Blue Light Enhanced Respiratory Activity under Photosynthetic Conditions in *Chlorella;* a Mass Spectrometric Analysis

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Mass spectrometric analysis shows that blue light enhances oxygen uptake during photosynthesis in *Chlorella fusca.* Assays in which all of the normal $^{16}O_2$ of air has been substituted by $^{18}O_2$ permit discrimination between photosynthetic O_2-evolution (measured as $^{16}O_2$, *i.e.* mass 32) and O_2-uptake (measured as $^{18}O_2$, *i.e.* mass 36). A chlorophyll-free *Chlorella kessleri* mutant for which in earlier studies the occurrence of blue light enhanced oxidative carbohydrate degradation has been demonstrated (W. Kowallik, H. Gaffron, Planta **69,** 92–95 (1966); W. Kowallik, Ann. Rev. Plant Physiol. **33,** 57–72 (1982)) has been used for comparison in the present study. The light intensity dependencies of the observed effect seem to differ in mutant and wild type cells. In the mutant a fluence rate of 1.5–2.0 $\mu E \cdot m^{-2} \cdot s^{-1}$ of blue light yields saturation, whereas in the wild type even ten times this value does not. A wavelength dependence of the effect measured with equal fluence rates at 422 nm, 457 nm, 488 nm, 555 nm and 649 nm shows maximal efficiency around 460 nm and no significant effect of red light. This agrees with earlier studies on the chlorophyll- free mutant. As a result of this correspondence, we think that the enhanced oxygen uptake during photosynthesis concerns oxidative carbohydrate degradation. The putative mechanism and significance of the observed blue light enhanced respiration in photosynthesizing *Chlorella* are discussed.

Introduction

In spite of great efforts, the question whether mitochondrial respiration of photosynthesizing plant cells is influenced by light or whether it remains unchanged in comparison with the rate in the dark is still unanswered. Literature of the past 50 years reports stimulations, inhibitions or no influence, the data usually being derived from different organisms and experimental approaches [1]. These unsatisfactory results were caused largely by the interference of the counteracting oxygen gas exchanges of photosynthesis and respiration, which are indistinguishable by usual techniques. Even the application of different oxygen isotopes in the water and in the gas phase yielded contradictory results [2–5]. Therefore, in the following indirect approaches have been attempted. In these experiments photosynthetically inactive cells were used, obtained either by mutation or by application of specific inhibitors. Among the former, two pigment mutants of *Chlorella,* the chlorophyll-free M 20 and the additionally carotenoid-deficient M 125, proved especially useful. They responded to illumination with a markedly increased loss of endogenous carbohydrates accompanied by an enhanced oxygen uptake and carbon dioxide output. The respiratory quotient remained around unity [6–10]. Test for photorespiration, using an increased supply of atmospheric oxygen and application of hydroxypyridinemethane-sulfonate, resulted negatively [8]. Therefore, the light effect was considered to reflect mainly enhanced mitochondrial respiration. Comparably enhanced gas exchanges were also obtained with DCMU-poisoned wild type cells [9, 11–13]. Closer analysis of the phenomenon revealed in all cases tested an induction period of 5–10 min and – most characteristic – an effectiveness of blue light only. Fairly well resolved wavelength dependencies showed two maxima, one around 460 nm and the other around 370 nm, and no effect whatsoever of wavelengths longer than 550 nm [6, 11, 14]. Finally, after turning the light off, the enhanced gas exchange decreased only slowly reaching the initial rate after more than 60 min [15].

Based on this information, Kowallik and Kowallik [16] made another attempt to answer the

Abbreviation: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea.

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point in question. Analysing the kinetics of photosynthetic oxygen liberation under various wavelengths of light, they found very short-lived induction phenomena, excluding a constant rate in red light from the beginning, but an only initially comparable high rate in blue light which decreased slowly within 5 min to a constant rate. The wavelength dependence of the drop in apparent oxygen liberation resembled quite closely the wavelength dependence of the enhancement of respiration in suitably mutated and specifically inhibited cells. This was interpreted to indicate the existence of such an increased respiration also during photosynthesis. This assumption received further support by the wavelength dependence of the slowly declining, in the beginning differently enhanced oxygen uptake after turning the light off. With these results the authors confirmed Emerson's data. He had observed and discussed 50 years earlier the same responses by *Chlorella* cells examined for their photosynthetic quantum requirement in different wavelengths of light [17]. A blue light dependent and slowly developing enhancement of oxygen uptake in darkness was induced by flashes of 5 s duration in wild type *Chlorella* by Pickett and French [18] and by Ried [19]. All these results served as good indicators for an enhancing effect of specific wavelengths of light on oxidative carbohydrate degradation in a photosynthesizing green alga comparable with that established for the non-photosynthetic cells [20]. None of them, however, provided unequivocal proof. In the present paper we have addressed the problem again using mass spectrometry and a device for extremely sensitive measurement of oxygen isotope ratios in photosynthetic oxygen evolution [21, 22]. We hereby demonstrate a specifically blue light enhanced oxygen consumption during photosynthesis, probably indicating enhanced respiration.

Materials and Methods

Strains and growth conditions

Chlorella fusca Shihara et Krauss (formerly *Chlorella pyrenoidosa*) and a chlorophyll-free mutant of *Chlorella kessleri* Fott et Nováková (formerly *Chlorella vulgaris*), Nos. 211-8b and 211-11h/20 respectively, of the Culture Collection of Algae of the Inst. for Plant Physiol. at Göttingen University, F.R.G. were used. Both algae were cultivated in an inorganic nitrition solution [23] which in the case of the non-photosynthetic mutant was supplemented by 1% glucose. Wild type cells were grown autotrophically in continuous white light of 3500 lux, while mutant cells were kept in the dark. Both cultures were continuously aerated with air, in the case of the wild type enriched with 1.5% CO_2. Growth temperature was 30 ± 1 °C. Further details on culture tubes, thermostat and light sources are given by [23]. For the experiments cells were separated from their growth medium by centrifugation at 3×10^3 g for 5 min, washed twice with distilled water and resuspended in 0.1 M Na_2HPO_4/KH_2PO_4 buffer pH 7.5.

Mass spectrometry

Oxygen exchange measurements were carried out with the *Stable Isotope Ratio Mass Spectrometer* "delta" from Finnigan MAT (Bremen, Germany).

The device operates with a two directional focussing Nier type ion source. The ion source (tungsten filament) is operated at 140 °C and has a high stability regulation of electron emission.

Fast responses of the detector to changes in the partial pressures of the gas phase were achieved by direct connection of the reaction chamber to the main vacuum of the ion source, by-passing the usual inlet system [22, 24]. Detection and recording of the oxygen signals at $m/e = 32$, $m/e = 34$ and $m/e = 36$ were performed simultaneously.

The *reaction chamber* used is a home-made massive steel cell with a plexiglass screw cap [22], whose total internal volume of 19 ml was separated from the gas phase of the ionic source by a teflon membrane at the bottom of the chamber. The total membrane spanned surface is 12 cm^2. Into this chamber 2 ml of a suspension usually containing 4–6 µl of packed *Chlorella* cells with generally 5–10 µg chlorophyll per µl packed cell volume (pcv) were given. The diameter of the cells varied between 4–10 µm. With an average cell diameter of 6 µm, the sedimented layer of 6 µl packed cell volume in the reaction chamber is calculated to be a monolayer of 6 µm thickness covering of the 12 cm^2 surface between 80 and 100%. The liquid phase in the reaction chamber is uniformly 1.7 mm high.

Calibration of the unstirred system is performed as follows: For instrumental calibration all meas-

urements (also qualitative ones in which only the isotope distribution matters) are started with the determination of masses 32, 34 and 36 of normal air (*e.g.* Fig. 3a in ref. 21) and the signals compared to the known % atomic abundance of ^{16}O (99,7587) and ^{18}O (0,2039) in air. Usually we determine isotope ratios with an internal precision of at least 0.1‰ (*e.g.* Tables I and II in ref. [21]). Thereafter, for kinetic measurements signals are calibrated on the basis of the equilibrium with air exactly as described by Peltier and Thibault [25] or by decomposition of various defined amounts of H_2O_2 by catalase in the reaction vessel. For correction of isotope dilution the equation for calculation of the O_2-uptake rate and gross O_2-evolution rate in a stirred assay, given by Peltier and Thibault [25] (compare also Shiraiwa *et al.*, 1988, [26]) is valid by principal. The assay with a sedimented monolayer offers some experimental advantages. Thus, the rate constant of oxygen decrease due to mass spectrometer consumption, measurable in the presence of inactivated algae, is much smaller (more than 10 times) than under those conditions. Photosynthetically produced $^{16}O_2$ of a sample containing 35 µg chlorophyll results, at the highest intensity used, in a dilution of $^{18}O_2$ in the gas phase of maximally 0.55% within 10 min. Therefore measurements starting with only $^{18}O_2$ in the gas phase and only $H_2{}^{16}O$ in the aqueous phase not exceeding 10–15 min have not been corrected.

For the *measurements* it should be kept in mind that the mass spectrometric set-up represents a closed gas system in which the gas phase is constantly pumped off by the vacuum system. Hence, all recorded O_2-signals are superimposed on an oxygen uptake due to this mass spectrometer consumption. However, the loss of the atmosphere over the liquid phase due to this consumption takes under our experimental conditions more than 10 h and is therefore beyond the measuring precision if experiments are carried out within minutes (see Fig. 1, 2 and 3). The system measures the *quantity of oxygen molecules* being evolved or taken up per time interval by the sources (algae or chloroplasts) on the membrane. Therefore, the time course for *O_2-evolution* shown in Fig. 2 represents the time course of an evolution rate: Upon illumination the sources emit oxygen with an increasing rate until after approx. 2 min a constant rate is reached. Upon switching off the light source the signal falls immediately back to the initial dark rate (*e.g.* Fig. 2). The linear dependence of the measuring signal on the amount of emitting sources (measured as chlorophyll) and on light intensity has been verified and confirmed for our system. Correspondingly, a course of *O_2-uptake* in the light is superimposed, this time in the same reaction sense, onto the mass spectrometer consumption rate and that of any dark O_2-consumption rate, due, for example, to respiration. Illumination diminishes the O_2-concentration per time interval that reaches the detector system if the sources exhibit an enhanced O_2-uptake in the light. Upon switching off the light, a signal-jump in direction to the original dark rate occurs (just visible in Fig. 2b for the uptake curve in red light) if the reaction does not continue for some time in the dark, which is in fact the case for blue light enhanced respiration as shown already by Kowallik in 1966 [15] and by Fig. 2a.

Illumination

Light of various spectral regions was produced by passing the light beam of a Leitz projector, Prado Universal, through interference filters, type IL or AL, from Schott & Gen., Mainz, F.R.G. with λ_{max} 422 nm (T_{max} 43%, HW 24 nm), λ_{max} 457 nm (T_{max} 59%, HW 18.5 nm), λ_{max} 488 nm (T_{max} 38%, HW 11 nm), λ_{max} 555 nm (T_{max} 56%, HW 22 nm) and λ_{max} 649 nm (T_{max} 64%, HW 22 nm). For high fluence rates of blue light a blue plexiglass filter (2 mm, Röhm & Haas, Darmstadt, F.R.G.) had to be used. The resulting light field exhibited wavelengths from 410–530 nm with a pronounced maximum around 460 nm and also wavelengths longer than 660 nm. Quantum fluence rates were determined with the quantum spectrometer QSM 11-2500 from Techtum Instruments, Umea, Sweden. The quantum fluence rates used are indicated in the figure legends.

Results

Oxygen uptake in non-photosynthesizing cells

First of all we tested the feasibility of the mass spectrometric method by comparing its signals with those of existing and widely confirmed manometric and polarographic measurements. For this purpose the chlorophyll-free *Chlorella* mutant 20 proved especially useful because of its inability to produce interfering oxygen by water oxidation.

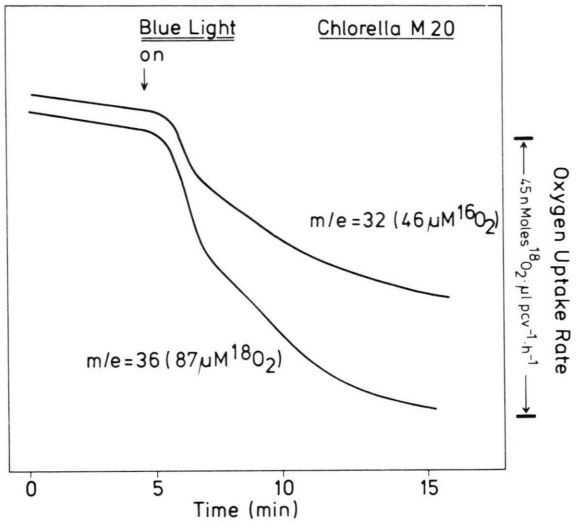

Fig. 1. Dependence of the rate of blue light (λ 457 nm) induced oxygen uptake on time in the non-photosynthetic *Chlorella* mutant 20 measured by mass spectrometry. Fluence rate 1.2 $\mu E \cdot m^{-2} \cdot s^{-1}$. The picture shows an experiment in which the oxygen atmosphere contained a defined mixture of $^{16}O_2$ (46 μM = 35%) and $^{18}O_2$ (87 μM = 65%).

Exposing the cells to an atmosphere of 35% $^{16}O_2$ and 65% $^{18}O_2$ we examined the applicability of different isotopes simultaneously for the metabolic reaction under discussion. Fig. 1 shows that the concentration of both oxygen isotopes reaching the detector system decreases markedly upon irradiation with blue light. In detail the time course shows no response within the first minute of illumination followed by a strong transient response which lasts about 1 min, then passing into a smaller response. This had not been seen before. We made no effort to pursue this further because the elucidation of the mechanism of the blue light action was not the objective of the present investigation. The overall phenomenon corresponds to the increase in respiratory oxygen uptake by blue light in this organism detected by manometry (Kowallik and Gaffron, 1966 [7]; Kowallik, 1966 [15]). Therefore, the method should be appropriate to follow respiratory and photosynthetic oxygen exchange simultaneously in illuminated wild type cells.

Oxygen exchange in photosynthesizing cells

We tackled the problem of respiration during photosynthesis by using 100% $^{18}O_2$ in the gas phase and $H_2{}^{16}O$, *i.e.* normal water, in the aqueous phase. This is an approach which had been used by Brown and his coworkers 40 years ago, yielding however, ambiguous results [2–4]. Exposing wild type *Chlorella* to blue or to red light of 5.5 $\mu E \cdot m^{-2} \cdot s^{-1}$ the cells evolve ^{16}oxygen resulting from photosynthetic water splitting with a fast increasing rate (Fig. 2a, b). At this light intensity, a

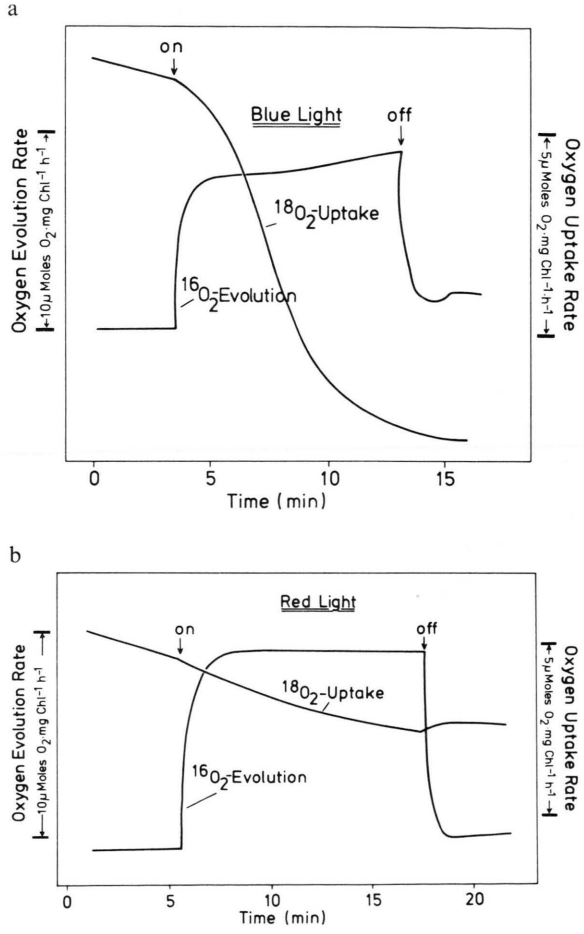

Fig. 2. Dependence of the rate of photosynthetic oxygen evolution ($m/e = 32$) and that of the simultaneously occurring oxygen uptake ($m/e = 36$) on time of *Chlorella fusca* exposed to blue (λ 457 nm) (Fig. a) or to red (λ 649 nm) light (Fig. b) of equal fluence rates of 5.5 $\mu E \cdot m^{-2} \cdot s^{-1}$. The gas phase contained only $^{18}O_2$ (in equilibrium with the aqueous phase) whereas the aqueous phase contained only $H_2{}^{16}O$. The experiment was measured with an $^{18}O_2$-background of 178 μM. The 2 ml assay contained 6 μl of packed cells corresponding to 35 μg chlorophyll. The culture in this figure exhibits a well pronounced blue light effect and represents an experiment of a series carried out with 10 different culture batches.

fairly constant rate of 8 to 10 μmol per mg chlorophyll per hour is reached in both cases after about 2 min. Simultaneously, $^{18}O_2$-uptake increases upon illumination with blue light reaching a constant rate after about 10 min. The extent of this increase may differ considerably from culture to culture. It ranges from less than 1 to up to 10 μmol mg chlorophyll^{-1} h^{-1}. Variations of this magnitude have been reported also for non-photosynthesizing mutant cells [6, 15]. In the mutant this means enhancement of the oxygen uptake rate in darkness by factors of 2 to 8. For the photosynthesizing cells examined here, we have no mass spectrometric data on their dark O_2-uptake. Adopting the data of polarographic measurements which are 2–3 μmol mg chlorophyll^{-1} h^{-1} and assuming their enhancement, the effect would range between less than 50 and 300%. Effects of up to 65% have been reported for DCMU-poisoned *Chlorella* cells earlier [11]. Whereas in the mutant this different behaviour has been correlated with the supply of endogenous carbohydrate reserves [6, 15, 20], we have not been able yet to demonstrate this for the photosynthesizing wild type cells.

In Fig. 2a we present an example for a very strong blue light response. At the fluence rate of 5.5 μE·m^{-2}·s^{-1} applied, a change in the O_2-uptake rate per hour is observed of about 7 μmol mg chlorophyll^{-1}. This is a rate which compensates photosynthetic O_2-production at this low light intensity almost completely. For comparison it may be mentioned that a quantum fluence rate of 5.5 μE·m^{-2}·s^{-1} of blue light corresponds roughly to about 300 lux of white light. At this intensity, compensation of O_2- and of CO_2-exchange has been found for many plants. The data presented is the first direct proof of a strongly enhanced oxygen consumption during photosynthesis in blue light. The result supports the earlier assumption of an increased respiration in photosynthesizing *Chlorella* cells under these specific conditions. Moreover, Fig. 2a shows that the blue light-enhanced $^{18}O_2$-uptake rate is maintained after switching off the light. This, too, complies with the observation in mutant cells [15]. In contrast to this, the only slightly increased O_2-uptake rate in red light shown in Fig. 2b returns immediately to a lower uptake rate after switching off the light.

Intensity and wavelength dependences

To corroborate the assumption that it is respiration which is specifically increased in photosynthesizing cells, intensity and wavelength dependencies of the enhanced oxygen consumption during photosynthesis have been compared with those of the light-enhanced loss of endogenous carbohydrates and of the concomitantly increased oxygen uptake of the chlorophyll-free *Chlorella* mutant [8]. Fig. 3 and 4 show that the intensity dependencies differ markedly. In the non-photosynthetic mutant fluence rates around 0.15 μE·m^{-2}·s^{-1} of blue light suffice for half saturation and fluence rates of 1.5–2.0 μE·m^{-2}·s^{-1} yield saturation of this effect. Both data corresponds to results obtained polarographically earlier [6, 14]. In photosynthesizing wild type cells however, even the highest fluence rate of about 18 μE·m^{-2}·s^{-1} tested, does not indicate light saturation of O_2-uptake. This is completely different from the situation in DCMU-treated green *Chlorella* cells, for which Kowallik [11] had shown that the light intensity dependence of the putative blue light enhanced oxygen uptake should more or less compare to that of the not photosynthesizing yellow *Chlorella* mutant. Therefore, the explanation offered the

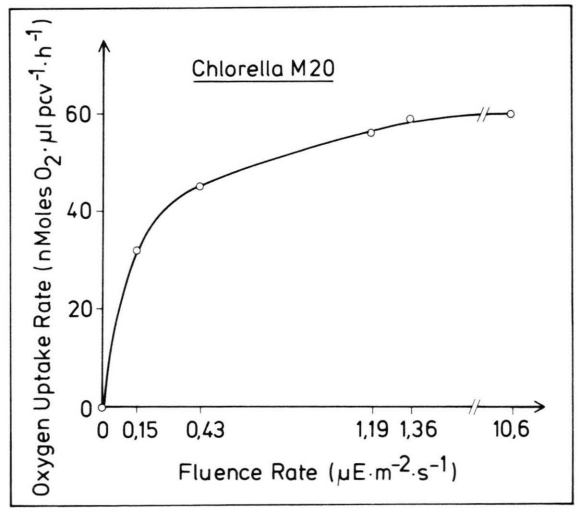

Fig. 3. Dependence of the blue light (λ 457 nm for the low intensities up to 1.19 μE·m^{-2}·s^{-1} and 410–530 nm with maximum at 460 nm for the intensities 1.36 and 10.6 μE·m^{-2}·s^{-1}) enhanced oxygen uptake in the chlorophyll-free *Chlorella* mutant 20 on the quantum fluence rate.

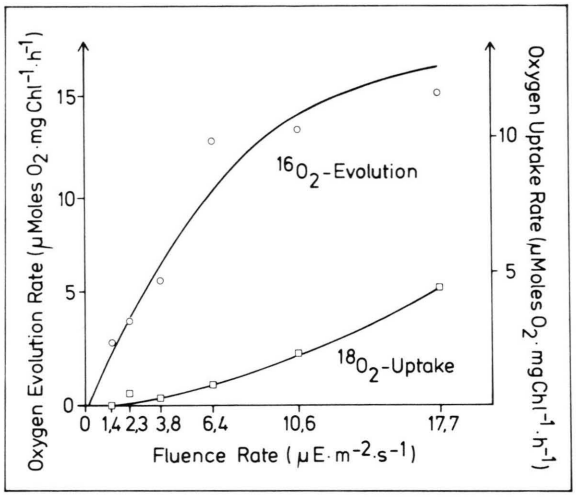

Fig. 4. Dependence on the fluence rate of blue light (λ 410–530 nm with max at 460 nm) of rates of oxygen evolution and of oxygen uptake of *Chlorella fusca*. The figure is an experiment of a series of 9 all exhibiting similar gas exchanges.

photoreceptor responsible might be shaded by green pigments, does not apply. Pickett and Meyers [27] observed in studies at such fluence rates hardly half-saturation of photosynthetic oxygen evolution. The wavelength dependence (Fig. 5) obtained at equal fluence rates of 5.5 μE · m^{-2} · s^{-1} exhibits the highest effectiveness

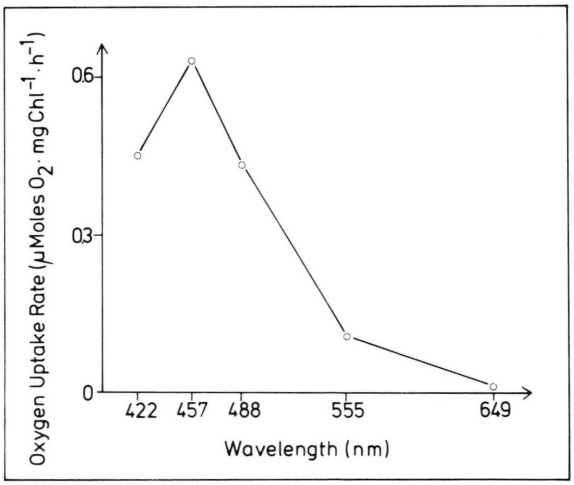

Fig. 5. Dependence of the enhanced $^{18}O_2$-uptake during photosynthesis of *Chlorella fusca* on the wavelength of light. Fluence rate 5.5 μE · m^{-2} · s^{-1} at all wavelengths. The curve is a representative experiment of a series of 4.

at wavelengths around 460 nm. It reveals comparably steep drops to shorter and to longer wavelengths with a minor effect of green light. Together with the inefficiency of red light, this corresponds to the respective action spectra for the chlorophyll-free *Chlorella* mutant [14] and for DCMU-treated wild type cells [11], and also that for an enhanced loss of endogenous carbohydrates in the mutant [8]. This corroboration supports the assumption that enhanced carbohydrate degradation is also taking place in the photosynthesizing cell.

Discussion

The assumption that the enhanced oxygen consumption during photosynthesis in blue light is connected with an increased breakdown of carbohydrate has no doubt yet to be proven. However, if we accept it as a working hypothesis because of the good correspondence with the respective behaviour of the non-photosynthetic mutant described, we have to take into account the situation in both cell types. Looking for a common source of usable substrate, there is, except a rather small amount of sucrose, only starch to be found. This is deposited inside the chloroplast as assimilatory starch from photosynthetically produced hexoses, or as starch granules built up from exogenously supplied glucose in the mutant [15]. On a first view, this correspondence might point to an influence of blue light on breakdown of these stored polymers. However, under autotrophic conditions *Chlorella* cells accumulate considerable amounts of reserve carbohydrates only when grown in strong white or in red light. They are largely devoid of starch reserves even after extended periods of time in weak white or in blue light [23]. Assuming this latter behaviour for the cells examined in the present study and expecting the enhanced oxygen consumption to continue also for longer periods of blue illumination than those actually followed for technical reasons, an influence on metabolites common in starch production and in starch breakdown appears more likely. Such substances can partly be found in photorespiration, a metabolic pathway suggesting itself in case of respiratory activity of plant cells in light. However, photorespiration does not originate from reserve carbohydrates. It is not specifically blue light dependent and its specific inhibitors

have not been effective in the cells under consideration [8]. Therefore, we feel photorespiration to be excluded. Common intermediates can also be found by taking into consideration chloroplast respiration. This metabolic pathway has been proposed by Gibbs and coworkers to perform polyglucan decomposition in the darkened chloroplast in order to supply the cell with stored energy under these conditions. From studies with [^{14}C]-glucose and specific inhibitors, and from the enzymatic profiles determined, these authors provide evidence for the functioning of reactions of the oxidative pentose phosphate cycle and of an incomplete glycolysis in chloroplasts of algae and of higher plants [28–30]. Obviously, glucose 1-phosphate resulting from phosphorolytic cleavage of starch [31] cannot pass the chloroplast envelope in major amounts. Being dependent on the translocator systems for photosynthetic products in the light [32], triosephosphate or glycerate 3-phosphate have to be produced. This can be achieved *via* fructose 1,6-bisphosphate or, in the course of glucose 6-phosphate regeneration, from ribulose 5-phosphate resulting from oxidation and decarboxylation of the former substrate. Triosephosphate, the substrate for the most active transfer system across the envelope, has probably to be partly oxidized inside the organelle in order to cope with the continuous demand of ATP necessary to keep these pathways going. The thereby and by direct glucose 6-phosphate oxidation produced NADPH is reoxidized for further use by transferring the electrons *via* ferredoxin to suitable acceptor molecules such as atmospheric oxygen. Carbon dioxide liberated in the overall process originates from gluconate 6-phosphate oxidation and from further degradation of the exported glycerate 3-phosphate *via* the common routes in cytosol and mitochondrion.

A supposed influence of light on the fate of intermediates in starch metabolism could not be brought about indirectly by the often discussed [1] alterations in metabolite concentrations resulting from photosynthetic activities; firstly, because the effect is also expressed in the non-photosynthetic mutant and, secondly, since it is only expressed in blue light. Since we have no information on the nature of the photoreceptor involved nor on its localization we can only speculate on its putative action. To make an attempt, we might suppose that its incorporation in the chloroplast envelope would alter the properties of these membranes on excitation, thus influencing metabolite export. However, the speeding up of syntheses in the cytosol might indirectly lead to an increased drain off from the chloroplast as well. The significance of an increased supply of ligh-energy molecules of the cytosol during illumination can easily be seen. The photoautotrophic cell produces mainly under these conditions lipids and amino acids for protein biosynthesis for which carbon skeletons such as acetate and 2-oxocarboxylic acids are needed, many of them not being intermediates of the chloroplast's metabolism [33]. Here it should be noted that Miyachi *et al.* have shown that blue light specifically enhanced $^{14}CO_2$ incorporation into amino acids and lipids, deriving from blue light stimulated anaplerotic reactions in chlorophyll-free *Chlorella* [34]. The question however, why the above proposed process requires a specific regulatory system instead of being accomplished by photosynthetic products alone cannot be answered. Information concerning the behaviour of translocator systems and the concentrations of various metabolic intermediates in the cell under specific illumination might help to clarify the situation.

Acknowledgements

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