Photosynthetic and Atmospheric Evolution

Questions re Behrenfeld's paper

1. H. Griffiths

To what extent is phenotypic plasticity of clonal populations in the lab confounded in the field by contrasting molecular ecotypes that result from genotypic variation - thus the 'Live Fast Die Young' or 'Slow but Sure' populations would coexist and vary with resource limitation in the field, rather than the need for phenotypic plasticity seen in the lab?

Response by M. Behrenfeld: Field populations of mixed genotypes have, at the population level, a much greater plasticity for resource optimization over the time scale of environmental change than that of a clonal lab population exposed to the same environmental perturbation. My anticipation, therefore, is that the degree of population optimization for a given integrated growth condition with be significantly greater in the natural population than in the monoculture.

2. Peter Nixon

Regarding your suggestion about the role of PTOX's in electron flow from Photosystem II, as far as I am aware they have a di-iron centre and in general occur at low abundance, although they could still have a role in that pathway.

Response by M. Behrenfeld: Yes. We refer to these terminal oxidases in the short water-PSII-water pathways as MOXs. While they do require a di-iron center, the combined PSII-MOX pathway is still an ‘iron-cheap’ way to balance ATP supply with demand compared to the PSI cyclic option adopted in iron-replete cells, which requires iron rich $b_6 f$ and PSI concentrations beyond that necessary for linear photosynthetic electron transport. With respect to the significance of the PSII-MOX pathway, I believe additional work is still needed for iron limiting conditions, particularly studies employing natural phytoplankton strains from low iron environments. If my proposed importance of these paths in iron limited cells is wrong, then we are still left with the question of why phytoplankton over express PSII under iron limiting condition (i.e., high PSII:PSI ratios) when these additional PSII’s represent a significant sink for iron.

4. William Martin

How far down in the photic zone do these pictures from space reflect what is going on in the water column?

Response by M. Behrenfeld: The short answer is approximately one optical depth for the wavebands being used to derive a particular product. To expand on this, an ‘optical depth’ is approximately the depth at which a particular waveband is attenuated to 10% of its surface value. Thus, the signal depth is dependent on the clarity of the water, which generally covaries with the concentration of phytoplankton. In very clear waters, the signal in the blue-green spectral region can emanate from 10’s of meters, while in turbid water it is much shallower. For chlorophyll fluorescence, the signal depth is approximately 2 meters everywhere. It should also be noted that the signal is double exponentially weighted, as light is attenuated in the downward direction and then attenuated again in the upward direction before it leave the ocean surface. This being said, one should also recognize that, irrespective of the depth with which the signal emanates, the derived satellite product should be representative of the entire mixed layer. Thus, even if your signal is from only a few meters, it could be representative of a water column more than 100 meters deep if that layer is truly mixed.

3. PJL Williams

Light variations can occur in natural aquatic systems on short time scales: what mechanism exists for phytoplankton to cope with this? What about clouds and turbulence in the water?

Response by M. Behrenfeld: This is always an interesting aspect of photoacclimation. Generally, I think about photosynthesis in the surface mixed layer as a challenge to achieve light saturation early in the photoperiod and then maintain a relatively low, but constant flow of electrons for the duration of the day and to do this in a light climate that is changing constantly at all time scales. The strategy that I think phytoplankton employ is to regulate pigment concentrations on long time scales (days), with the objective of achieving light saturation early irrespective of where they might be within the mixed layer when the photoperiod begins. The problem with this strategy, of course, is that it increases the risk of photodamage. But if we look at evolved photoacclimation mechanisms, we see that the true diversity exists in ways to deal with too much light, not too little. At the extremely short time scales, the PQ pool can act as a sort of 'capacitor'. At somewhat longer times scales, nonphotochemical quenching can track changes in light due factors such as passing clouds. Even longer, phytoplankton can use reversible down-regulation of PSII (i.e., what we often refer to as 'photoinhibition') to follow change in sunlight from the daily solar cycle, and so on.

5. Tony Walsby

We carried out detailed studies in a much smaller system in the English Lake District on two plankton species, one green containing phycocyanin and one red containing in addition phycoerythrin. In winter the lake tends to be mixed to the bottom and the red species is limited on four days whereas the green is limited for 31 days in winter. The green organism has an intrinsically higher growth rate and during summer outgrows the red which has to expend a lot of energy making these extra pigments.

Response by M. Behrenfeld: This is a very interesting case. Although I don't have a complete explanation for your observations, one factor that may be important is basal metabolic rate. For example, in culture, one can take a diatom strain and put it in the dark for a long period of time and then give it light again and it will bloom like nothing ever happened. Do that to a green, and in a few days you can see a strong expression of programmed cell death and a population crash that takes a long time to recover from after returning them to the light. This makes me wonder, therefore, whether the red species you're looking at has a similar advantage over the green during the winter that allows it to deal better with the low light, deep mixing period. As for the importance of energetic costs in the red strain for making extra pigments and the relationship between this cost and the green's success in the summer, I'm not certain. It would be interesting to evaluate exactly how ‘costly’ those pigments are relative to the total cell’s energy budget.

6. John Raven

Intrinsically there's a lot more resource cost for making more light harvesting pigment in terms of photons than there is nitrogen cost making more nitrogen assimilation proteins. That is going to cause an asymmetry between light limitation and nitrogen limitation where there isn't this tremendous nitrogen cost of making more nitrogen assimilating machinery relative to the rest of the nitrogen of the cell, whereas there is a large energy cost of making more energy harvesting machinery. This could explain why the PI curve falls off, they simply can't make enough chlorophyll.

Response by M. Behrenfeld: It is not clear to me yet how this difference in cost between nitrogen assimilation proteins and light harvesting complexes is going to directly influence the PI curve (i.e., carbon fixation – irradiance relationship), but it certainly is important when considering the transition between nitrogen limited growth and light limited growth with respect to the shape of the light-chlorophyll curve and corresponding changes in growth rate. In our manuscript, we show a ‘typical’ photoacclimation – growth relationship for *Dunaliella* under conditions of replete nutrients (F/2). The question thus arises, how does this relationship change when nitrogen levels are reduced in the medium? For the two end points, we know that, at extremely low light levels, the nitrogen concentration is irrelevant and the cellular chlorophyll concentration will equal that of the F/2 medium (i.e., the chlorophyll-irradiance curve will have the same intercept at light = 0). At very high light, photon supply is irrelevant and the chlorophyll concentration will be dictated by the nitrogen available and can be calculated using the expression given in our manuscript in Section 8. The interesting question is what happens in the middle? Specifically, as light begins to decrease from supersaturating to light limiting, nitrogen-demanding light harvesting components must be increased. This will have a severe impact on nitrogen available for cell division, causing the light-growth rate relationship to show a stronger decrease at higher light levels than observed under nutrient replete conditions.