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RESEARCH ARTICLE

THE PHOTOSYNTHETIC SYSTEM OF THE SEAWEEDS: THE SEAWEED PARADOX

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ABSTRACT

In theory Seaweed biomass production is severely hampered by a 10,000 fold slower diffusion rate of a Carbon source or Dissolved Inorganic Carbon (DIC) in the biophysical medium water in comparison to terrestrial C3 crops. Despite this inflicting property pelagic seaweeds outcompetes C3 crops for annual green biomass production which is called “the seaweed-paradox”. Here we have reported our findings and hypothesized that for four seaweed species that due to an internal acidification the abundant oceanic bicarbonate ion (HCO₃⁻) is introduced into the cell which will in the inner acidic mitochondrial environment (matrix) rapidly be converted to CO₂ which is the only C-form photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) can react with to produce with solar energy and water green biomass. We hypothesize this intracellular acidification is performed by reversal of the fifth pump of the chemi-osmotic model of Mitchell. It can be expected that in nearby future seaweeds may play a prominent role in providing the unfettered growth of the world population -estimated at around 10 billion people at the midst of the 21st century: food, fuel and other bioactive ingredients.

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INTRODUCTION

Natural photosynthesis is the process by which sunlight is captured and converted into the energy of chemical bonds of organic molecules that are the building blocks of all living organisms. Pelagic seaweed ecosystems in our oceans are in comparison to terrestrial crops the most productive on Earth (Hurd *et al*, 2014; van Ginneken and de Vries 2016a) but the photosynthetic mechanism is not fully understood because it is aquatic. In theory biomass production is severely hampered by a 10,000 fold slower diffusion rate of a Carbon source or Dissolved Inorganic Carbon (DIC) in the biophysical medium water in comparison to terrestrial C3 crops (Black *et al*, 1981; Larkum 2010). Despite this inflicting property pelagic seaweeds outcompetes C3 crops for annual green biomass production which is called “the seaweed-paradox” (van Ginneken and de Vries 2016a). We state that although the mechanisms of aquatic photosynthesis for unicellular algae have detailed been elucidated (Falkowski and Raven, 2007), there is a historic lack at research at seaweed photosynthesis (Raven *et al*, 2002). Seaweed culture needs the Cartesian model to elucidate the challenging evolutionary ancient photosynthetic mechanisms (Raven *et al*, 2008) to grow out to a global seaweed aquaculture industry humanity urgently needs (Cottier-Cook *et al*, 2016). Therefore a photosynthetic model for oceanic water (The Royal Society, 2005) -similar to

existing terrestrial photosynthesis models (Farquhar *et al*, 1989)- needs at first to be hypothesized and finally proven, going back to the roots of the classical biochemistry (Mitchell 1961). Here we pose such a model partly substantiated with laboratory data. Demand for green biomass for energy and food is projected to increase at least 70% by mid-century relative to the present global consumption due to an unfettered growth of the world population estimated at around ≈10 billion people at the midst of the 21st century (van Ginneken and de Vries 2016, United Nations 2008). Overall, the rate of energy capture by photosynthesis –conversion of carbon dioxide using solar energy directly into Life (primary production) or indirectly into food- is immense, approximately 100 Terawatts (10¹² Watt) or to make a more comprehensible statement: 1 h of sunlight falling on our planet is equivalent to all the energy consumed by humans in an entire year (van Ginneken and de Vries 2016b, Larkum 2010). Facing the problems of “global warming” and “ocean acidification”, carbon-neutral energy production on a scale commensurate with, or larger than, the entire present-day energy supply from all sources combined is urgently needed. If solar energy is to be a major primary energy source, then it must be stored and dispatched on demand to the end user e.g. via green biomass. However, terrestrial agriculture is presently at its limits (Foresight, 2011). Another option would be artificial photosynthesis (Voloshin *et al*, 2015) which is especially an attractive approach to store solar energy in the form of chemical bonds as occurs in natural photosynthesis. As a major advantage it is carbon-neutral (Farquhar *et al*, 1989). However upscaling is

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being very difficult, if not impossible on the global scale required (Barber and Tran, 2013).

So a smart creative innovative approach to increased primary production can be accomplished by exploiting our oceans - which cover around $\frac{3}{4}$ of our globe- by culture of seaweeds the “unforeseen crop of the future”. Seaweeds, in principle, as primary producers that are easy to harvest, can make a significant contribution to the production of green biomass. However, their photosynthesis is aquatic and therefore barely understood. In contrast, terrestrial photosynthetic systems have been described in detail by C3, C4, Crassulacean Acid Metabolism (CAM-photosynthesis) for terrestrial plants in which Carbon fixation is an important biological process in all photosynthetic organisms in order to convert light into chemical energy with a photosynthetic efficiency of 3–6% (Larkum, 2010, Farquhar *et al.*, 1989). Luckily from freshwater studies with aquatic angiosperm (Maberly & Madsen 2002) and submerged aquatic macrophytes like *Hydrilla* (Chen and Coughenour 1996) or the amphibious plant *Rumex palustris* (Mommer *et al.*, 2005) much “pre-knowledge” has been collected one decade ago with aquatic (freshwater) photosynthesis.

From these literature it becomes clear the major issue related to aquatic photosynthesis is in general solely related to the biophysical constraint and limitations for a suitable Carbon source -in most cases still CO_2 - in the biophysical medium water for photosynthesis because CO_2 diffuses 10,000 times slower in the medium water than in air, and is also slow to equilibrate (Black *et al.*, 1981; Larkum 2010). From the studies at aquatic angiosperms and submerged aquatic macrophytes it became clear two major strategies can be distinguished related to severely restricted availability of a Carbon source in the medium water for photosynthesis. Some macrophytes may lower photosynthetic capacity matching the low supply of CO_2 (and light) (Maberly and Madsen, 2002). Others apply one or several Carbon Concentrating Mechanisms (CCM) mechanisms like e.g. usage of HCO_3^- which is the most widespread carbon acquisition strategy present in about half of the tested submerged angiosperms (Maberly and Madsen, 2002). In contrast, research at oceanic aquatic photosynthesis of seaweeds is still in its infancy.

MATERIALS AND METHODS

The following materials were used in the experiments:

Seaweeds

- *Ulva lactuca* (Chlorophyta): Katse Heule, Easters-Scheldt, The Netherlands; approximate coordinates: 51°32'30 N and 3°52'E.
- *Caulerpa sertularioides* (Chlorophyta): (origin: Denpasar, Bali, Indonesia) purchased by Burgers' Zoo, Arnhem, (the Netherlands). Approximate coordinates: 8° 41' S and 115° 17' E.
- *Caulerpa cf. brachypus* (Chlorophyta): (origin: Cuba), was obtained from “De Jong Marinelife”, Spijk, (The Netherlands). Approximate coordinates: 23° 50' S and 82° 50' W.
- *Undaria pinnatifida*, (Wakame) (Phaeocophyceae): Kilcar, West-Donegal, Ireland, approximate coordinates: 54°37'N and 8°37'W.

While seaweeds were collected, a water sample of the surrounding oceanic water was sampled at the same time stored at -80°C pending analysis.

Experimental set up

In this experiment we determined for four seaweed species under mechanical pressure until 10 barr the percentage of moisture weight. All investigated four pelagic seaweeds species gave moisture and with ICP-techniques we investigated it among else for macro- and micro-elements. Also in the surrounding oceanic water, at the same time sampled during collection of the seaweeds, with the same ICP-techniques the macro- and micro-elements were determined.

Mechanical pressure procedure

To be able to press juice out of the seaweed biomass the materials were first pulped using a laboratory homogenizer (manufacturer: Foss Tecator, type: Tecator 1094 homogenizer). For seaweed biomass a smooth knife was used, for others a serrated knife was used. For most materials the lower speed of 1500 rpm was sufficient, for other the higher speed of 3000 rpm was needed. Juice was pressed out of the pulp, approximately 100 grams of pulp was used, using a LLOYD INSTRUMENTS (type: LR30K) testing machine that was fitted with a specially constructed unit for pressing pulps at a maximum pressure of 60 bar (see Figure 1: PANEL 1,2). Pulps were first pressed for 5 minutes at a pressure of 2 bars, after that for another 5 minutes at a pressure of 10 bars (see Figure 1: PANEL 3). Applied pressure, thickness of the press cake and cumulative juice production (see Figure 1: PANEL 4), were continuously monitored. Afterwards press cake and samples of the obtained seaweed moisture of the four different seaweed species (n=4 per seaweed species) were immediately stored at -80°C pending analyses.

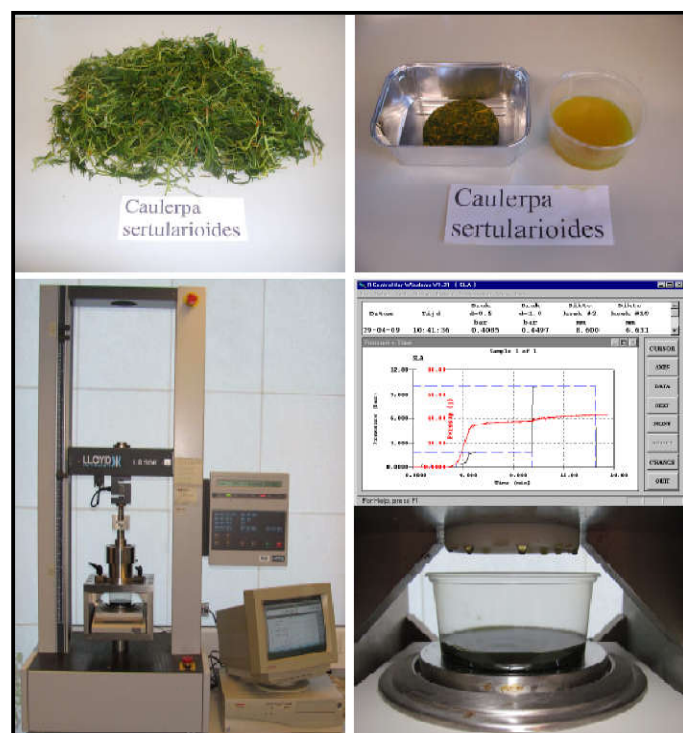


Fig.1. Pressure equipment to obtain press moisture from *Caulerpa sertularioides*

Salinity: Salinity of the seaweed moisture and oceanic water were determined using an EC meter (manufacturer: WTW; type Cond 315i/SET) fitted with a conductivity cell (manufacturer: WTW; type: TetraCon 325, cell constant 0.475 cm⁻¹).

pH: pH measurements were performed with a PHH-7011 pH-meter with automatic temperature compensation (Omega, the Netherlands).

N-total and P-total measurements: N-total and N-NH₄ measurement were performed on a Segmented Flow Analyzer (SFA) apparatus according to SWV E1417 guide lines at the Chemical Biological Laboratory for Soil Research, Wageningen University, Wageningen (The Netherlands). Determination of P₃- was performed on an HR-ICP-MS (Thermo Element-2) according pre-treatment SWV E-3404, measurement SWV E-1325 and conservation SWV E-3404 guide lines at the same laboratory.

Calculations: The amount of H⁺- ions was calculated from the pH-value according to 10^{pH} (The Royal Society, 2005).

properties of the pressed liquid. These will be discussed in other documents (V.van Ginneken *to be submitted*). pH values for the seaweed *Ulva lactuca* were slightly acidic (range pH: 6.44-6.57), for *Undaria pinnatifidia* pH: 6.51 ± 0.055, and the lowest for both *Caulerpa* species: *Caulerpa sertularioides* pH: 4.56 ± 0.058 and *Caulerpa cf. brachypus*, pH: 4.51 ± 0.055 and (*vide* Table 1).

DISCUSSION

CO₂ in the aquatic environment is expressed with "Dissolved Inorganic Carbon" ≈ (DIC): (acid-base dependent chemistry (DIC=Σ ([CO₃²⁻] + [HCO₃⁻] + [CO₂]), a reflection of the bicarbonate equilibrium) (The Royal Society, 2005). The physical determined diffusion rate of DIC in water which is in comparison with CO₂ in the medium air ≈ 10,000 slower (Black *et al.*, 1981; Madsen & Sand-Jensen, 1991). The term 'Dissolved Inorganic Carbon' or [(DIC=Σ ([CO₃²⁻]+[HCO₃⁻]+[CO₂])] ignores to some extent the 'problematics' of defining [CO₂] in water because the relative proportions of the three inorganic forms of Carbon Dioxide dissolved in seawater is dependent on environmental parameters like water acidity such

Table 1. Some characteristics for the at 10 bar mechanical pressed seaweed moisture for salinity, nutrients like N& P, and calculated H⁺ value (mean ± Std of n=4 samples per seaweed species)

Seaweed origin	Sample number	Salinity Promille ‰	pH mg/l	H ⁺ mol/l	N-NH ₄ ⁺ mg/l	N-tot mg/l	P mg/l
<i>Ulva lactuca</i> Netherlands	Ulva1	9.60	6.53	0.015	40.9	420.0	88.9
	Ulva2	9.40	6.44	0.016	45.8	432.0	91.4
	Ulva3	9.40	6.55	0.015	42.7	360.0	83.1
	Ulva4	9.60	6.57	0.014	42.9	359.0	85.3
	Mean	9.501	6.51	0.015	43.08	392.75	87.18
	Stdev	0.115	0.055	0.001	2.027	38.71	3.694
<i>Caul.sert.</i> Indonesia	CS1	19.10	4.81	0.081	4.81	362.0	45.0
	CS2	19.30	4.20	0.150	4.61	344.0	45.0
	CS3	19.50	4.62	0.099	4.62	348.0	44.8
	CS4	19.30	4.62	0.099	4.71	351.0	45.20
	Mean	19.30	4.563	0.107	4.69	351.25	45.00
	Stdev	0.163	0.258	0.030	0.093	7.72	0.163
<i>Caul.brach.</i> Cuba	C-b-1	20.50	4.51	0.110	14.40	922.0	91.40
	C-b-2	20.60	4.51	0.110	14.50	917.0	92.80
	C-b-3	20.70	4.50	0.111	14.60	920.0	92.50
	C-b-4	20.50	4.51	0.110	14.70	917.0	93.40
	Mean	20.58	4.508	0.110	14.55	919.00	92.53
	Stdev	0.096	0.005	0.001	0.129	2.45	0.838
<i>Undaria</i> Ireland	Und-1	9.60	6.53	0.015	14.60	123.0	17.80
	Und-2	9.40	6.44	0.016	10.10	96.6	12.60
	Und-3	9.40	6.50	0.015	8.27	91.20	11.60
	Und-4	9.60	6.57	0.014	5.92	83.10	10.60
	Mean	9.50	6.510	0.015	9.72	98.48	13.15
	Stdev	0.115	0.055	0.001	3.674	17.27	3.206

RESULTS

For this experiment only the pH values -of importance for the hypothesis described in this manuscript about the "seaweed paradox" are given- but for completeness, salinity values of the pressed liquid including fertilizers (N & P) are also given because they give a more complete picture of the biophysical

as pH and the acid-base chemistry of the CO₂-carbonate system in the sea (The Royal Society, 2005). In principle, the surface waters of the oceans are slightly alkaline, with an average pH of about 8.2 ± 0.3 units because of local, regional and seasonal variations in the oceans (The Royal Society, 2005). Under these oceanic pH conditions the carbon source in seawater [CO₂] ≈ 10 μM and [HCO₃⁻] ≈ 2 mM which implies

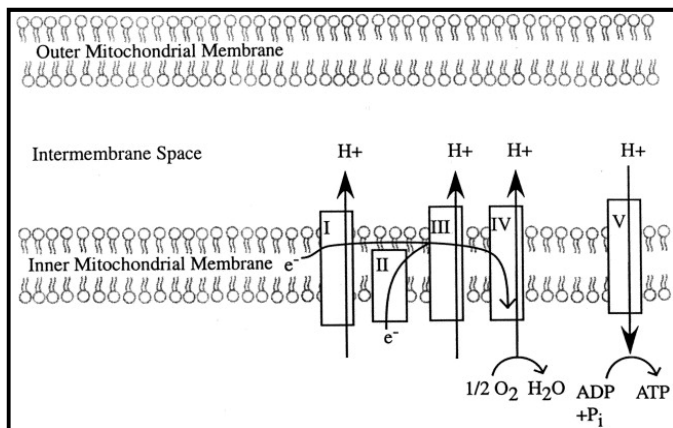


Figure 2. Our explanation for an efficient aquatic photosynthesis of the seaweeds –the so called “seaweed-paradox”, is that we assert that H⁺ ions produced in the respiratory energy event coupled to oxidative phosphorylation, do not connect oxygen to become neutral water. But these produced protons are pumped back via a reversed fifth pump of the model of Mitchell into the cell to acidify the internal environment of the seaweed cell so that HCO₃⁻ can be converted directly into carbon dioxide that can react directly with Rubisco and create green biomass with sunlight

that [HCO₃⁻] is ≈200 times more available than the carbon source in the form of [CO₂]. This abundant HCO₃⁻ source can easily pass the fluid mosaic bilayer in the aquatic oceanic environment of the seaweeds because it consists mainly out of cholesteryl esters while the energy is used stored in a proton gradient across a membrane to drive the synthesis of ATP from ADP and phosphate (P_i) (Boyer, 1997). Here we suggest the CCM in seaweeds is based on a cellular acidification of compartments by pumping protons and hydrolyzing ATP (Nelson *et al.*, 2000). In addition, intracellular acidification is associated with the operation of a carbon-concentrating mechanism (CCM) (Raven *et al.*, 2008). Their main function is to act as centers of carbon dioxide (CO₂) fixation, by generating and maintaining a CO₂ rich environment around the photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Mitchell (Mitchell 1961) proposed that energy is stored as an electrochemical gradient across a vesicular membrane which opened the door for understanding energy transformation by membrane systems. Most of the proteins required for the conversion of light energy and electron transfer reactions of photosynthesis are located in membranes. In the chemi-osmotic energy transduction of (Mitchell, 1961) it was suggested that cells can store energy by creating an electric field or a proton gradient across this membrane. The chemi-osmotic hypothesis suggests that the action of ATP synthase is coupled with that of a proton gradient. It is the action of the proton gradient that causes a proton motive force that allows ATP synthase to phosphorylate ADP and inorganic phosphate to ATP. In mitochondria, the key site of ATP production in oxidative phosphorylation is the inner mitochondrial membrane. This process was also discovered to take place in the thylakoids of chloroplasts as a means of generating ATP and reduced NADP in the light dependent reaction, key products needed for the light independent reaction to generate hexose sugars in plants (Mason *et al.*, 2013) and algae (Barsanti and Gualtieri, 2014). Our modification of the Mitchell model -based on an overall internal acidification of the internal environment for pelagic seaweed- is that we assert that H⁺ ions produced in the respiratory energy event coupled to oxidative phosphorylation, do not connect oxygen to become neutral water. But these produced protons are pumped back into the cell to acidify the

internal environment of the seaweed cell so that HCO₃⁻ can be converted directly into carbon dioxide that can react directly with Rubisco and create green biomass with sunlight. We postulate, in the closely related vacuolar type H⁺-ATP-ases, the hydrolysis reaction is used to acidify cellular compartments like chloroplasts, by pumping protons and hydrolyzing ATP (Alberts *et al.*, 2002). This solely can be accomplished -like we pose in this seaweed model- by a reversal of “complex V” in the Mitchell model (Mitchell, 1961) - resulting in an intracellular acidification.

Seaweeds had a convergent evolution with the terrestrial plants and their photosynthetic systems are very ancient. The first multicellular red algae arose during the Middle Proterozoic around 1250 mYr ago, while the first green macroalgae arose during the late Proterozoic around 750 Myr ago (Carroll 2001). So these evolutionary facts show us that their during a time period between 750-1250 Myr ago (Carroll 2001) the first photosynthetic systems evolved in the evolution which are completely different in comparison to the three nowadays existing photosynthetic systems C3, C4 and CAM. With a tremendous potential and diversity of seaweed sp. in our oceans of around 1200 green-, 2000 brown- and 6000 red seaweed species humanity has new perspectives in many areas for the next coming centuries in the feed (Nederlof *et al.*, 2017), in the food (van Ginneken *et al.*, 2011) in order to prevent our chronic modern welfare diseases like obesity and type 2 diabetes (van Ginneken & de Vries 2015) in order to produce green biomass (Cottier-Cook *et al.* 2016) and industrial applications (Se-Kwon Kim 2012). A statement like “the overseen crop of the future” is fully justified.

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