Review Article

Light Utilization Strategies in Photosynthetic Microbial Mats May Give Hints to Improve Cyanobacterial Biomass Production

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Abstract
Understanding the adaptations and the strategies adopted by microorganisms inhabiting environmental ecosystems may provide good guidance for many applications that involve microorganisms. These applications can be useful in different fields such as medicine and pharmaceutical products, industry, biofuels and agriculture. Cyanobacteria in photosynthetic microbial mats have developed fascinating strategies to utilize light at different light quantities and qualities. In this review, these strategies and their possible applications are discussed, especially that more attention has been recently given to algal and cyanobacterial biomass production for several important products. Additionally, an algal biofilm strategy is suggested as a potential approach for biomass production, which might be easier to control with respect to growth conditions and harvesting method than the traditional open pond approach.

INTRODUCTION
Microbial mats are stratified complex microbial ecosystems that inhabit wide range of environments [1-5]. They operate as almost closed systems with persistent oxidation-reduction gradients and restricted mass flow [6]. A photosynthetic microbial mat performs in a very similar way as a complex food web, because different members in the community depend on, and support each other. This is facilitated by remarkable strategies that they have to harvest light energy efficiently. These strategies have served them well as they were amongst the first complete ecosystem on the earth. Photosynthetic mats are also thought to be responsible for the emergence of oxygen in earth’s surface layers that allowed the evolution of oxygen-respiring life forms.

Typically, the thickness of a microbial mat does not exceed few centimeters and within this confined space all primary productivity, aerobic and anaerobic mineralization processes take place [7,8]. Steep gradients in physico-chemical microenvironments and the pronounced stratification of the microbial community composition and their associated activities in photosynthetic mats are formed because light enters the ecosystem from the top and gradually attenuates and because of mass transfer resistance (Figure 1). Obviously, energy-taxis provide cells with a versatile sensory system and enable them to navigate to niches where energy generation is optimized. Therefore, energy-taxises is fine-tuned to the environment where a cell finds itself in and allows efficient adaptation to changing conditions that affect cellular energy levels.

MICROBIAL MATS DRIVEN BY LIGHT
Species occurrence and abundance in microbial mat communities are strongly influenced by the physical properties and chemical parameters of the environment in which they live. Important physical properties include light (both quantity and quality), temperature, and pressure. Key chemical parameters include oxygen availability, pH, oxidation/reduction potential, salinity, and available electron acceptors and donors, as well as the presence or absence of specific chemical species [1]. Light is the main driving force of the photosynthetic microbial mats. It shines from the upper part and its energy powers the photosynthetic microorganisms (i.e., mainly cyanobacteria), which in return supply other layers in the mat with energy [7]. Cyanobacteria convert light energy into chemical energy stored in organic materials parts of which are excreted to the mat ecosystem. Other microorganisms in the ecosystem use part of
the stored chemical energy through degradation of the organic material using suitable terminal electron acceptors available for each layer in the microbial mat. Additionally, part of the simple organic material is fermented by fermenting bacteria in the deeper layers resulting in re-mineralizing part of the nutrients, which will be reused again in the upper layer.

The quality and quantity of incident irradiance vary in response to diurnal cycle and also at different depths within microbial mats. Incident irradiance attenuates steeply inside microbial mats reaching less than 1% of that received at the mat surface already few millimeters below the surface. This behavior is likely to govern vertical species stratification as the active of motile cells migrate in response to shifting gradients of light [9]. Cyanobacteria have developed several behavioral and functional adaptations to cope with these changes in light quantity and quality. Specifically, they can migrate up and down and adjust themselves to the layer with suitable incident irradiance [10,11]. They can also adjust their absorption cross section in response to the incident irradiance [12]. Furthermore, at high incident irradiance, cyanobacteria in the upper layers produce a special pigment, called scytonemin, that act as sunscreen to protect the cells from the virulent effect of the UV spectra [13,14].

**LIGHT BEHAVIOR IN MICROBIAL MATS**

Light behavior in marine sediments and microbial mats drew the attention of the pioneers in marine microbiologists [15,16]. Using scalar irradiance microsensor, it was shown that few micrometers below the mat surface (i.e., 100 µm) incident irradiance was boosted a bit relative to that at the surface (>100%) [17-20]. This increase is due to the accumulative effect of down willing irradiance (i.e., from light source) and the backscattering of incident irradiance because of the pigmented microorganisms and sand particles. Below this layer incident irradiance is substantially filtered and attenuated due to selective absorption of certain wavelengths by the pigments and different sediment components (Figure 1). The attenuation of incident irradiance below mat surface is a common trend in cyanobacterial mats from different locations around the globe [21]. Cyanobacteria adjust their location in the euphotic zone to utilize light energy efficiently [11]. The ones in the lower layers of the euphotic zone are photosynthetically more efficient than those in the upper layer, because the latter will be affected by the high light energy, thus saturate their photosynthesis.

Recently, light utilization efficiency was compared between three different microbial mat ecosystems [22]. It was shown that the mat with thin, compact, and densely pigmented euphotic zone had the highest light utilization efficiency and the one with the spread, and loosen euphotic zone had the lowest (Figure 2). This discrepancy is mainly because in mats with loose euphotic zone, light would be unspecifically absorbed by sediment, organic material, detritus and metals [22]. On the other hand, in mats with condensed cyanobacterial layer, most of light energy would be utilized in photosynthesis efficiently. However, even in the mats with condensed cyanobacterial layer, the efficiency is still way less than the maximum theoretical efficiency (27.7% of the absorbed light; [11]. In addition to losses on the cellular level
that were described earlier [23], the unspecific light absorption by sediment and other organic and inorganic compounds wastes considerable amount of light energy. Because of that, it was assumed that the canopy ecosystem is far more efficient in utilizing light energy than microbial mats ecosystems; mainly because of limited unspecific light absorption [22].

**CAN WE LEARN FROM CYANOBACTERIA HOW TO INCREASE LIGHT UTILIZATION FOR BIOMASS PRODUCTION?**

In the recently decades, more attention has been paid to the use of algae and cyanobacteria in biomass production for several industrial uses. Because of limited petroleum reserves and the environmental consequences resulting from combustion of gases, biofuel production has emerged as a viable alternative for generating environmentally friendly energy, [24-28]. There are many research priorities that aim to increase light utilization efficiency by photosynthesis in different photosynthetic organisms. There are many advantages of using them over the traditional plant crops. Their productivity per area is high, they grow faster and using them does not negatively affect human food as using the crops does. Interestingly, they can thrive in lower quality water (e.g. the effluent of waste water treatment facilities, or saline water), and remove CO$_2$ and NOx gases that are produced by combustion (e.g. coal-fired power station emissions). Moreover, any algal species produces valuable products, such as colorants, polyunsaturated fatty acids and bioactive compounds, which can be used in food and pharmaceutical industries [24,29].

The major technical challenges regarding these systems are to (i) sustain highest photosynthesis and biomass productivity, and (ii) increase the capability of the system to expand to an industrial scale production [29]. Therefore, it is of vital importance to fully understand the limitations of light utilization efficiency, or the conditions by which the highest yield of biomass production is achieved with the lowest possible damage or energy losses from the photosynthetic system. The base of such knowledge can be gained from naturally occurring ecosystems and the adaptations that they have developed to cope with environmental conditions.

A possible approach for cyanobacterial biomass production that can be tested is a biofilm formation based technology. The thickness of the biofilm and its cell density can be adjusted to improve light utilization efficiency and subsequently enhance biomass production. Adopting the biofilm approach for biomass production may have more advantages than the suspension approach (i.e., open ponds). One of the plausible advantages has to do with harvesting. In open ponds, biomass harvesting could be done by filtration, dewatering and drying. All of these methods are time consuming and expensive. However, harvesting biomass using the biofilm approach is faster and easier because the cells are already packed.

Genetic manipulation of the cyanobacterial cells, which will be used for biofilm, toward increasing lipid production and/or leaking lipids outside the cells could be good strategy for biofuel production. However, intensive work in that direction is still required to be done to reach the suitable (i.e., environment-friendly and economically) setup. Recently, metabolic engineering has contributed to the production of different high-value products from cyanobacteria such as ethanol, isobutanol, D-lactate [30-33].

**CONCLUSION**

In conclusion, investigating the adaptations of microorganisms in their ecosystems is crucial to understand how they succeed in their environments. Furthermore, understanding the strategies adopted by photosynthetic microorganisms in their natural ecosystems may represent good guidance to increase algal biomass production for several industrial applications. For example, applying the strategy adopted by cyanobacteria in photosynthetically efficient microbial mats, by aggregating to form thin photic zone that is densely populated with cyanobacteria, on metabolically modified algae might result in promising approach that can be used in several applications. It is anticipated that dealing with thin biofilm would be easier than growing algae in open ponds, especially with respect to harvesting.

**REFERENCES**


