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Synergistic carbon metabolism in a fast growing mixotrophic freshwater microalgal species *Micractinium inermum*

Richard T. Smith ^{a,b,*}, Krys Bangert ^{a,b}, Stephen J. Wilkinson ^{b,1},
D. James Gilmour ^a

^a Department of Molecular Biology and Biotechnology, University of Sheffield, Western Bank, Sheffield, South Yorkshire, S10 2TN, United Kingdom

^b Department of Chemical and Biological Engineering, University of Sheffield, Mappin Street, Sheffield, South Yorkshire, S1 3JD, United Kingdom

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ABSTRACT

In recent years microalgae have attracted significant interest as a potential source of sustainable biofuel. Mixotrophic microalgae are able to simultaneously photosynthesise while assimilating and metabolising organic carbon. By combining autotrophic and heterotrophic metabolic pathways biomass productivity can be significantly increased. In this study, acetate-fed mixotrophic *Micractinium inermum* cultures were found to have a specific growth rate 1.74 times the sum of autotrophic and heterotrophic growth. It was hypothesised that gas exchange between the two metabolic pathways within mixotrophic cultures may have prevented growth limitation and enhanced growth. To determine the extent of synergistic gas exchange and its influence on metabolic activity, dissolved inorganic carbon (DIC), dissolved oxygen (DO) and photosynthesis and respiration rates were measured under different trophic conditions. A 32.7 fold and 2.4 fold increase in DIC and DO concentrations, relative to autotrophic and heterotrophic cultures respectively, were coupled with significant increases in rates of photosynthesis and respiration. These data strongly support the hypothesis of mixotrophic gas exchange within *M. inermum* cultures. In addition to enhanced growth, this phenomenon may provide reductions in aeration and oxygen stripping costs related to microalgae production.

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* Corresponding author. Department of Molecular Biology and Biotechnology, University of Sheffield, Western Bank, Sheffield, South Yorkshire, S10 2TN, United Kingdom. Tel.: +44 (0) 114 222 4412.

E-mail address: r.t.smith@sheffield.ac.uk (R.T. Smith).

¹ Present address: Department of Chemical Engineering, Thornton Science Park, University of Chester, Chester, Cheshire, CH2 4NU, United Kingdom.

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1. Introduction

Microalgae derived biofuels have the potential to meet a significant fraction of global transport fuel demand, enabling a reduction in our dependency on finite fossil fuels and their associated greenhouse gas emissions. Although microalgae have similar photosynthetic machinery to higher plants, their simpler cellular structure and planktonic mode of growth allow efficient access via diffusion to CO₂ and other nutrients, enabling high biomass productivities. Furthermore, oleaginous microalgae accumulate significant proportions of their biomass as lipids (typically 20–50% compared to <5% for oil palm); lipid being the desired feedstock for biodiesel production [1]. Consequently, compared to terrestrial crop biofuel feedstocks such as soybean or sugarcane, microalgae have orders of magnitude higher land use efficiencies [2]. In addition, microalgae can be grown on non-arable degraded land using wastewater as a nutrient source [3]. These attributes are particularly important because, unlike first generation biofuels, they allow extensive microalgal cultivation while avoiding the economic and environmental issues associated with food production competition.

Unfortunately, the numerous advantages of microalgal biofuels are matched by several technical challenges that must be overcome to reach full environmental and economic feasibility. One such challenge is achieving a high enough productivity to drive down processing and harvesting costs, which, due to the microscopic and aqueous nature of microalgae, are considerably higher than terrestrial crops [3]. Biomass productivity, expressed, for example, in units of grams of dry cells per litre of culture per day, depends on both cell density and specific growth rate [4]. Photoautotrophic (henceforth referred to as autotrophic) algae rely entirely on solar energy for growth, consequently cell density is inversely proportional to light penetration and as cell density increases specific growth rate declines due to self-shading [5]. Achieving a high cell density and biomass productivity can therefore be limited by light availability. For large-scale cultivation systems, photosynthetic autotrophic growth is usually considered as the dominant mode for engineering design purposes. For this mode of growth, reactors and ponds are designed to ensure adequate access to sunlight for photosynthesis, with operating cell densities maintained at a reasonably low level to prevent excessive shadowing of other cells. On the other hand, heterotrophic cultivation of microalgae by promoting aerobic respiration on an organic carbon source enables biomass production to be maintained during the night hours, and at higher cell densities due to light independent growth. Cultivation using both modes of carbon metabolism therefore offers the potential to maximise productivity; particularly when a source of cheap organic carbon is available such as acetate in the effluent of anaerobic digestors [6].

Mixotrophic algae are capable of simultaneously photosynthesising while assimilating and metabolising organic carbon as both a carbon and energy source. This mode of growth reduces dependency on light penetration, enabling higher cell densities than autotrophy, while using considerably less organic material per unit of biomass than dark heterotrophic growth [7]. Mixotrophic growth can enable

significantly enhanced biomass productivity, which in turn leads to enhanced lipid productivity [5]. These characteristics make mixotrophy a promising alternative strategy for microalgal biofuel production, especially when coupled with the use of waste organic carbon sources [8].

A frequently overlooked challenge facing microalgal biofuel commercialisation is CO₂ supply. Autotrophic algal growth is highly dependent on the availability of CO₂, which provides the main source of elemental carbon for the production of new biomass and energy carrying molecules. Carbon dioxide is freely available in the atmosphere, but at a low concentration of around 0.04% which limits the diffusive mass transfer of CO₂ into an algal culture. In order to reach economically feasible productivity rates, this mass transfer limitation to autotrophic growth can be removed by sparging cultures with external sources of concentrated CO₂. Anthropogenic CO₂ sources such as waste flue gases from power plants are envisaged to meet the requirement for large scale microalgal production. However, providing sufficient CO₂ to produce a quarter of US annual transport fuel demand (roughly 227 billion litres of biodiesel) would require harnessing a large proportion (36–56%) of total CO₂ emissions from all US power plants [9,10]. Furthermore, in the US, without an extensive and costly infrastructure of CO₂ capture and transportation, only a limited number of these concentrated emission sources are within range of areas suitable for large scale algal cultivation. Consequently the availability and cost of supplying CO₂ is a significant bottleneck for large scale microalgal production and further research is needed to reduce reliance on external concentrated CO₂ sources [10,11].

Mixotrophic growth could mitigate this problem by providing an endogenous source of CO₂ through the respiration of organic carbon [12]. One of the earliest experiments comparing trophic modes in the green alga, *Chlorella regularis*, discovered that the two metabolic pathways, photosynthesis and heterotrophic respiration, can act non-competitively under mixotrophic growth [13]. Consequently the mixotrophic specific growth rate should equate to the sum of the autotrophic and heterotrophic growth rates. This can be expressed as a specific growth rate ratio (Equation (1));

$$\frac{\mu_M}{\mu_A + \mu_H} = 1 \quad (1)$$

where μ_M , μ_A , μ_H , equate to mixotrophic, autotrophic and heterotrophic specific growth rates respectively. Subsequent studies have reported a similar relationship in *Chlorella vulgaris*, *Haematococcus pluvialis*, *Chlamydomonas humicola*, but not in *Scenedesmus acutus* [14–17]. The species specific nature of non-competitive mixotrophic growth is largely influenced by both the degree to which organic carbon assimilation inhibits the production of chlorophyll and the degree to which illumination inhibits the production of organic carbon uptake enzymes [12,16]. However, conformity to this ratio is also governed by the aeration conditions under which the cultures are grown. Martinez and Orus [15] reported that when the *C. vulgaris* cultures were aerated with 2% CO₂-air the ratio was recorded as 1.00, in line with earlier aerated studies. However when the cultures were aerated with air or grown under non-aerated conditions this ratio increased to 1.10 and 1.28 respectively. A possible explanation for this phenomenon is

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