Biology | Susana Enríquez

Integrative plant responses

How seagrasses adjust to light

The shallow coastal waters that house tropical seagrass meadows are often highly illuminated. In the Caribbean, the main habitat builder is the species Thalassia testudinum, characterised by a leaf physiology adapted to shade. Dense canopies allow the seagrass to survive in such environments, but depth colonisation requires canopy and underground mass adjustments. These integrative plant responses are essential to adjusting to light gradients. Dr Susana Enríquez, at the National Autonomous University of Mexico, studies these responses, which could inform about the role of light in the formation of plant communities and help in the development of better programmes for seagrass restoration in the future.

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 photoinhibition – a decline in the photosynthetic rates associated with the accumulation of photodamage – but also due to the increasing costs of maintenance of photosynthetic activity. 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 seagrass 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 meristem, 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 80% in the first 5 cm of the seagrass canopy, and that intense sun-flecks 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.

The researchers have collected samples of *T. testudinum* to study their leaf physiology and morphological variability along a depth gradient (Mexican Caribbean, 2004).

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 very inefficient to develop the high-light phenotype. This conclusion was based on two key 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 photoinhibition.

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 photoprotection of these leaves and found not only an efficient mechanism, similar to their terrestrial plant congeners, but that it is expressed differentially along the leaf, from the more pigmented basal-low light acclimated segments to the light green-yellow apical and high-light acclimated portions of the leaf.

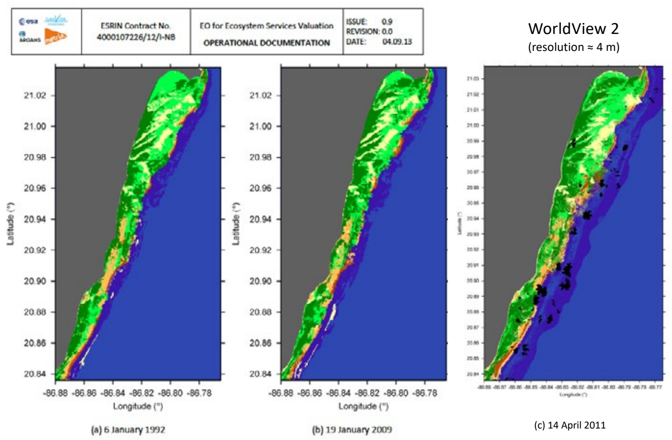
Taking into consideration all these characteristics, it was necessary for Dr Enríquez to explain how *T. testudinum* had achieved such an ecological and evolutionary success in the Caribbean, and be able to modulate the costs of maintenance of its photosynthetic activity in these shallow and highly illuminated reef environments.

MORPHOLOGICAL CHANGES

Canopy leaf area varies largely in response to changes in light. The Leaf Area Index (LAI) is the parameter that allows measuring the total canopy leaf area per unit ground surface area in plant communities. This parameter is key for predicting plant productivity and the magnitude of light intensity attenuation within the canopy, known as leaf self-shading. The group of Dr Enríquez demonstrated for the first time in their 2019 paper that LAI is also a determinant of seagrass production and developed a model to quantify this variation with depth. According to the model, LAI and leaf production variation in seagrasses is governed by changes in shoot size and density. Based on this, the model quantifies the differential effect of changes in shoot density and shoot size on LAI and seagrass productivity due to their different pattern of variation with depth. Shoot density declines exponentially with depth, but there is an initial increase in shoot size in shallower waters until a maximum value; beyond this maximum, shoot size also declines. 'The consequence of this variation', according to Dr Enríquez, 'is that LAI reaches maximum values on a shallow coastal platform formed by the accumulation of belowground seagrass biomass and sediment, which not only presents the largest productivity but is also the major contributor to below-ground carbon storage (blue carbon) of this seagrass'. This platform, however, is not always present in the coastline of reef lagoons, and usually represents a small fraction of the total area potentially colonisable by the seagrass.

Dr Enríquez has characterised the photosynthetic physiology of T. testudinum and its phenotypic plasticity in response to a variable light field.

In their 2005 publication, Dr Enríquez and her collaborators described for the first time the canopy model, which recognises form-function associations or 'cause-effect' relationships between changes in canopy form (i.e., changes in shoot density and shoot size) and their physical consequences for seagrass function (i.e., leaf photosynthesis and meadow production). The fact that the seagrass responds along a depth gradient as predicted by the model supports the key contribution of a common 'physical driver', such as light, to induce an integrative plant response for the control of light penetration within the canopy. For example, in the deeper sites investigated, the decrease in the overall mass of *T. testudinum* was mainly due to large reductions in shoot density, confirming its primary role in the control of canopy light attenuation and leaf self-shading. In shallow areas, by contrast, the formation



Remote sensing analysis offers excellent tools to evaluate the status of seagrass habitats.

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 as 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 ecosystem 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, seagrass 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, and seagrass meadows could present true signs of ecosystem deterioration. An improved awareness of the changes in seagrass canopy, and particularly LAI, as a function of depth and habitat nutrient condition, can enhance our ability for assessing the impacts 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 light and depth enables the comparison of habitat's condition against a 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.

Behind the Research

Dr Susana Enríquez

E: susana.enriquezdominguez@gmail.com **E:** enriquez@cmarl.unam.mx

Research Objectives

Dr Enríquez studies plant responses to environmental cues; in particular, she analyses the response of the tropical seagrass *Thalassia testudinum* to light gradients.

Detail

Susana Enríquez
Unidad Académica de Sistemas Arrecifales (Puerto Morelos) ICML-UNAM, Apdo. 13,
77500 Cancun, Quintana Roo, Mexico

Bio

Born in Spain, Susana Enríquez studied Biology at the Autonomous University of Madrid, developed her PhD project in plant allometry at the Mediterranean coast, and her UE postdoctoral project in Denmark with a Marie Curie Fellowship. In 1998, she was hired by the National Autonomous University of Mexico (UNAM), where she has developed her independent scientific career as a coral reef photobiologist.

Funding

- The PAPIIT program of the Universidad Nacional Autónoma de México (project: IN206710)
- The Mexican CONACYT (Conv-CB-2009; project 129880)
- The Foreign Affairs Mexican Secretary (SRE, Mexico), for financing the one-year stay of the Philippine student Napo Cayabyab
- The Program of Academic Mobility of the Iberoamerican University Association (Salamanca, Spain), for financing the stay of the Spanish student Irene Olivé
- The annual Institutional funding by the Institute of Marine Sciences and Limnology (ICML) at the UNAM

Collaborators

- Dr Enríquez would like to acknowledge Dr John D. Hedley for his collaboration in upscaling the biological processes to large-scale quantitative models, extremely useful to interpret with less subjective bias remote-sensing images. Her gratitude has also to be extended to Dr Roberto Iglesias-Prieto, who opened for her the opportunity to work in the most fascinating ecosystem for a marine biologist, the coral reef.

Instituto de Ciencias del Mar y Limnología

Universidad Nacional Autónoma de México

References

- Enríquez, S., Olivé, I., Cayabyab, N., & Hedley, J. (2019). Structural complexity governs seagrass acclimatization to depth with relevant consequences for meadow production, macrophyte diversity and habitat carbon storage capacity. *Scientific Reports*, 9, 14657. Available at: https://doi.org/10.1038/s41598-019-51248-z
- Enríquez, S., & Pantoja-Reyes, N. (2005). Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia*, 145, 235-243. Available at: https://doi.org/10.1007/s00442-005-0111-7
- Enríquez, S., Merino, M., & Iglesias-Prieto, R. (2002). Variations in the photosynthetic performance along the leaves of the tropical seagrass *Thalassia testudinum*. *Marine Biology*, 140, 891-900. Available at: https://doi.org/10.1007/s00227-001-0760-y
- Cayabyab, N., & Enríquez, S. (2007). Leaf photoacclimatory responses of the tropical seagrass Thalassia testudinum under mesocosm conditions: a mechanistic scaling-up study. *New Phytologist*, 176, 108-123. Available at: https://doi.org/10.1111/j.1469-8137.2007.02147.x
- Schubert, N., Colombo-Pallota, M., & Enríquez, S. (2015). Leaf and canopy scale characterization of the photoprotective response to high-light stress of the seagrass *Thalassia testudinum*. *Limnology and Oceanography*, 60, 286-302. Available at: https://doi.org/10.1002/lno.10024
- Belgrano, A., Allen, A. P., Enquist, B. J. & Gillooly, J. F. (2002). Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecology Letters* 5, 611-613

Personal Response

How can your research be utilised for remote sense applications?

"Satellite remote sensing offers an excellent opportunity, as a complementary tool to *in-situ* field surveys, to understand the large-scale patterns of the LAI-depth model and comparing habitat changes across a certain period of time. The spatial scale of a remote sensing analysis can easily cover the area size required, in km^2, to elucidate specific environmental problems or to obtain a true regional picture. This is not so easy to derive from isolated field surveys. This approach can also quantify the area with the largest contribution to store blue carbon and identify areas of particular interest for management that may require *in-situ* surveys."