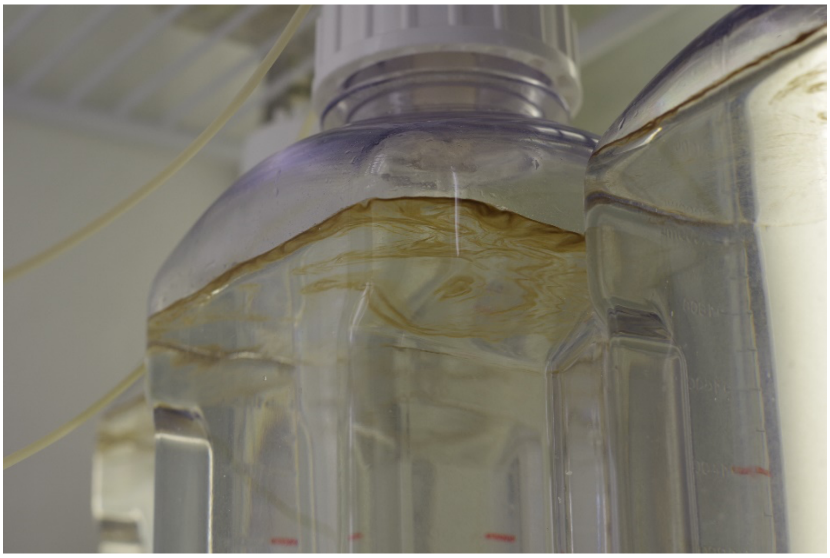
Physiological and elemental changes of *Trichodesmium* in response to growth limitation by phosphorus, iron and zinc



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Summary

Trichodesmium spp. is a colonial, diazotrophic (N_2 fixing) cyanobacterium found in the oligotrophic (sub-)tropical ocean. It contributes an estimated 50% of the total N_2 fixed in the ocean. In regions where *Trichodesmium* is abundant, concentrations of dissolved inorganic phosphorus (DIP) can be depleted, potentially to growth-limiting levels. To cope with low DIP concentrations, *Trichodesmium* are able to utilize part of the more abundant dissolved organic P pool (DOP; e.g., phosphoesters and phosphonate). To obtain P from the DOP pool, *Trichodesmium* requires the utilization of enzymes such as alkaline phosphatase (AP), which hydrolyses phosphoesters, and C-P lyase, which is responsible for the catabolism of phosphonate. Both AP and C-P lyase are metalloenzymes, specifically, (i) the AP enzyme PhoA requires zinc (Zn) and magnesium (Mg), PhoD/X requires calcium (Ca) and iron (Fe); and (ii) C-P lyases contain Zn and Fe. As the concentrations of these metals in the open ocean can often be extremely low and their physicochemical speciation further constrains their bioavailability, the potentially enhanced trace element requirements for P acquisition enzymes under stronger P limitation has the potential to exert control on the growth of *Trichodesmium* and thereby impact global nitrogen and carbon cycles. In this thesis, I applied a continuous culture technique under trace-metal-controlled conditions to vary the supply of DIP, DOP, Fe and Zn to test the impact of the relative availability of P sources, Fe, and Zn availability on the growth and physiological changes in *Trichodesmium*. First, to explore effects of different P sources on the growth of

Trichodesmium, *Trichodesmium* was grown with either DIP or DOP (methylphosphonic acid, MPA). This study (Chapter 2) revealed 3.5-fold elevated Zn requirements of *Trichodesmium* when MPA was used as the sole source of P in comparison to growth on DIP, which I hypothesize was due to enhanced Zn requirements for P scavenging enzymes. This observation suggested an important level of interaction between the cycles of P and Zn in the ocean. Next, *Trichodesmium* were grown from a gradient of Fe depleted to repleted conditions, with P again supplied as either DIP or DOP (MPA). To track the physiological response of *Trichodesmium* to Fe limitation, changes in the concentration of the particulate targeted metabolites were also examined. This study (Chapter 3) found a shift from P limitation, or P-Fe co-limitation, into stronger Fe limitation in the Fe depleted DIP treatment and a shift from strong P limitation through to Fe-P co-limitation in the Fe depleted DOP treatment. Reduced Fe supply resulted in increased intracellular Zn:C, Mn:C, Cu:C and Mo:C ratios and a decreased Fe:C ratio in the Fe depleted DIP treatment. Conversely, reduced Fe supply resulted in an increased intracellular Zn:C ratio and decreased Fe:C, P:C and N:C ratios in the Fe depleted DOP treatment. No significant changes were observed in the carbon-normalized abundance of targeted metabolites produced by *Trichodesmium*, whether in the Fe depleted, Fe recovery condition or transition phase from Fe depleted to Fe recovery condition. These findings provided for the first time the elemental stoichiometry of *Trichodesmium* grown under Fe limitation and Fe-P co-limitation conditions and revealed the response of *Trichodesmium* to nutrient limitation from the perspective of metabolite changes. The final study (Chapter 4) explored the response of *Trichodesmium* to Zn limitation. This study revealed ~10-fold elevated nickel (Ni) requirement of *Trichodesmium* under Zn limitation, regardless of whether the supplied source of P was DIP or DOP. This finding provided for the first time (i) a novel perspective on the relatively high Ni demand for *Trichodesmium*, and (ii) the elemental stoichiometry of *Trichodesmium* grown under Zn depleted conditions. Together, the research presented in this thesis demonstrates that *Trichodesmium* can significantly change its elemental stoichiometry in response to different elemental limitation conditions. Ultimately, these data will provide a useful resource for ocean biogeochemical models that may in the future resolve P, Fe and Zn.