grove, California, on comparative physiology; and (3) Alan H. Brown (1917–2004) at



Fig. 1. C.P. Whittingham at a coffee break in 1980, Botany Department, Imperial College. Photograph by G.P. Holbrook.

the University of Minnesota on the CO₂ burst in algae (see Brown and Whittingham 1955).

Whittingham served in three academic institutions in the UK: in 1958–1964 as Professor of Botany, Queen

Highlights

- Charles Whittingham, photosynthesis pioneer, who excelled in research and education
- He emphasized physical sciences in the study of physiology of plants and algae
- Whittingham worked on light reactions, glycolate production, and photorespiration

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Mary College, London University; in 1964–1971 as Professor of Plant Physiology, Imperial College of Science and Technology and Head of the Agricultural Research Council Unit of Plant Physiology; in 1971–1982 as Head of the Botany Department, Rothamstead Experimental Station.

We now present his important thoughts, which some of us share, by reminding us of his Inaugural Lecture at Imperial College, London, entitled '*The Schizophrenic Botanist*' (Whittingham 1964b). He dwelt on issues arising from his background and training in the physical sciences before turning to botany and photosynthesis. This background led him to the belief that postgraduate researchers in botany and biological subjects should receive supplementary training in the physical sciences.

Whittingham's initial research interests included the light-harvesting mechanisms in photosynthetic organisms that provide the energy to drive CO₂ assimilation. This included, particularly, the way in which energy absorbed by the photosynthetic pigments is used to generate electron transfer, split water, and create reducing power and oxygen (Whittingham and Bishop 1961). For his work on the two-light effect in isolated chloroplasts, see Bishop and Whittingham (1963). Thereafter, he directed his research activities to work on the green alga *Chlorella* and on higher plants, relating to glycolate production and metabolism (Marker and Whittingham 1966). Using [¹⁴C] glycolic acid he showed that glycolate is oxidized to glyoxylate and aminated thereafter to glycine and serine during photosynthesis, finally ending as sucrose (Waidyanatha *et al.* 1975). These studies laid the foundation of the photorespiratory pathway that functions alongside photosynthesis.

Professor Whittingham initiated newer studies on glycolate metabolism at Rothamstead, which has had a long history of measuring productivity and yield in various crops. Studies on photosynthetic gas exchange revealed that a burst of CO₂ was produced following the transition from light to dark. This post-illumination burst, which was used as a measure of photorespiration, was shown to decrease at low oxygen concentrations or under high CO₂. It was concluded that inhibition of photorespiration could increase photosynthesis, and hence plant productivity. However, glycolate oxidase inhibitors also proved to be inhibitors of photosynthesis (Kumarasinghe *et al.* 1977).

In addition to photosynthesis, Whittingham's interests spanned environmental issues in the field such as the effects on crops of gases produced by local brickwork. The considerable crop damage observed downwind of brickwork was attributed to fluoride release (Brough *et al.* 1978). Professor Whittingham therefore instigated a new line of research to discover the nature of fluoride-induced effects on crop productivity. While crop physiologists in the Department were not particularly enthusiastic about this turn of events, he was able to apply knowledge gained in the laboratory concerning plant physiology and biochemistry to the field (Bishop and Whittingham 1968). His research was funded by the British Council, the Potato Marketing Board, and the UK Agricultural

Research Council. Whittingham was a shrewd judge of the ability of others and often directed students and staff into appropriate employment. The text of his books was carefully constructed with students in mind and was largely based on his own lecture material. In addition, Professor Whittingham had several important international collaborations. For example, he made annual lecture visits to the Department of Botany, University of Lisbon, at the invitation of a former fellow student at Cambridge, Professor J. Contreiras.

In conclusion, there is no doubt that Charles Whittingham was a pioneer of photosynthesis research in the UK. He created a dynamic research environment that stimulated several novel research areas leading to important discoveries such as the pathway of nitrate assimilation and the engineering of Rubisco.

Whittingham's colleagues from Rothamstead have wonderful memories of this great man. Martin Parry, who was one of his last PhD students, and one of the authors, said: "*He believed that only seminal work should be published and had a firm commitment to excellence that inspired all his colleagues. He appreciated a sound analytical mind and always rewarded success*". Alfred Keys, one of his collaborators, and one of the authors, commented: "*Whittingham inspired research that facilitated the different pieces in the puzzle of the photorespiratory pathway to be fitted together. While he often seemed more interested in the bigger picture than the details of the research, he inspired approaches and research directions that were generally successful*".

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