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A barren ocean

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SUMMARY

The Southern Ocean is the largest ocean on our planet, and it covers more than 10% of the surface of the earth. The world oceans play an important role in our climate system. The oceans are a buffer not only for heat, but also for CO₂. CO₂ is a greenhouse gas that absorbs thermal radiation that is emitted from the earth. The excess anthropogenic CO₂ produced over the last decades may give rise to a global increase of the temperature of the atmosphere with several degrees. The oceans may take-up part of the atmospheric CO₂, and thus control the potential warming of the atmosphere. Over the last ten years, the oceans took up at least one third of the CO₂ emitted from fossil fuel burning and tropical deforestation. The Southern Ocean is considered to significantly influence the earth's climate system. The role of biochemical cycles is hereby very important, via the biological pump. The incorporation of CO₂ in phytoplankton can lead to undersaturation of CO₂ in the seawater, which may result in an uptake of CO₂ from the atmosphere.

Productivity in the Southern Ocean has a high variability. Phytoplankton blooms occur only in restricted areas. Large parts of the Southern Ocean are barren of phytoplankton, in spite of the fact that concentrations of the major nutrient are high enough to warrant a high level of primary production. This "Antarctic Paradox" is the consequence of a combination of biological, chemical and physical factors that act to control phytoplankton abundance in the Southern Ocean. *Biomass build-up* may be prevented through a tight coupling between microzooplankton and the flagellates that constitute the phytoplankton community. The grazers have equally high growth rates as their prey, and can therefore respond rapidly to any potential increase in phytoplankton biomass. Phytoplankton *growth rates* may be controlled by resource availability. Iron is an essential nutrient for phytoplankton growth, but it is found in very low concentrations in large areas of the Southern Ocean. Iron is required in many metabolic processes in the cell, and most important, in photosynthesis. Iron limitation may act simultaneously with light limitation to control algal growth. The Antarctic Ocean is governed by the most strongest winds in the world, which induce wind mixed layers often in excess of 100m. Phytoplankton frequently experience light conditions that are too low to support algal growth.

The basic process of phytoplankton growth is photosynthesis. Phytoplankton cells carry photosystems that convert light into chemical energy. The photosynthetic apparatus requires iron for synthesis of several structural components. Iron limitation is known to result in a decrease in photosynthetic capacity: in the cell, the conversion of light into energy is the first process to suffer from iron deficiency. Iron limitation and light limitation may act synergistically to control growth. Under low light conditions, the iron requirement of phytoplankton increases, because the cells have to expand their photosystems to capture enough light to sustain growth. Iron-limited cells may then become severely energy-limited.

Iron is required in various other biochemical pathways in the cell. Iron acts as a catalyst in many reduction/oxidation processes that are involved in the biosynthesis of cell components. In addition, many of these processes require energy and reductant that is supplied by photosynthesis and respiratory processes. In both processes, again, iron is required. The biochemical pathways of the cell are highly interdependent, and it is therefore very difficult to get insight in the mechanisms that control the various processes. This thesis focused on effects of iron limitation on photosynthesis. Effects of iron limitation on cell biochemistry have been considered mainly as a function of light availability. Laboratory experiments have been performed to study the mechanisms of iron limitation under controlled conditions. Field studies have been carried out to study the physiological status of natural phytoplankton communities, and to confirm whether or not the endemic community in the Southern Ocean was iron-limited.

Pyramimonas sp., a common Antarctic flagellate species, was cultured under high and low iron and light conditions, to study effects of iron limitation on photosynthesis (chapter 6). Carbon incorporation was measured to establish Photosynthesis-Irradiance relationships, which provide information on the efficiency of photosynthesis. It was found that iron limitation resulted in a reduction in photosynthetic efficiency, under both high light as well as low light conditions. These experiments confirmed earlier findings by other investigators, who by means of fluorescence observed analysis that iron limitation resulted in a decrease in efficiency of electron transfer within the photosystems. This led to an overall decline in the quantum yield of photosynthesis. It was surprising to find that the effects of iron limitation were not reinforced under low light conditions: the photosynthetic efficiency measured for *Pyramimonas*, was no more suppressed under low light than under high light conditions.

The effects of iron limitation on the light harvesting and photoprotective capacity of the cell appear less critical. For two Antarctic flagellates, *Pyramimonas* sp. (the same species as used for the photosynthesis measurements) and *Phaeocystis* sp., it was found that iron limitation resulted in a decline in cellular pigment content as determined by HPLC (chapter 5 & 6). Notably, iron limitation resulted in a shift in carotenoid composition. The general decline in pigment composition was, however, largely compensated for by a reduction in cell size and cellular carbon. By recording *in vivo* absorption spectra, it was found that the light harvesting function of the alga *Pyramimonas*, was not affected by iron limitation when expressed per unit carbon, not even under low light conditions (chapter 6). Similarly, when exposed to high light intensities, concentrations of photoprotecting pigments were not affected by iron limitation. The laboratory studies thus revealed that iron exerts its effect on photosynthesis mainly on light utilisation efficiency, rather than on the light harvesting capacity of the cell.

Experiments carried out in 1992 and 1995, confirmed the hypothesis that, in the Southern Ocean, iron governs phytoplankton growth via its control on

photosynthesis. Moreover, iron-enrichments performed in 1995, confirmed the laboratory findings that iron limitation exerted its effect on photosynthesis mainly through its control on quantum efficiency rather than on pigment synthesis (chapter 7). Iron addition resulted in a decrease in cellular fluorescence as recorded by flow cytometry, which indicated an increase in the efficiency of electron transfer. Little effect was observed on pigment synthesis by the plankton communities.

Light conditions appear to determine the way in which iron limitation is reflected in the biochemical composition of the cell. Under iron limitation, carbon and nitrogen assimilation have to compete for a limited supply of reductant. Under low light conditions, nitrogen assimilation competes stronger for electrons than carbon fixation. Under high light conditions, a relatively large proportion of electrons flows into carbon fixation. This may induce N deficiency, as observed in experiments with the Antarctic flagellate *Phaeocystis* sp. (chapter 4). When the alga was cultured under high light and iron-limited conditions, the cellular concentrations of DMSP increased. Because DMSP might replace N-containing organic solutes under nitrogen deficiency, the increase in DMSP concentrations was interpreted as an indication of a reduced ability to assimilate nitrogen.

In the field, growth of iron-limited phytoplankton is apparently controlled by a reduced rate of carbon fixation (chapter 2). Iron enrichment of natural plankton communities did not result in significant changes in the major biochemical pools (proteins, polysaccharides, lipids and low-molecular-weight metabolites) of the cells. Rather, an overall enhancement of several rate parameters that could be linked to growth (chl.*a*-synthesis and nutrient consumption) indicated that the endemic plankton community had been iron-limited.

Whereas it was observed that iron resulted in an overall decrease in metabolic rates, phosphate metabolism of the plankton communities was apparently not affected. The iron-enrichment experiments revealed a relative increase in nitrate vs. phosphate consumption, as measured by nutrient uptake in the incubations (chapter 2 & 3). The differential control by iron on N and P metabolism was also reflected in the nutrient inventories of the ambient seawater in areas of dense blooms of *Fragilariopsis kerguelensis*. (chapter 3). These observations not only underlined the role iron can play in balancing biochemical pathways of the cell, they also show that iron can significantly influence the nutrient signatures of ambient watermasses.

Iron and light control phytoplankton growth in the Southern Ocean. In this thesis it is described how natural plankton populations respond to iron addition by an increase in photosynthetic capacity. The incubation experiments using natural phytoplankton communities also emphasized the impact light availability may have on phytoplankton growth; biomass developed also in the unamended incubation bottles, which could well be attributed to enhanced

light levels. In the Southern Ocean, the availability of the resources light and iron largely controls the spatial variability in phytoplankton abundance. Phytoplankton biomass can only develop in those areas where the supply of iron and the continuity of a stable light climate is warranted. During both expeditions to the Southern Ocean, those conditions were met at frontal zones (chapter 2 & 8). Given the simultaneous absence of any phytoplankton development at the marginal ice zone, these observations underline the importance of frontal systems for phytoplankton productivity in the Southern Ocean.