Integrative plant responses

How seagrasses adjust to light

Seagrasses build highly productive coastal habitats all over the world, with the exception of Antarctica. Seagrass meadows are often areas of high biodiversity and operate as nursery and feeding grounds for a large array of marine species. They can also work as green filters by absorbing excess nutrients from the environment, which allows them to maintain good water quality as well as trap and stabilise sediments. In the last decade, it has become generally accepted that seagrasses also play an important role as blue carbon sinks, storing into the sediment significant amounts of organic carbon.

Like all photosynthetic organisms, seagrasses need light to survive. Light affects both the growth and distribution of seagrass meadows and is the main factor that limits the depth at which seagrass meadows can survive. However, light in excess can also limit plant growth due to photo-inhibition—a decline in the photosynthetic rates associated with the inhibition of photosynthesis by light. Hence, light triggers a large number of plant responses to optimise growth and minimise the adverse effects of light at different levels of plant organisation, from the biochemical composition of the pigment-protein antenna complexes to the canopy and whole-plant morphological adjustments.

All these responses need to be integrated in a common plant response. Thus, understanding how the different morphological and functional plant traits are coupled in a distinctive response is a central challenge in functional plant ecology. Large seagrasses can modify the light environment of their leaves within the canopy, providing more stable light fields that are less dependent on external variation. This particular characteristic of large species may require less leaf physiological adjustments and instead is more dependent on the structural changes of the canopy.

Dr Susana Enríquez, at the National Autonomous University of Mexico, studies this complex response of seagrasses to light, focusing on the species Thalassia testudinum (T. testudinum), a large seagrass and habitat builder distributed all over the Gulf of Mexico and the Caribbean Sea.

A MATTER OF LIGHT AND DEPTH

In a 2002 paper, Dr Enríquez and colleagues first described how light attenuation affects the seagrass canopy. Seagrass leaves are arranged in shoots, with older leaves covering the younger ones. Hence, the young leaves tend to be exposed to lower light conditions. Since cell division occurs at the midrib, found at the base of the leaf, the leaves are also younger at the basal portions and grow upwards from the sediment towards the top of the meadow canopy. As the leaves elongate, the younger basal portions occupy a higher position in the canopy and must respond to a progressively more intense and variable light environment.

Dr Enríquez’s team characterised this variability in detail in a dense coastal meadow, as well as the strong light gradients formed within the thin (~20 cm) seagrass canopy. The researchers found that light can be attenuated by 81% in the first 5 cm of the seagrass canopy, and that intense sun-fields can also illuminate the shaded deepest layers.

This early work revealed that at shallow sites, T. testudinum is exposed to potentially damaging light intensities for most of the day. Therefore, it is important for this species to maintain low light levels within the canopy of shallow meadows. However, further along the light gradient, at deeper sites, light attenuates exponentially with depth and a progressive expression of the seagrass response to shade is required.

PHOTOSYNTHESIS LEAF PHYSIOLOGY

To characterise this response and understand the photosynthetic physiology of T. testudinum and its phenotypic plasticity in response to a variable light field, Dr Enríquez and colleagues performed an experimental analysis, published in a 2007 paper, concluding that leaf physiology is well adapted to shade but is still necessary to develop the high-light phenotype. This conclusion was based on two main physiological features of shade-adapted leaves: (1) the estimated quantum photosynthetic efficiency defined by the number of oxygen molecules produced per photon of light absorbed, is close to the theoretical minimum of 8 quanta (i.e., between 8 and 14), and (2) the capacity to increase the maximum photosynthetic rate under high light is limited. In addition, the irradiance at which photosynthesis rates saturate, Ek, is consistently low, another characteristic not appropriate for leaves exposed to high light levels, as low Ek represents the irradiance above which the excess of light absorbed induces significant pressure on the photosynthetic membranes and potentially photodamage and photosynthesis photo-inhibition.

Nevertheless, the leaves were very efficient in dissipating heat as the excess of solar energy absorbed. This was discovered in a 2015 paper, where Dr Enríquez’s team described the capacity of seagrass canopy photosynthesis to protect the leaves and functional photosynthetic apparatus from photodamage similar to their terrestrial plant congeners, but that it is expressed differentially along the leaf. This was the first description of a high-light phenotype. This conclusion was based on two main physiological features of shade-adapted leaves: (1) the estimated quantum photosynthetic efficiency defined by the number of oxygen molecules produced per photon of light absorbed, is close to the theoretical minimum of 8 quanta (i.e., between 8 and 14), and (2) the capacity to increase the maximum photosynthetic rate under high light is limited. In addition, the irradiance at which photosynthesis rates saturate, Ek, is consistently low, another characteristic not appropriate for leaves exposed to high light levels, as low Ek represents the irradiance above which the excess of light absorbed induces significant pressure on the photosynthetic membranes and potentially photodamage and photosynthesis photo-inhibition.

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The understanding of seagrass response to changes in light availability with depth can enhance our ability for assessing the impacts of environmental changes on seagrass habitats.

of deep light gradients within the canopy provides shade for the leaves. The study of Dr. Enríquez offers a mechanism and a useful hypothesis in support of the ability of a clonal plant to respond to an integrated system in order to provide optimal light conditions for the leaves and optimise plant productivity under a variable light environment.

Quantitative models are not so common in seagrass ecology, but they are fundamental for enhancing the predictive capacity of ecology. The particular interest of the models documented by Dr. Enríquez is that they are based on a physical mechanism/hypothesis that can be tested, and allow the biological processes to be upscaled to the landscape level in order to better understand the spatial and temporal variability of seagrass abundance. Furthermore, the interpretation that light has a key role in the induction of canopy changes also underlines a possible mechanism behind important trends in plant ecology such as the self-thinning rule.

PIGMENT SELF-SHADING AND THE PLANT SELF-THINNING RESPONSE

Pigments within leaves and plant canopies absorb light for the purpose of photosynthesis and therefore, pigment self-shading can limit the photosynthetic activity, when light reaching the pigments is largely reduced due to its absorption by other pigments. Accordingly, pigment self-shading determines the net photosynthetic activity of complex multicellular structures such as leaves and canopies. The plant self-thinning response, known also as Yoda law, that could be recognised in the simultaneous opposite trends between shoot density and shoot size, has been so far only described for terrestrial plant communities but not yet for aquatic ecosystems. The fact that the changes predicted by the Yoda law were only observed on the seagrass platform constructed by the seagrass at the coastline, suggests that this self-thinning seagrass response is only expressed when light is not limiting plant growth. According to the researchers, this result is of high relevance as it offers an explanation for the physical mechanism behind this universal trend, supporting a key role of light in the control of this response. Hence, seagrass meadows would respond as predicted by this universal law under no limiting light conditions, but as light limitation increases with depth, the maximum for seagrass abundance will be reduced. This finding highlights the critical role that light plays in the determination of the maximum biomass that a plant community can pile up, underlining the fundamental contribution of one of the most important constraints of the photosynthetic metabolism, pigment self-shading, to the construction of plant communities. Accordingly, pigment self-shading and the light gradients formed within canopies in relation to the external light environment (i.e., air or water column) may determine the maximum photosynthetic biomass that can be piled up in a particular ecosystem in order to maintain sufficient photosynthetic activity at the lowest layers. The study of Dr. Enríquez affords an interesting discussion, as the researchers conclude that this physical constraint of the photosynthetic metabolism is universal and affects all photosynthetic structures, from cells to tissues and canopies.

FUTURE IMPLICATIONS: UNDERSTANDING HABITAT LOSS

Over the last decades, coastal environments have experienced significant environmental deterioration, particularly in the areas more affected by anthropogenic transformations. This has strongly affected seagrass meadows, which are, apparently, declining worldwide. In tropical areas, however, seagrasses growth is often limited by nutrients and this condition is reverted when anthropogenic pressure results in considerable nutrient enrichments, leading to large increases in seagrass abundance. These habitat changes can be detected before seagrass abundance declines. Seagrass meadows would respond true signs of ecosystem deterioration. An important open question is how changes in seagrass canopy, and particularly LAI, as a function of depth and habitat nutrient condition, can enhance our ability for assessing the impact of environmental changes on seagrass habitats and species diversity. Accurate predictions of how the overall mass of seagrasses and their LAI change in response to depth and light enables the comparison of how habitat condition affects stable and more objective reference at the climax of seagrass colonisation. In this sense, remote sensing analysis offers excellent tools to evaluate the status of seagrass habitats from the knowledge of seagrass LAI variation with depth and due to changes in nutrient availability. This information can be used to better understand critical processes that are occurring in seagrass meadows and other associated ecosystems such as coral reefs, and can also help the development of better seagrass bed restoration projects in the future.