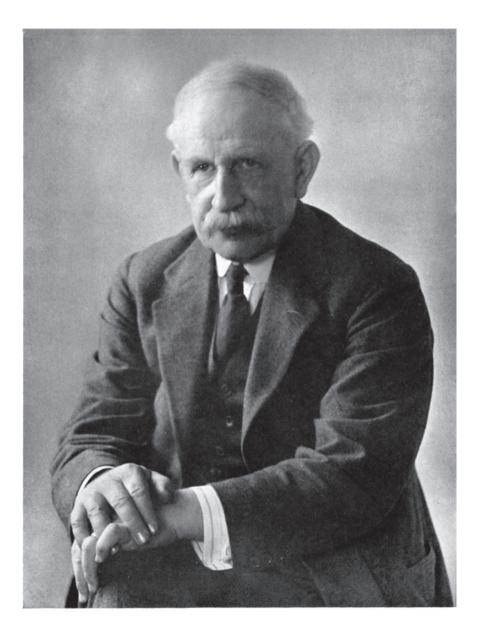


# ANALYTIC STUDIES IN PLANT RESPIRATION





F. F. BLACKMAN



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BY THE LATE
F. F. BLACKMAN

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#### PREFACE

In 1936, at the age of 70, F. F. Blackman retired from his position as Reader in Botany in the University. During his retirement he hoped that, with the secretarial help of one of his research students, he would be able to prepare for publication much of the work on which he had been engaged. But the Second World War came and his hopes were not to be realized. Until January 1947 he had been continuously occupied with this work, and on his death left much in varying stages of completion; some had been made nearly ready for publication many years before. The carefully documented editions of some of the papers make clear, what was already known to his friends, that Blackman was a man not easily satisfied. Now that he had gone, ought these papers (which apparently had not satisfied him) to be left unpublished; or ought a wider circle than his students to have the privilege of seeing how his mind worked? There was a series of six papers dealing with the effect of varying oxygen concentrations on the respiration of the apple, to which he had given much thought, and as these could be prepared for publication without material alteration to the typescript, it was decided, with Mrs Blackman's consent, to publish these. To make the account more nearly complete it has been necessary to include three papers already published by the Royal Society, and for permission to reprint these we have to thank the Council.

These nine papers show Blackman's ideas developing. The incompleted drafts of further work leave little doubt that before he died his ideas had developed yet further, and that he would not have subscribed to some of the views published now.

The experimental work on which these writings of Blackman are founded was done by one of his research students, P. Parija. One of the published papers bears his name alone, another his name in conjunction with Blackman's; Parija's name also appears on one of the typescripts, but it is quite clear that all these papers show the work of Blackman's mind, and that he himself wrote the papers, and the book therefore bears Blackman's name alone; information about names appearing in these papers is supplied in editorial footnotes. Professor Parija has approved this procedure. It did not seem necessary to distinguish the editorial footnotes from the others.

Having explained the origin of this book it is necessary for us to say something more about the writer and its contents.

Blackman was never content to publish unanalysed data. His interest was in metabolic concepts, and any set of data was analysed exhaustively to establish and interpret the underlying correlations. In this way Blackman subjected to his own special methods of analysis many series of results; some of these were obtained in researches carried out under his supervision, but others were from published results of other workers. Little of this careful analysis reached the stage of publication; nevertheless, these analytical studies of experimental data comprised the bulk of his lectures and gave them their unique character.

The nine papers published here are based almost entirely on the data collected



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in one year (1920–1) with twenty-one apples. Under his guidance research students investigated other aspects of apple respiration as is shown in Appendix II. The results would have formed the subject of other contributions, but no doubt they influenced his lines of thought as he wrote the present papers. And this is probably true also of investigations made by others of his students on the respiration of other plant material.

The six unpublished papers in this book were written mainly between 1930 and 1938, and it might be thought that the material is now out of date. This is not so. The experimental data here printed are still among the most important material in this particular field, and Blackman's analysis of the data in these papers provides the most comprehensive picture yet available of the influence of oxygen on respiration. Blackman's initial analysis of one section of the data, published in the three papers of 1928, was recently referred to as follows: 'The classical paper of 1928 remains far and away the most careful and critical analysis of respiration data in the field of plant physiology.'

In the three published papers Blackman was considering mainly the effect of nitrogen and of air on the respiration of apples. In the six additional papers he is concerned with the influence of the full range of oxygen supply, from zero up to 100% oxygen. Many physiologists have investigated the influence of nitrogen and of air on respiration, but few have realized the importance of studying the effect of the intermediate concentrations of oxygen, and it was the results obtained with these that Blackman found so revealing. He writes in Paper V: 'We may present fig. 4a as the first comprehensive schema that has been put forward, for a higher plant, for the effects of oxygen supply upon the full range of respiratory metabolism between the points of the air supply and the zero supply in nitrogen.'

Fig. 4a, just mentioned, shows the changes in the relative rate of CO<sub>2</sub> production in relation to oxygen supply. As such it represents only experimental facts and provides no metabolic concepts. Blackman said of it in Paper VII: 'This set of curves was slowly built up from a multitude of observations by the empirical procedure described in Papers IV and V. We have now to...carry out upon the set an analytic procedure which aims at disentangling the functional determinants that lie behind its graphic features.' From this analytic procedure as carried out in Papers VII and VIII emerges fig. 10 of Paper VIII, in which is put forward schematically a new concept, namely, that in plants a main influence of oxygen concentration on respiration is through an effect on the rate of supply of carbohydrate substrate; to this process Blackman gave the term carbactivation. The importance of this aspect of oxygen supply was indicated in the published Paper III in the following words: 'Should it be established that the primary effect of varying oxygen supply in respiration lies in the control of carbohydrate equilibrium, then our biological outlook on this function will be considerably modified.'

But although there is in the papers more than one important metabolic concept which will provide a stimulus for further research, the scientific contribution which the series makes may be of less ultimate importance than their influence on the analysis and presentation of physiological data. Each of the nine papers is remarkable for the scrupulously careful arrangement of the sequence of ideas and



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the clarity of the writing. Scrutiny of Papers VII and VIII will reveal the stages in Blackman's analytical approach. First came an exhaustive graphical analysis of the experimental data, to establish physiological relations; this was followed by careful consideration of the existing theory, the outcome being that the theory was stated in its simplest form, and certain independent physiological determinants were selected. By graphical analysis the influence of variations in the independent determinants was then investigated, and in this manner it became possible to compare theoretical schemes with the experimentally observed relations. Finally, the analysis led to the presentation of a simple schema indicating the physiological systems involved. Much of Blackman's approach is summarized in the following phrase, which is taken, not from his papers, but from a cutting found with his notes—'the compulsion of theoretic possibilities pushed to their logical conclusion'.\*

To some Blackman may seem to be too dogmatic; to others this characteristic will indicate his search for simplicity and clarity. To quote from Paper IX: 'Though, in order to economize words these views are expressed as antithetically as possible, it is not intended to give dogmatic support to the view that has been developed out of observations on plants. The intention...is rather to formulate the opposition of views as clearly as possible so that further data may be collected to clear up the critical issues between the theories.' And from Paper III: 'After that it may become necessary to take the present schema to pieces and reconstruct it, but at least we shall have consolidated a mass of relations to which any future system must conform.'

The papers were not prepared as chapters of a book. There are repetitions, and in some places the treatment in later papers replaces that in early. To try to make a unity would involve risks that we were not prepared to take. By leaving the papers essentially as they were we have left it possible for a reader to trace the development of the author's ideas.

Although the individual papers and their different editions had been prepared by Blackman with ultimate publication in mind, their assembling has involved Dr J. Barker, one of Blackman's pupils, in much devoted labour.

Appendix II contains a list of the names of Blackman's research students, as complete as we have been able to make it. Where the results of the investigation were embodied in a dissertation submitted for a research degree, the title has been given. Some of the results have already appeared as published papers.

\* Bukharin, The Times, 8 March 1938.

G. E. BRIGGS

Cambridge 1952