PHYSIOLOGICAL STUDIES ON NITROGEN-FIXING BLUE-GREEN ALGAE

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SUMMARY

The various types of blue-green algae known to fix nitrogen are considered. Particular attention has been paid to the effects of oxygen and other physiological parameters on nitrogenase activity and on the ecological distribution of the group. Data on nitrogen fixation by cell-free extracts of blue-green algae are presented.

INTRODUCTION

Blue-green algae, together with the photosynthetic bacteria, are probably the most primitive photosynthetic organisms found on Earth to-day. Present day species range through unicellular, colonial and filamentous types and morphologically some resemble fossil forms which occurred 1–3 billion years ago in the early-, mid-, and late-Precambrian periods of the Earth’s history, and later (see Plate 1). Schopf refers to the similarity in morphology between fossil and living forms as evolutionary conservatism. Physiologically also there may be evolutionary conservatism because studies on nitrogen fixation by blue-green algae suggest that at least some species are perhaps better adapted to the micro-aerophilic conditions of the Pre-cambrian period than to the present day atmosphere which has high concentrations of oxygen, because oxygen may inhibit nitrogenase activity. In this paper I should like to summarise some recent developments in the physiology of nitrogen fixation by algae and to indicate some ways in which these may relate to the present day ecological distribution of the group.
Until recently unequivocal evidence for nitrogen fixation by algae was available only for heterocystous forms of the orders Nostocales and Stigonematales. Recent evidence for nitrogen fixation by pure cultures of unicellular and filamentous non-heterocystous forms suggests that a re-assessment is now necessary.

a) Heterocystous algae

Drewes first demonstrated convincingly that blue-green algae fixed nitrogen by showing that pure cultures of *Nostoc punctiforme* and two *Anabaena* species increased in total nitrogen content in culture solution without adding combined nitrogen. Fogg was the first to take the necessary precaution of removing any traces of ammonia and oxides of nitrogen from the atmosphere to which the alga (*Anabaena cylindrica*) was exposed. Later nitrogenase activity in heterocystous algae was confirmed using N$_2$ and by the acetylene reduction technique. There is now evidence for nitrogen fixation by approximately 50 species and strains of heterocystous algae.

Heterocysts are large thick-walled, empty-looking cells which, under the light microscope appear empty, but which at the ultrastructural level have a complex lamellar network. Fay *et al.* argued on the basis of diverse morphological and physiological data that the heterocysts were probably the sites of nitrogen fixation in heterocystous algae, and additional indirect evidence for this has been obtained subsequently by other workers. Stewart *et al.* finally obtained direct evidence of nitrogenase activity in heterocysts when they showed that preparations of isolated heterocysts possessed a nitrogenase and that ATP and a source of reducing power (Na$_2$S$_2$O$_4$) were required for its efficient functioning. Smith and Evans consider that the vegetative cells of *Anabaena cylindrica* also possess the enzyme. The latter supposition will be referred to again later.