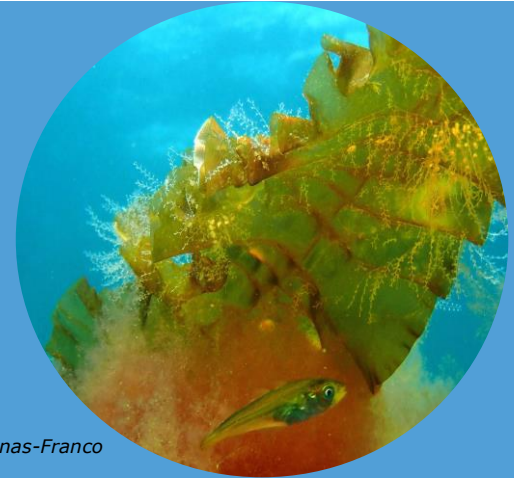


Seaweed Factsheet: Carbon

Carring capacity in seaweed cultivation

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Introduction

Carbon (C) serves as a common element of all known life and it is the second most abundant element in the human body and in plants by mass, after oxygen. Due to its molecular structure, carbon is able to form more compounds than any other known element. Seaweeds play a considerable role in the world's carbon cycle (global primary production). Approximately 6 % of the global net primary production (NPP) of 104.9 Pg (104.9×10^{15} g) carbon per year is ascribed to seaweeds, although seaweeds only colonize 0.1 % of the seafloor. In theory, seaweed biomass production is severely hampered by a 10000-fold slower diffusion rate of a carbon source in the aquatic medium in comparison to terrestrial crops (for 3 C plants). Despite this inflicting biophysical property, seaweed outcompetes the relative terrestrial annual green biomass production - the so called "**seaweed paradox**".

1.2. Photosynthesis

The photosynthetic process in seaweeds, like in all photo-autotrophic plants, is driven by sunlight and uses CO_2 , which is thereby removed from the water, to form new biomass, which also requires a variety of minerals, and especially dissolved inorganic- phosphorus and nitrogen (DIN and DIP). Seaweeds can conduct photosynthesis in all their tissue, whereas most terrestrial plants photosynthesize only in their (green) leaves.



Overall equation for photosynthesis in plants.

The produced oxygen (O_2) originated from water (H_2O). Carbon dioxide (CO_2) is soluble in water and dissociates to give bicarbonate ion (HCO_3^-), hydrogen ion (H^+), and carbonate ion (CO_3^{2-}) in the aquatic medium. In addition, methane (CH_4) uprising from the ocean floor can dissociate in the water column into hydrogen (H_2) and carbon monoxide (CO),

which forms CO_2 and dissociates into HCO_3^- . The relative proportions of these forms of inorganic carbon depend on pH, salinity and temperature. During photosynthesis in seaweed, aquatic bicarbonate ions are introduced into the mitochondrial matrix of the cell, which rapidly converts the HCO_3^- into CO_2 . Photosynthesis stops during night, when the light level is low, and seaweeds begin to take up oxygen, burn glucose and release carbon dioxide.

Carbon fixation

Seaweeds use inorganic carbon (CO_2) as their only carbon source. The main abiotic factors that affect the rate of carbon fixation (and thus growth) in seaweed are light intensity (PAR, UV), carbon dioxide concentration, temperature and salinity (Table 1). Growth also depends on the seaweed's internal growth limitations and nutrient status, like nitrogen (N) and phosphorus (P) availability, as well as pest and diseases. The carbon fixation reaction only takes place, if the end products of the photosynthetic light reactions (ATP, NADPH^+) are available, and may develop and/or progress differently, depending on species. Basically the Calvin cycle (light independent redox reaction) with light dependent regulators to the cycle's activation of enzymes, is the only means of net carbon fixation in most seaweeds (and plants) see figure 1.

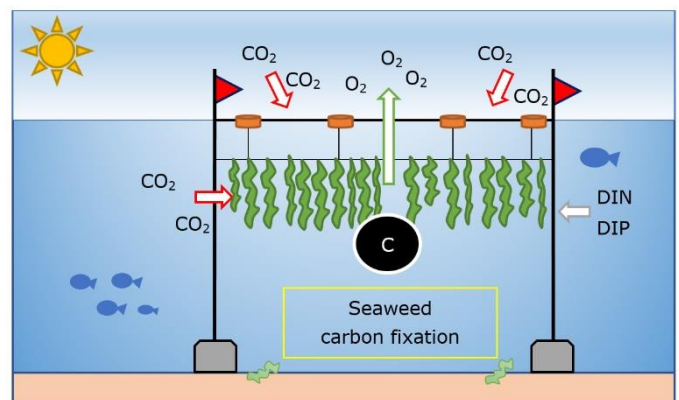


Figure 1. schematic of a seaweed cultivation site where carbon fixation takes place.

Table 1. Main abiotic factors that affect carbon fixation in seaweeds

Factor	Effect
PAR / UV	Irradiance and light quality vastly affect photosynthesis. Seaweeds are well adapted to low light concentrations, thus excessive radiation damages important compounds in the cell and consequently reduces its photosynthetic and general metabolic activity, resulting in a reduction in growth.
CO₂	High CO ₂ concentrations, respectively bicarbonate concentration, increase growth.
Temperature	Chemical reaction that combines CO ₂ and water to produce glucose and O ₂ are controlled by enzymes, which reaction rate is affected by temperature
Salinity	Unsuitable salinity reduces the photosynthetic efficiency, thus affects growth (Lanping et al. 2013).
Nutrient status	Nutritional history of the cells: filled internal nutrient pools/storages (e.g. C, N, P) supply building blocks, whereas depleted storages cannot contribute to biosynthesis.

The light dependent photosynthesis, which provides key products, like NADPH⁺, for the Calvin cycle, is depressed, during times of strong sunlight in many seaweeds. This depression primarily occurs to protect the photosynthetic apparatus by photo-inhibition and typically follows a diurnal pattern with lowest photosynthetic activity between noon and afternoon. Variations in this midday decline are dependent on species, developmental stage, derived habitat, and diurnal light history.

Carbon balance

The carbon balance of plants and seaweeds is dominated by photosynthesis and respiration. Dark respiration (non-photo-respiratory mitochondrial respiration), which occurs in both the dark and in the light, is not only critical for biosynthesis, including growth, in plants and seaweeds, but also plays an important role in modulating the carbon balance in individual cells and also whole plants, as well as is regarded as an essential part to photosynthesis to sustain the cytosolic redox potential. During daytime, respiration is partly depressed

by the light and the ratio of respiration to photosynthesis is low, whereas the ratio increases during darkness. Empirical evidence suggests a respiration to photosynthesis ratio of about 0.4 – 0.5 for vegetation in general. A ratio of 1 shows homeostasis between respiration and photosynthesis, while a ratio >1 eventually leads to autolysis and death of the cell. Photorespiration in seaweed could not be detected in experiments, unless the seaweeds were treated simultaneously with high O₂ and low CO₂ concentration.

Carbon uptake and sequestration

Macro algae and some of the brown seaweeds in particular, are known for their fast growth. This makes them an attractive plant for cultivation purposes. In natural ecosystems these kelps contribute to several ecosystem services. Which are now being researched in a cultivation context as well. However the non-value ecosystem services, kelp forests provide have often been overlooked. Two of the main points of interest are the potential for nutrient removal in eutrophic area's and carbon sequestration. The role of macroalgae in carbon sequestration has long been overlooked due to their main habitat being on hard substrate. Direct burial in the sediment is not possible in these environments. However, large part of the kelp blades can get worn down by storms that can uproot vast parts of a cultivation site. The uprooted kelps can then enter the detritus pool and be buried in the sediment elsewhere. Furthermore, kelp exude large portions of dissolved organic matter (DOM) which is partly bioavailable and thus can be utilised by bacteria. Other parts of the DOM cannot be broken down, these are called Refractory DOM (RDOM). This portion, has the potential to contribute to carbon sequestration once transported below the mixed layer.

Carbon an nutrient ratio's

In addition to environmental parameters, different seaweeds inherit different metabolic carbon fixation rates, hence general C requirements also differ between species. Besides C, as a major element in biosynthesis, nitrogen (N) and phosphorus (P) are essential for growth. However, the different forms of N an P require an active transport the enter the cell while C can enter the cell in the form of bicarbonate ion (HCO₃⁻) through diffusion. In phytoplankton the Redfield ratio, or C:N:P ratio, of 106:16:1 is fairly constant under repletion conditions, which is not the case for seaweed. Most seaweeds have a higher nutrient ratio. A mean of 92 species showed a ratio of 550C:30N:1P.

This ratio shows that seaweeds are more carbon rich and require a lower concentration of P than of N, compared to phytoplankton. Table 2 shows the C:N:P ratio of some of the seaweed species which are being considered for cultivation in the North sea. Seaweed cultivation in open systems, means that there are limiting nutrients, for seaweed these are N and P, C is generally not a limiting nutrient because the ocean is a natural sink for atmospheric CO₂. Additionally there is a natural input of C through biological and geothermal activity in the sea where CO₂ and CH₄ are released. Nevertheless the amount of C should be monitored in extensive cultivation sites as a C limitation could locally occur during the growth season.

Table 2. Showing the stoichiometry of different seaweed species.

Seaweed Species	Common name	C:N:P ratio in tissue
Winter sp.		
<i>Saccharina latissima</i>	Sugar kelp	117:13:1 630:70:1
<i>Laminaria digitata</i>	Oarweed	80:8:1 606:25:1
Summer sp.		
<i>Ulva lactuca</i>	Sea lettuce	450:30:1 711:79:1
<i>Ulva rigida</i>	Sea lettuce	110:10:1
Year round		
<i>Fucus vesiculosus</i>	Bladder wrack	782:34:1
<i>Ascophyllum nodosum</i>	Knotted wrack	814:37:1
<i>Palmaria palmata</i>	Dulse	100:10:1 180:12:1