



Review



Colouring applications of microalgae and cyanobacteria photosynthetic pigments: Challenges for industrial and market acceptance

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ABSTRACT

Microalgae and cyanobacterial photosynthetic pigments possess immense potential for sustainable colouring applications in industries such as food, feed, cosmetics and textiles, primarily because of their vibrant colours, safety and eco-friendliness. These photosynthetic pigments align with the growing demand for eco-conscious products. However, substantial challenges persist at the industrial level, particularly in scaling up production and achieving acceptance in niche markets. This review highlights the critical roles of abiotic factors such as light quality, temperature, pH, nutrient availability and salinity in enhancing pigment production using conventional production methods. Additionally, issues related to the cost, purity and stability of the pigments must be addressed to facilitate broader acceptance. Looking forward, the focus must be on developing innovative cultivation techniques that optimise and define the abiotic conditions most favourable for maximum pigment production or even incorporate genetic engineering tools. Additionally, exploring untapped species from inhospitable environmental sources and integrating the residual biomass through biorefinery processes represent effective approaches for enhancing the sustainability of microalgae and cyanobacterial pigment production on an industrial scale. Overcoming these barriers utilising targeted research and industry collaboration as well as fostering market acceptance is essential for fully harnessing the potential of these natural pigments and driving the transition towards more sustainable industrial colouring practices.

1. Introduction

Colour plays a central role as a sensory characteristic that influences the visual appeal and acceptability of almost all products. Thus, various colouring agents are widely used in the food, feed, cosmetic, pharmaceutical, nutraceutical and textile industries. However, it is crucial to acknowledge that despite their positive attributes, the majority of these colourants are chemically synthesised, non-biodegradable and potentially harmful to human health and the environment. The extensive use of synthetic colourants has led to alarming levels of environmental pollution, with particularly detrimental effects on aquatic ecosystems (Uddin et al., 2022). In this context, there has been a growing focus on natural colouring alternatives, particularly eco-friendly and sustainable biopigments derived from microorganisms (Kaur et al., 2020).

To ensure conceptual clarity, particularly from an industrial perspective, it is essential to establish a precise classification of pigments and dyes within the broader category of colourants. Colourants impart colour to materials and can be classified based on their structure, origin, hue, application method and solubility (Guerra et al., 2018). The two primary subcategories of colourants, pigments and dyes, are differentiated by their solubility. Pigments consist of fine insoluble particles that require a binding agent to adhere to the surface, whereas dyes are soluble colourants that dissolve in their application medium and chemically bond to the substrates (Broadbent, 2001; Hefford, 2011). Thus, the application and performance of pigments and dyes are typically determined by their chemical properties and their interactions with the target material (Broadbent, 2001; Pfaff, 2022). However, in biology, the term pigment is frequently used to describe natural colourants found in cells, tissues, or body fluids (Pfaff, 2022), which may lead to terminological

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Abbreviations










CAGR	compound annual growth rate
Chl	chlorophyll
DW	dry weight
EGD	European Green Deal
M&C	microalgae and cyanobacteria
PBPs	phycobiliproteins
Scy	scytonemin
WTP	willingness to pay
WW	wet weight

inconsistencies. Given that this study focuses on the photosynthetic pigments of microalgae and cyanobacteria (M&C), the term pigments is used within the broader classification of colourants, regardless of their solubility.

Pigment-producing microorganisms are quite common in nature

Table 1

Key photosynthetic pigments of M&C: Chemical structure (Supplementary data), commercial launch year of pigments production, global market value, main production species and bioactive properties.

Pigment	Chemical Structure	Colour ^a	Commercial Launch Year	Global Market Value + CAGR ^b (Year)	Main production species (Content Range)	Bioactive Properties	References
Chls	Chl a		–	USD 164.7 million + 8.5 % (2024; 2025)	<i>Chlorella</i> sp. (4.5 % of DW)	Anti-cancer Anti-inflammatory Anti-obesity Anti-diabetic Anti-microbial Antioxidant Neuroprotective	Christaki et al., 2015 ; Fernandes et al., 2017 ; Freitas et al., 2019 ; Kang et al., 2018 ; Li et al., 2019 ; Mulders, 2014 ; Wang and Wink, 2016
	Chl b		–				
Carotenoids	β-carotene		1986	USD 561.4 million + 5.45 % (2024; 2025)	<i>Dunaliella salina</i> and <i>D. bardawi</i> (10 %–14 % of DW)	Anti-cancer Anti-inflammatory Antioxidant Neuroprotective	Borowitzka, 1999 ; Cordero et al., 2011 ; Karmakar et al., 2021 ; Kelman et al., 2009 ; Koo et al., 2012 ; McClure et al., 2018 ; Mulders, 2014 ; Nethravathy et al., 2019 ; Pagels et al., 2020 ; Patias et al., 2017 ; Yaqoob et al., 2021
	Zeaxanthin		–	USD 189.2 million + 7.4 % (2024)	<i>C. ellipsoidea</i> (0.06 % of DW)		
	Astaxanthin		1994	USD 1.1 billion + 8.5 % (2024)	<i>Haematococcus pluvialis</i> (4 % of WW; 5 % of DW)		
	Lutein		–	USD 386.6 million + 5.7 % (2023; 2024)	<i>Chlorella</i> spp. (2 % of WW)		
	Fucoxanthin		–	–	<i>Phaeodactylum tricornutum</i> (5.92 % of DW)		
PBPs	PC ^c		1977	USD 165.4 million + 8.3 % (2020; 2023)	<i>S. platensis</i> (20 % of DW)	Anti-ageing Anti-cancer Anti-inflammatory Anti-obesity Anti-diabetic Anti-microbial	Favas et al., 2022 ; Gammoudi et al., 2019 ; Mulders, 2014 ; Pagels et al., 2022 ; Pourhajibagher et al., 2019 ; Prabakaran et al., 2020 ; Qi et al., 2019 ; Rahman, 2020 ; Ulagesan et al., 2021
	PE ^c		–	USD 11.34 million + 8.2 % (2023; 2025)	<i>Porphyridium</i> sp. (15 % of DW)	Anti-neurodegenerative Antioxidant Hepatoprotective	
Scy			–	–	<i>Chroococcidiopsis</i> sp. and <i>N. commune</i> (0.1 %–0.4 % of DW)	UV-protective	Rastogi et al., 2014 ; Rastogi and Incharoensakdi, 2014 ; Rath et al., 2012 ; Vega et al., 2020

^a The colour presented is merely an illustrative depiction of the most representative colour approximation for this set of pigments, although variations may occur.

^b Estimated global market value, based on the mean between global market values, with the respective CAGR from 2023/2024/2025 to 2033/2034/2035.

^c The presented structures depict the phycobilins associated with the respective BBP.

(Dufossé et al., 2005). M&C, which are photosynthetic organisms, can be highlighted among these microorganisms, once they synthesise diverse pigments to efficiently harvest light energy (Pagels et al., 2021a). Typically, these pigments are categorised into three major classes: chlorophyll (Chl), carotenoids and phycobiliproteins (PBPs) (Pagels et al., 2021a; Assunção et al., 2022).

The attractiveness of M&C photosynthetic pigments lies in their vibrant colours and bioactive properties, making them suitable for a range of industrial applications (Table 1). Additionally, their appeal stems from their natural origins and eco-friendly characteristics (Pagels et al., 2021a). Currently, the use of M&C pigments is becoming increasingly prevalent in the food, feed and cosmetics industries (Favas et al., 2022; Sandybayeva et al., 2022; Di Salvo et al., 2023; Sun et al., 2023), with this review offering a comprehensive exploration of their applications in these fields. Furthermore, the textile industry has emerged as one of the most innovative sectors harnessing M&C pigments (Metwally et al., 2021; Kramar and Kostic, 2022), and it is also a focal point of discussion in this review. Despite being less referred in the literature, there are some reports of the application of M&C pigments for other colouring applications, at an industrial level, such as biopaints

(Prathiksha et al., 2024), printing inks (such as those produced by @LIVING INK) (Hozzein, 2022), and colour enhancer in animal feed (Pagels et al., 2021b). Some of the referred M&C pigments are also used for fluorescence purposes in medical and chemical applications (Kovaleski et al., 2022; Saini et al., 2018).

Although numerous pigment production processes are currently operating on an industrial scale (Hozzein, 2022; Sandybayeva et al., 2022; Sun et al., 2023; Di Salvo et al., 2023; Prathiksha et al., 2024), it is worth noting that the journey from laboratory cultivation to widespread industrial and commercial implementation remains lengthy. The industry continues to face multiple challenges in effectively adopting M&C pigments and requires strategic solutions to overcome technical and economic barriers.

The production of M&C pigments is highly influenced by environmental conditions, particularly abiotic factors such as (1) light intensity and quality, (2) temperature, (3) pH, (4) nutrient availability and (5) salinity (Assunção et al., 2023; Khazi et al., 2021). Optimising these parameters is essential for improving the pigment yield and ensuring cost-effective production on an industrial scale. However, large-scale adoption of M&C pigments faces several challenges, including high production costs, process inefficiencies, pigment stability issues and limited scalability (Rather et al., 2023; Sandybayeva et al., 2022). Addressing these challenges via technological advancements is crucial for making M&C pigments viable and competitive alternatives to their synthetic counterparts. Furthermore, educating consumers regarding the benefits of natural M&C pigments and leveraging green marketing strategies can drive their adoption. Aligned with industry trends, increasing consumer awareness of health and environmental issues is driving the growing acceptance and preference for naturally sourced colourants as alternatives to their synthetic equivalents (Nwoba et al., 2020).

Several factors influence consumers' increased willingness to pay (WTP) for green products (Li and Kallas, 2021; Gomes et al., 2023). Generally, there is a growing tendency among consumers to pay a premium for sustainable alternatives, particularly when trust and innovation are emphasised. This trend is in line with the increasing market acceptance of sustainable products such as M&C pigments, driven by heightened environmental awareness, regulatory advancements and corporate sustainability initiatives.

This review examines the potential of M&C photosynthetic pigments for sustainable colouring applications, focusing on industrial challenges, such as production factors, scalability, cost and stability. It further explores strategies for scaling up production, including optimisation of cultivation by controlling abiotic factors. Additionally, this study identifies and analyses the key factors influencing market acceptance and the drivers behind the adoption of these pigments by both industries and consumers.

2. Microalgae and cyanobacteria pigments

Biopigments can be sourced from various microorganisms, including microalgae, cyanobacteria, fungi and bacteria (Saini et al., 2018). Among these, M&C stand out as the simplest and most efficient photosynthetic organisms owing to their rapid response and adaptability to environmental stimuli that are unmatched by any other life forms (Pagels et al., 2020). Associated with their photosynthetic metabolism, these microorganisms possess a diverse array of chromatic compounds, ranging from Chl to carotenoids and PBPs, the latter comprising phycoerythrin (PE), phycocyanin (PC) and allophycocyanin (APC) (Hachicha et al., 2022; Sandybayeva et al., 2022), which exhibit fluorescence at specific wavelengths and display distinctive colours (Rastogi et al., 2015a,b). These pigments not only facilitate the absorption of solar energy during photosynthesis but also play crucial roles in photoprotective mechanisms. Furthermore, they exhibit a wide array of beneficial properties, including antioxidant, anti-inflammatory, anti-carcinogenic, anti-obesity, anti-angiogenic and neuroprotective

activities (Table 1) (Hachicha et al., 2022).

In this regard, the importance of natural pigments sourced from M&C cannot be overstated, particularly in the food, feed, cosmetic, pharmaceutical and nutraceutical sectors, where various industries have found numerous applications, ranging from food colourants to health products (Mourelle et al., 2017; Pagels et al., 2020).

2.1. Chlorophylls

Chls are the primary light-absorbing pigments universally found in autotrophic organisms and serve as the driving force behind the conversion of light into biological energy (Saini et al., 2018). These green, lipid-soluble pigments constitute approximately 0.5 %–1.5 % of the dry matter in M&C and play a major role in photosynthesis (Hachicha et al., 2022). Although cyanobacteria do not possess chloroplast-based systems, unlike plants or green algae, these pigments perform the essential functions of light-harvesting and charge separation (Assunção et al., 2022).

The structure of Chl comprises four pyrrole rings arranged in a tetrapyrrole ring, known as porphyrin, which is formed from protoporphyrin IX (Saini et al., 2018). Various classifications of Chl molecules exist, including Chl a, b, c and d, distinguished by differences in the side-group substituents on the tetrapyrrole ring.

All Chls have two major absorption bands, 450–475 nm for blue or blue–green and 615–675 nm for red, which result in the characteristic green colour of Chls (López-Hernández et al., 2022). This enables Chl to absorb light energy from the visible spectrum, which can be used for photosynthesis (photochemistry) or released as heat (heat dissipation) or light (fluorescence) (Sandybayeva et al., 2022).

The production of Chls by M&C, highly linked to the genus *Chlorella*, can achieve up to 4.5 % of dry weight (DW), in certain conditions (Christaki et al., 2015). This mode of production may prove more viable than that of terrestrial plants, particularly when evaluated from a commercial and economic perspective (Alam et al., 2020; Ferreira and Sant'Anna, 2017). The market value of Chls colour market is of USD 164.7 million in 2025, with a Compound Annual Growth Rate (CAGR) of 8.5 % until 2035 (Future Market Insights, 2025; Verified Market Reports, 2025).

2.2. Carotenoids

Carotenoids serve as light-harvesting pigments associated with Chl and are widely distributed among a broad range of organisms, including cyanobacteria, algae, fungi and plants. These pigments complement Chl absorption in the light-harvesting system by absorbing light at specific wavelengths within the visible spectrum that are not covered by Chl (Assunção et al., 2022; Sandybayeva et al., 2022). Furthermore, carotenoids play a crucial role in protecting photosystems from excessive light irradiation. This is achieved by quenching both the singlet and triplet states of Chl (Saini et al., 2018), neutralising reactive oxygen species produced when exposed to light, and absorbing light in the visible spectrum (Assunção et al., 2022). In addition, carotenoids contribute to the dissipation of excess energy and stabilise the structure of the photosynthetic apparatus (Sandybayeva et al., 2022).

Carotenoids absorb light in the 400–550 nm range, at which wavelength they exhibit strong absorption, giving them a yellow–orange colour (López-Hernández et al., 2022). Biologically, carotenoids belong to the class of terpenoid pigments, featuring strongly conjugated polyene chains, which are responsible for the various colours of carotenoids, such as violet, red, orange and yellow (Assunção et al., 2022). More than 600 carotenoids have been identified in nature (Pagels et al., 2021b).

These pigments have commercial value because of their antioxidant properties, brilliant colours and health-promoting properties. M&C produce various carotenoids, including β -carotene, astaxanthin, lutein, zeaxanthin, lycopene, echinenone, canthaxanthin and fucoxanthin (Saini et al., 2018; Sandybayeva et al., 2022). Currently, carotenoids

production by M&C is mainly associated with *Dunaliella* sp. and *Haematococcus pluvialis* with production yields ranging from 4 % to 15 % of DW (Nethravathy et al., 2019; Yaqoob et al., 2021).

While the commercial production of certain carotenoids remains undocumented in the literature, others, such as astaxanthin and β -carotene, have been commercially available since the 1980s (Yaqoob et al., 2021). Carotenoids market value is of USD 1.8 billion in 2024 and is expected to grow at a CAGR of 5.5 % from 2024 to 2034, proving the relevance of these pigment group, with most of the industrial-scale production being carried out by M&C cultivation companies (BCC Research, 2025; Verified Market Reports, 2025). For each specific carotenoid, astaxanthin global market value represents USD 1.1 billion in 2024, with an expected CAGR of 8.5 % over 10 years, highlighting the great industrial potential of this pigment (Global Market Insights, 2025; Verified Market Reports, 2025). Despite being available for sale since 2018, the application of fucoxanthin focuses on its nutritional value and not on its application as a colouring agent (Algatech, 2018), emphasising the absence of a real current market for this pigment.

2.3. Phycobiliproteins

PBPs are a group of colourless and water-soluble molecules responsible for light-harvesting in cyanobacteria, red algae, cryptomonads and cyanelles (Pagels et al., 2019). The wavelength absorption range of these accessory pigments is 500–650 nm, with colours ranging from blue–green to blue, orange and red (López-Hernández et al., 2022).

These proteins are complexed with specific pigments (or chromophores) known as phycobilins. In addition, the distinct colours of PBPs depend on the nature of the attached phycobilins, namely phycocyanobilin (blue), phycoerythrobilin (red), phycourobilin (orange) and phycoviolobilin (purple) (Assunção et al., 2022). All PBPs have the same monomer as the basic unit, composed of α and β subunits. Each monomer can carry one, two, or three chromophores, depending on the molecular species. Nonetheless, depending on the PBP, different phycobilin combinations may occur, leading to specific spectral and optical identities (Kovaleski et al., 2022).

In terms of their classification, PBPs can be categorised according to the number and type of chromophore-binding subunits and light absorption spectra: PC (610–625 nm), PE (490–570 nm) and APC (650–660 nm) (Favas et al., 2022); or based on the expressed colour, into only two main groups: PC and PE (Saini et al., 2018). Notably, PC is the predominant PBP found in cyanobacteria, which is why these organisms, despite being distinct photosynthetic bacteria, are commonly referred to as blue–green algae (Pagels et al., 2019).

Currently, industrial-scale production of PBPs is almost exclusively associated with the blue pigment (PC). This pigment global market value is of USD 165.4 million in 2023, with a forecasted CAGR of 8.3 % from 2023 to 2033 (Allied Market Research, 2025; Grand View Research, 2025). Although there are studies into the use of PE as a food colouring, its real industrial application is still based on its fluorescence (García et al., 2021). The global market value for PE is USD 11.34 million in 2025, and its projections infer a CAGR of 8.2 % from 2025 to 2035 (Data Horizon Research, 2025; Future Market Insights, 2025). The highest production of these pigments is obtained by *Spirulina platensis*, in the case of PC, and by *Porphyridium* sp. for PE, with yields of 20 % and 15 %, respectively (Rahman, 2020).

2.4. Other pigments: scytonemin

Scytonemin (Scy), a yellow-brown pigment found in cyanobacterial extracellular sheaths, has been identified in over 30 species of cyanobacteria that thrive in habitats exposed to intense solar radiation (Rastogi et al., 2015a,b). Its photoprotective properties enable cyanobacteria to flourish in harsh, rocky and highly radiated environments (Saini et al., 2018). This small hydrophobic alkaloid serves as both a yellow-brown pigment and a secondary metabolite and is gaining

importance in adaptation to harsh environments (Assunção et al., 2022; Saini et al., 2018).

Scy exists in two forms: (1) oxidised (yellow-brown) and (2) reduced (red) (Pathak et al., 2021). It exhibits exceptional stability, is lipid-soluble and consists of indolic and phenolic subunits that bind to an olefin carbon atom (unique among natural products) (Assunção et al., 2022). This pigment have a prominent absorption maximum in the near-ultraviolet spectrum (386 nm) that extends to the infrared region (Rastogi et al., 2015a,b). Additionally, they absorb light at wavelengths of 252, 278 and 300 nm (Assunção et al., 2022; Rastogi et al., 2015a,b).

Apart from their crucial role as UV protectors and functioning as a shield for cyanobacterial cells, certain Scy variants play a role in photoprotection within the photosynthetic apparatus and are potentially involved in energy dissipation (Saini et al., 2018; Assunção et al., 2022).

Scy production by *Nostoc commune* has yields of production that represent 0.1 % of the DW (Wright et al., 2005), but studies with *Chroococcidiopsis* sp. achieved yields of production of 0.4 % of the DW (Casero et al., 2024). According to the authors' knowledge, there is no industrial production of Scy.

3. Industrial colouring applications of microalgae and cyanobacteria pigments

In recent years, microorganisms have been extensively used owing to their biotechnological potential, especially in industrial processes. The importance of expanding our knowledge of microorganisms lies in the creation of innovative and sustainable technologies that can positively impact human health and the environment. Among microorganisms, M&C represent a diverse group with the potential to produce valuable colourants suitable for several industrial applications (Patel et al., 2019). A notable example of M&C applications involves the domain of coloration.

Colour plays an important role in influencing consumer perception, as it is often the primary characteristic noticed in a product. Furthermore, colour enhances the attractiveness of products and aids in distinguishing and selecting them compared with similar items (Galetović et al., 2020). Additionally, natural pigments offer more than just colour, as they also harbour potential health-beneficial bioactive compounds such as antioxidants and anti-inflammatory agents (Di Salvo et al., 2023).

The main features that contribute to the widespread industrial application of M&C pigments are related to consumer awareness of more sustainable and less dangerous options, as well as their higher demand for natural products. The availability of an extensive colour palette and the wide range of bioactive properties of these compounds are also among these attributes. Other sought-after characteristics include a reduced risk of adverse health effects and compliance with environmental regulations (Fig. 1).

Despite these favourable characteristics, some M&C species are known to produce certain compounds, such as toxins, which may have harmful effects on human health and the environment. Therefore, a preliminary assessment is required to ensure their safety. Additionally, a 100 % industrial process based on M&C pigments may not be economically viable, due to the difficulties of large-scale production, but also due to other factors such as high production costs and the industrial acceptance of products with lower performance. An industrial application of M&C pigments might still demand applied research to ensure their feasibility and large-scale operability.

3.1. Food and feed

In the food industry, there has been a noteworthy shift towards embracing natural pigments instead of synthetic alternatives owing to their exceptional colouring abilities and potential health benefits, such as antidiabetic, photoprotective and antioxidant properties (Favas et al., 2022; Sandybayeva et al., 2022; Sun et al., 2023). Natural pigments,

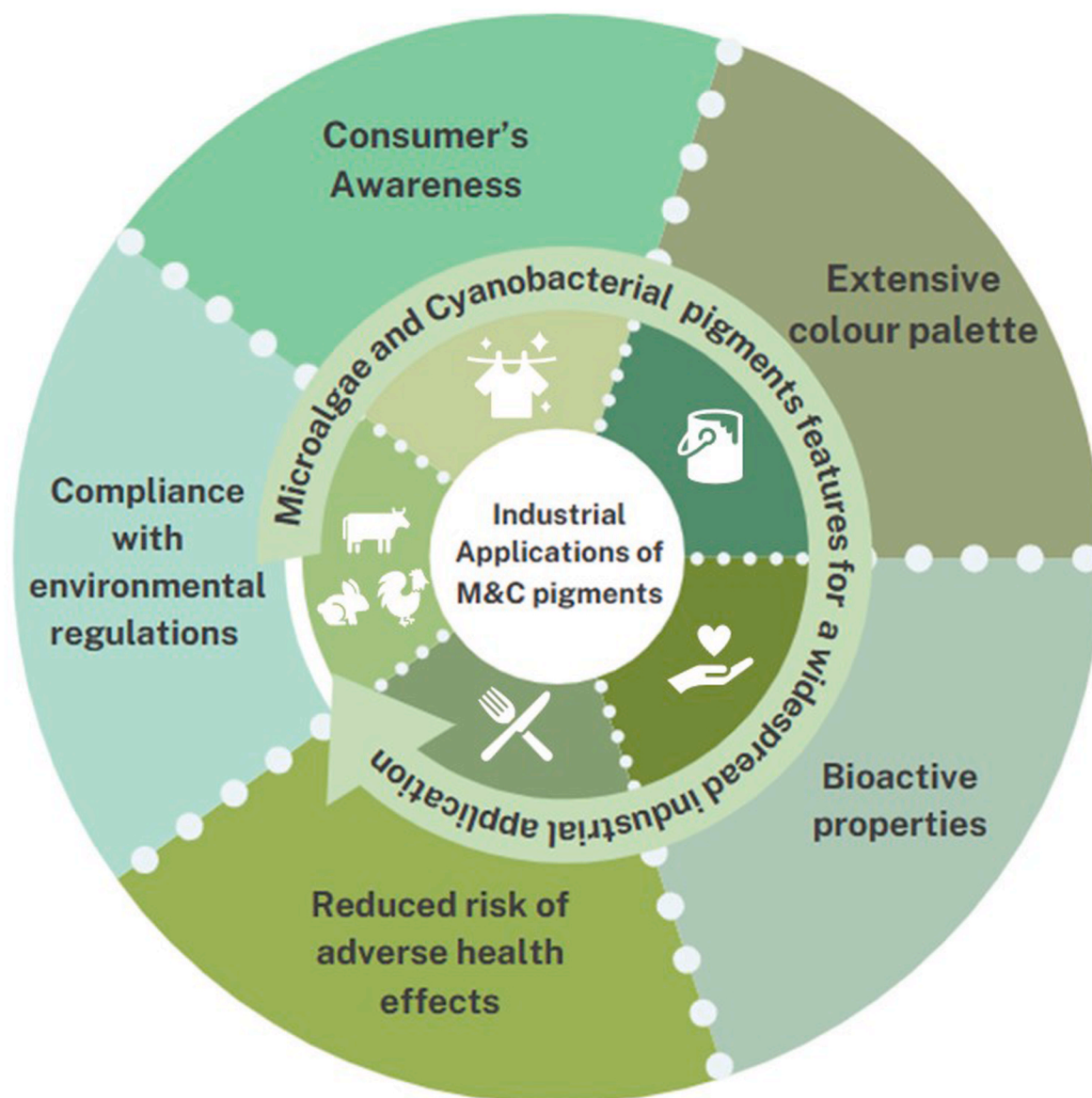


Fig. 1. – General promising attributes of M&C pigments and their widespread industrial applications.

especially those derived from M&C, exhibit unique colours and molecular structures, along with distinct physiological and health benefits when consumed (Di Salvo et al., 2023; Sun et al., 2023). In addition to their role as colourants, these pigments exhibit auxiliary preservation and antiseptic effects during food storage owing to their inherent physiological properties (Sun et al., 2023).

Among the natural pigments extracted from M&C, carotenoids are the preferred choice for the food industry, particularly in the production of cooked sausages, soft drinks and baked goods (Sun et al., 2023). Their outstanding antioxidative and preservative qualities contribute to maintaining the original colour and flavour of food during storage while preventing the oxidation and deterioration of fatty acids and other compounds (Sun et al., 2023). β -carotene is gaining prominence as a natural colourant in the food industry, with concentrations ranging from 2 to 50 ppm in products such as juices, drinks, butter, margarine and cheese (Di Salvo et al., 2023). Yellow zeaxanthin, extracted from *Flavobacterium* spp., serves as both an antioxidant and a food colourant. Similar properties have been observed for the orange/deep-pink canthaxanthin pigment from *Bradyrhizobium* spp. (Di Salvo et al., 2023). Astaxanthin, another valuable carotenoid with natural colouring properties, is extracted from *H. pluvialis* and is approved for use as a

dietary supplement in Japan, the USA, and some European countries (Sun et al., 2023). These pigments have also been used in animal feed, particularly for poultry, to guarantee stronger colours in their byproducts (Guedes et al., 2011).

Furthermore, PC, a PBP produced by cyanobacteria, is widely used in the food and beverage industry. *Spirulina* spp. are extensively studied cyanobacteria known for their high PC content, constituting up to 20 % of their DW (Di Salvo et al., 2023). For instance, aqueous extracts of non-purified blue PC from *Spirulina* have been incorporated into ice creams, yogurts, isotonic beverages, confectionery and jellies (Galetović et al., 2020). PE, mainly obtained from *Porphyridium* sp., can be used for red coloration of gelatine deserts and dairy products, and colour stability in dry food products is ensured at relatively high temperatures (60 °C) for 30 min (Dufossé et al., 2005).

3.2. Cosmetics

Cosmetics have become a daily staple for millions of people. Although traditionally associated with enhancing one's aesthetic appearance, in recent years, there has been a noticeable shift towards prioritising skin health. This growing concern has fuelled a substantial

demand for skincare products. M&C have emerged as a noteworthy source of skincare compounds, with numerous derivatives from these microorganisms demonstrating valuable properties including UV protection, hydration and antioxidant capabilities, in addition to their colouring properties. These include mycosporine-like amino acids, Scy, exopolysaccharides and phenols (Derikvand et al., 2017).

Carotenoids have also garnered considerable interest in the field of cosmetology because of their ability to identify key indicators of unhealthy and ageing skin (D'Orazio et al., 2012; Sathasivam and Ki, 2018). In addition, carotenoids exhibit antioxidant properties that are beneficial for skin care (Favas et al., 2022). The inclusion of cyanobacterial extracts, particularly those rich in carotenoids, in cosmetic products has been associated with anti-ageing effects (Favas et al., 2022; Sandybayeva et al., 2022). Furthermore, Pagels et al. (2020) noted that cyanobacteria belonging to the genus *Cyanobium* are rich in β -carotene and other pigments such as echinenone, lutein and zeaxanthin that offer a wide range of benefits, including photoprotection, anti-inflammatory properties, antioxidant protection and cancer prevention (Pagels et al., 2020).

Moreover, PBPs constitute another M&C pigment highly valued in the cosmetics industry owing to their vibrant coloration and health benefits (Pagels et al., 2019). An example of their application is *Spirulina* extract Spiralin®, found in products like Skinicer® Repair cream and Spirularin®, with regenerative effects on damaged skin cells, collagen production promotion and UV protection (Sandybayeva et al., 2022). Other studies have demonstrated that PC can be used as a hair dye as it is not toxic to keratinocytes (Kraseasintra et al., 2022).

Notably, Scy, an extracellular pigment found in cyanobacteria, has been explored for its potential as a photoprotective agent (Mourelle et al., 2017).

3.3. Textiles

The textile industry is a pioneering and advanced application of M&C photosynthetic pigments. Over the past decade, research has increasingly focused on pigments derived from microorganisms as innovative and promising resources for the textile industry (Venil et al., 2013; Rao et al., 2017; Usman et al., 2017; Metwally et al., 2021; Kramar and Kostic, 2022). Among the various sources of microorganisms, M&C are the most promising candidates for pigment production owing to their numerous advantages (Fig. 1) (Ren et al., 2021; Srivastava et al., 2022; Sun et al., 2023).

In addition to scientific research exploring the potential utilisation of microbial pigments in the textile industry, there has been a growing trend in recent years involving designers and companies using bacterial, fungal and microalgal pigments in fabrics (Fried et al., 2022; Lagashetti et al., 2022; Mutaf-Kilic et al., 2023). For instance, as the importance of technical textile products continues to grow, there is increasing interest in natural colourants with functional properties to enhance the eco-friendliness and multifunctionality of textile fabrics (Mutaf-Kilic et al., 2023).

Several researchers have studied the application of M&C pigments as colourants in the textile industry. Jorge et al., (2024) investigated the use of microalgae Chl for wool dyeing and emphasised the need of mordants for an efficient dyeing (Jorge et al., 2024). Moldovan (2021) obtained interesting results when Chl, carotenoid, PC and PE liquid extracts were used for dyeing wool (Moldovan, 2021). Cotton and silk fabrics have been dyed with PC, and promising results have been achieved by co-mordanting fabrics with common metal mordants (Baek et al., 2022). Despite these promising applications, several operational challenges must be addressed to ensure the fastness of M&C pigments on textile fibres. The feasibility of an all-natural industrial process needs to be explored, as it may be necessary to apply some synthetic compounds to facilitate the application of M&C pigments to textile fibres.

4. Challenges and strategies for enhancing the industrial adoption of microalgae and cyanobacteria pigments

The industry, along with the increasing demand from consumers, shows a strong willingness to shift towards a greater use of colourants of natural origin, such as M&C pigments. However, several constraints hinder the development of this process on the desired scale. Studies have consistently highlighted that one of the main factors affecting the use of M&C pigments is their time-consuming and cost-intensive production. A significant challenge in the large-scale manufacturing of cyanobacterial pigments is their high upfront and operational expenses (Ferreira and Gouveia, 2020).

From an industrial production perspective, the primary obstacles revolve around efficiently separating the biomass, extracting the pigments and addressing the instability of the isolated compounds, which ultimately results in low yields of the active substances and markedly affects their cost (Sandybayeva et al., 2022). For instance, the cost of producing pure pigments remains high, limiting their application in high-value markets such as the cosmetics industry (Mehta et al., 2018). The natural capability of microalgae to produce pigments creates a crucial obstacle to their commercial use, which is typically insufficient for profitable exploitation (Srivastava et al., 2022).

Pigment stability is also a challenge in industrial-scale production and applications. Temperature and pH are abiotic factors related to pigment stability, light intensity and oxygen (Rather et al., 2023). Similarly, other compounds such as proteins, metal ions and other chemical molecules may react with these pigments and compromise their industrial applications (Rather et al., 2023). Given that abiotic factors markedly influence the pigment yield, this review provides detailed insights into their effects on M&C pigment production, along with strategies to mitigate challenges and optimise production for enhanced effectiveness and efficiency.

Therefore, several technological improvements are required to make M&C pigments economically competitive in established markets. Genetic and metabolic engineering techniques can be highly useful to address this issue; however, they can also be costly. Indeed, successful large-scale production of some M&C pigments has already been implemented in the food, pharmaceutical and cosmetics industries (Bhattacharya and Goswami, 2020; Silva et al., 2020), proving the effectiveness of this biotechnological application.

4.1. Abiotic factors affecting microalgae and cyanobacteria pigment production

Similar to all living organisms, M&C can be influenced by numerous abiotic and biotic factors (Fig. 2). These factors play a crucial role in shaping their growth and metabolite production (Pagels et al., 2019). Among the abiotic factors, elements such as light (Tables 2–4), temperature (Table 5), pH (Table 6), nutrient levels (Table 7) and salinity (Table 8) can modulate an organism's metabolic processes (Begum et al., 2016; Nwoba et al., 2020; Pagels et al., 2019). Consequently, variations in these factors can lead to important changes in pigment production, as these organisms respond adaptively to these fluctuations (Assunção et al., 2023; Begum et al., 2016; Sandybayeva et al., 2022).

Given these dynamics, a comprehensive investigation of the impact of environmental conditions and growth parameters on pigment production in M&C cultures is essential. This arises from the necessity of optimising the culture and growth conditions to achieve maximum pigment yield, especially when large-scale cultivation is required. By gaining insights into the distinct contributions of each influencing factor, it is feasible to generate both biomass and pigments in the desired quantities.

4.1.1. Light intensity, light quality and photoperiod

The effect of light on microbial growth is well-known, and some M&C species reproduce in dark environments (Zittelli et al., 2023).

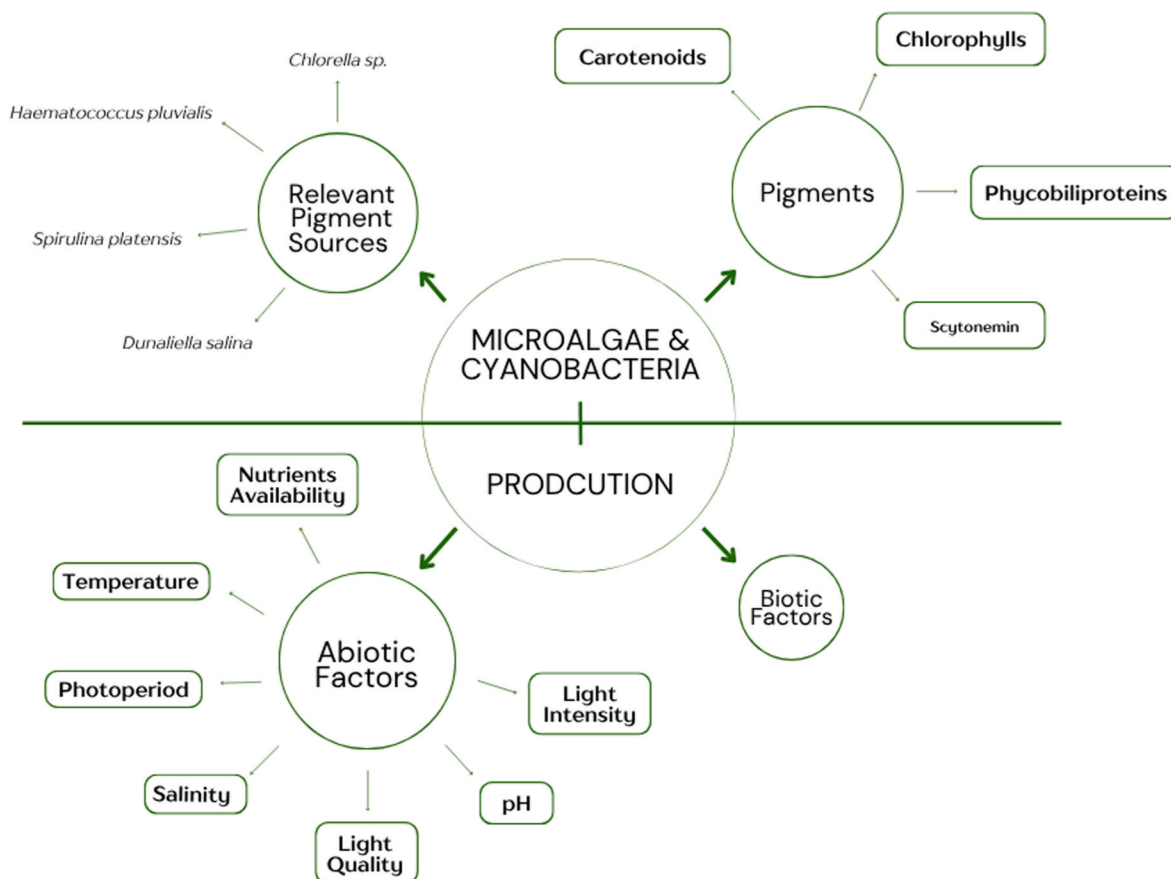


Fig. 2. – M&C pigments, their main sources and the factors influencing their production.

Likewise, the production of certain pigments seems to be related to light intensity, light colour and photoperiod to which microorganisms are exposed (Chen et al., 2022; Zittelli et al., 2023). Depending on the species, higher pigment production can be achieved at low or high light intensity.

The correlation between the production of Chls is reported to be inversely proportional to light intensity, when analysing the production of these pigments by *Dunaliella salina*, *Chlorella* sp., *Microcystis aeruginosa*, *Monoraphidium dybowskii*, *Scenedesmus dimorphus*, *Pavlova lutheri*, and *Chlamydomonas reinhardtii* (Carvalho et al., 2009; Bonente et al., 2012; He et al., 2015; Ferreira et al., 2016; Hotos and Antoniadis, 2022; Huang et al., 2023).

Carotenoid production (total carotenoids, β -carotene, and astaxanthin) differs among species (Assunção et al., 2022; Fábregas et al., 2003; Gris et al., 2017; Hotos, 2023; Huang et al., 2023; Imamoglu et al., 2009; Seyfabadi et al., 2011; Singh et al., 2019). For example, high light intensity ($200\text{--}1000 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) decreases β -carotene content in *M. aeruginosa*, whereas astaxanthin production increases with increased light intensity ($1000 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Huang et al., 2023).

Literature describes increased PBP production with low light intensities (under $50 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) by *Synechocystis* sp., *Anabaena* sp., *Gloeocapsa* sp., *Lyngbya* sp. and *Anabaena* NCCU-9 (Castro et al., 2015; de Oliveira et al., 2014; del Rio-Chanona et al., 2015; Gris et al., 2017; Hemlata and Fatma, 2009; Hifney et al., 2013; Hong and Lee, 2008; Lee et al., 2016; Ma et al., 2015; Maurya et al., 2014). However, some studies have shown that increased light intensity ($75\text{--}150 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) leads to high PBP content in *Arthronema africanum* and *S. platensis* (Chaneva et al., 2007; Hotos, 2023; Kumar et al., 2011; Maurya et al., 2014; Mohite and Wakte, 2011). Low light intensity (under $20 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) increases PC content in *Pseudanabaena*

sp. ABRG5-3, *S. subsalsa* and *Limnithrix* sp. SK1–2–1 (Aoki et al., 2024; Jiang et al., 2023). In *Arthrospira platensis* NIES-39, higher intensities ($100 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) enhance PC production (Aoki et al., 2024). C-PC production by *Potamosiphon* sp. UFPS008 increased at higher light intensities ($200 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than at lower light intensities ($50 \mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Contreras-Ropero et al., 2024).

The differences between species are even more evident in terms of light colour/light quality. Mohsenpour et al. (2012) found that the Chl content in *C. vulgaris* was boosted by red light and was lower under violet light. However, for *Dunaliella* sp., the Chl content seemed to be increased by blue light (Hotos, 2023). For Chl a, based on the strain assessed, higher content can be obtained under green (Assunção et al., 2022; Hotos and Antoniadis, 2022), pink (Vadiveloo et al., 2017), blue–green, blue and red light (Vadiveloo et al., 2015, 2017).

Despite being less explored, light colour may have an impact on carotenoid pigment production. In *A. platensis* (Zittelli et al., 2022), orange and white light led to a higher carotenoid content. Similarly, *Synechocystis salina* LEGE 06155 (Assunção et al., 2022) increased carotenoid production under white light, whereas *Asterarcys quadricellulare* PUMCC 5.1.1 (Singh et al., 2019) and *Dunaliella* sp. (Hotos, 2023) showed better results under blue light.

The influence of light quality on the production of PBPs (PC, PE, and APC) has also been described in the literature. In some cases (*Anabaena* sp., *Nostoc sphaeroides*, and *Synechococcus* sp.), blue light doubled PBP production (Khattar et al., 2015; Kim et al., 2014; Ma et al., 2015; Maurya et al., 2014). In other cases (*Nostoc* UAM 206, *Synechococcus* NKBG 042902, *Nostoc muscorum*, *S. salina* LEGE 06155, and *Pseudanabaena* sp.), red light enhanced the production of these pigments (Assunção et al., 2022; Keithellakpam et al., 2015; Mishra et al., 2012). For *Pseudanabaena mucicola*, higher PBP concentrations were obtained under white light (Khattoon et al., 2018). Assunção et al. (2022) reported

Table 2
– Effect of light intensity on the production of pigments by M&C.

Abiotic Factor	Pigment	Microalgae/Cyanobacteria	Effect on the Production	Condition	References	
Light Intensity	Chl	<i>Chlorella</i> sp.	Inverse relation		Carvalho et al., 2009; Bonente et al., 2012; He et al., 2015; Ferreira et al., 2016; Hotos and Antoniadis, 2022; Huang et al., 2023	
		<i>M. dybowskii</i> <i>S. dimorphus</i> <i>P. lutheri</i> <i>C. reinhardtii</i> <i>Phormidium</i> sp. <i>Cyanothece</i> sp. <i>M. aeruginosa</i>				
	Chl <i>a</i>	<i>Cyanobacterium aponinum</i> PCC 10605	↑	Light intensity higher than 150 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Gris et al., 2017	
	Carotenoids	<i>C. aponinum</i> PCC 10605 <i>Dunaliella</i> sp.	↓	Higher light intensities (when exceeded 150 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Gris et al., 2017; Hotos, 2023	
		<i>S. salina</i> LEGE 06155 <i>Phormidium</i> sp. <i>Cyanothece</i> sp. <i>A. quadricellulare</i> PUMCC 5.1.1	↓	Higher light intensities (between 60 and 160 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Singh et al., 2019; Assunção et al., 2022; Hotos and Antoniadis, 2022	
	β -carotene and Astaxanthin	<i>M. aeruginosa</i>	Inverse relation			Huang et al., 2023
		<i>C. vulgaris</i>				
	β -carotene		↓	Irradiance of 100 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a 16:8-h light/dark photoperiod	Seyfabadi et al., 2011	
	Astaxanthin	<i>Haematococcus pluvialis</i>	↓	Flashing light	Fábregas et al., 2003	
			↓	Light intensity of 546 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Imamoglu et al., 2009	
	PBPs	<i>Synechocystis</i> sp. <i>Anabaena</i> sp. <i>Gloeocapsa</i> sp. <i>Lyngbya</i> sp. <i>Oscillatoria</i> sp. KJ652541	↓	Light intensity of 2000 lux	Maurya et al., 2014; Hotos, 2023	
			↓	Light intensity of 6000 lux	Tiwari et al., 2019	
			↓	Medium and high light intensities (75–150 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Hifney et al., 2013; de Oliveira et al., 2014; Castro et al., 2015; del Rio-Chanona et al., 2015; Ma et al., 2015; Lee et al., 2016; Gris et al., 2017	
		<i>S. platensis</i>	↓	Light intensity of 25 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Hong and Lee, 2008; Hemlata and Fatma, 2009	
		<i>Anabaena</i> NCCU-9 <i>Synechocystis</i> sp. PCC6701	↓	Light intensity of 150 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a maximum temperature of 36 °C	Chanava et al., 2007; Kumar et al., 2011; Mohite and Wakte, 2011; Maurya et al., 2014	
<i>A. Africanum</i> <i>S. platensis</i> <i>Synechocystis</i> sp. <i>Gloeocapsa</i> sp. <i>Lyngbya</i> sp. <i>Anabaena</i> sp. <i>C. aponinum</i> PCC 10605 <i>Euryhalinema</i> sp. <i>Destifilum</i> sp.		↓	Lower light intensities (less than 100 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Gris et al., 2017; Khazi et al., 2021		
PBPs (PC)		<i>S. subsalsa</i>	↓	Light intensity of 500 lux	Jiang et al., 2023	
		<i>Pseudanabaena</i> sp. ABRG5-3 <i>Limnothrix</i> sp. SK1–2–1	↓	Light intensity of 20 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Aoki et al., 2024	
		<i>A. platensis</i> NIES-39	↓	Light intensity of 100 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Aoki et al., 2024	
		<i>Potamosiphon</i> sp. UFPS008	↓	Light intensity of 200 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Contreras-Ropero et al., 2024	
PBPs (PE)	<i>Anabaena</i> sp. BTA 903	↓	Light intensity from 4000 to 6000 Lux	Nath et al., 2024		

Table 3
– Effect of light quality (light colour) on the production of pigments by M&C.

Abiotic Factor	Pigment	Microalgae/Cyanobacteria	Effect on the Production	Condition	References
Light Colour	Chls	<i>C. vulgaris</i>	↓	Red light	Mohsenpour et al., 2012
			↑	Violet Light	
		<i>Dunaliella</i> sp.	↓	Blue light	Hotos, 2023
	Chl <i>a</i>	<i>S. salina</i> LEGE 06155	↓	Green light at high intensities	Assunção et al., 2022; Hotos and Antoniadis, 2022
<i>Phormidium</i> sp.		↓			
<i>Cyanothece</i> sp.		↓			
<i>Nannochloropsis</i> MUR 267		↓	Pink light	Vadiveloo et al., 2017	
		<i>Nannochloropsis</i> MUR 266	↓	Blue–green and blue lights	Vadiveloo et al., 2015
			↓	Red light	Vadiveloo et al., 2017
	Carotenoids	<i>A. platensis</i>	↓	Orange and white lights	Zittelli et al., 2022
		<i>S. salina</i> LEGE 06155	↓	White light at high intensities	Assunção et al., 2022
		<i>A. quadricellulare</i> PUMCC 5.1.1	↓	Blue light	Singh et al., 2019; Hotos, 2023
	PBPs	<i>Dunaliella</i> sp.	↓		
		<i>Anabaena</i> sp.	↓	Blue light	Hemlata and Fatma, 2009; Kim et al., 2014; Khattar et al., 2015; Ma et al., 2015
		<i>N. sphaeroides</i>	↓		
		<i>Synechococcus</i> sp.	↓		
		<i>Nostoc</i> UAM 206	↓	Red light	Mishra et al., 2012; Keithellakpam et al., 2015; Assunção et al., 2022
		<i>N. muscorum</i>	↓		
		<i>Pseudoanabaena</i> sp.	↓		
	<i>S. salina</i> LEGE 06155	↓			
		<i>P. mucicola</i>	↓	White light	Khatoon et al., 2018
	PBPs (PC)	<i>A. platensis</i>	↓	Blue light	Zittelli et al., 2022
		<i>S. salina</i> LEGE 06155	↓	White light under high intensities	Assunção et al., 2022
		<i>Phormidium</i> sp.	↓		
		<i>Nodularia sphaerocarpa</i>	↓	Green light	Kaushal et al., 2017; Hotos and Antoniadis, 2022; Hotos, 2023; Jiang et al., 2023
		<i>Anabaena</i> sp.	↓		
		<i>S. subsalsa</i>	↓		
		<i>Synechococcus</i> sp. PCC6715	↓	Blue light	Klepacz-Smółka et al., 2020
		<i>Potamosiphon</i> sp. UFPS008	↓	Ratio of red:blue lights (3:1)	Contreras-Ropero et al., 2024
		<i>Pseudanabaena</i> sp. ABRG5-3	↓	Green, red, and white lights	Aoki et al., 2024
		<i>Limnothrix</i> sp. SK1–2–1	↓		
	PBPs (PE)	<i>A. platensis</i> NIES-39	↓		
		<i>S. salina</i> LEGE 06155	↓	Red light under low intensity	Assunção et al., 2022
		<i>Phormidium</i> sp.	↓	Blue light	Hotos and Antoniadis, 2022
		<i>Cyanothece</i> sp.	↓	Green light	Hotos and Antoniadis, 2022
	PBPs (APC)	<i>S. salina</i> LEGE 06155	↓	Red light under low intensity	Assunção et al., 2022
		<i>A. platensis</i>	↓	Orange and white lights	Zittelli et al., 2022
			↑	Blue light	
		<i>Phormidium</i> sp.	↓	Coloured lights	Hotos and Antoniadis, 2022
		<i>Cyanothece</i> sp.	↓	Green light	Hotos and Antoniadis, 2022

Table 4

– Effect of photoperiod on the production of pigments by M&C.

Abiotic Factor	Pigment	Microalgae/ Cyanobacteria	Effect on the Production	Condition	References
Photoperiod (light: dark)	Chls	<i>A. falcatus</i>	↓	12 h:12 h and 18 h:06 h	George et al., 2014
			↑	00:24 h	
	β -carotene	<i>C. vulgaris</i>	↓	16:08 h and irradiance of 100 $\mu\text{mol}_{\text{photons}}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Seyfabadi et al., 2011
	PBPs	<i>Synechocystis</i> sp. <i>Anabaena</i> sp. <i>Gloeocapsa</i> sp. <i>Lyngbya</i> sp. <i>Oscillatoria</i> sp. KJ652541	↓	16 h:08 h	Hemlata and Fatma, 2009; Johnson et al., 2014; Maurya et al., 2014
	PBPs (PC)	<i>Synechococcus</i> sp. PCC6715	↓	14 h:10 h	Tiwari et al., 2019
	PBPs (PE)	<i>Anabaena</i> sp. BTA 903	↓	16 h:08 h	Klepacz-Smólka et al., 2020
				14:10 h	Nath et al., 2024

that *S. salina* LEGE 06155 produced more PC under white light and higher PE and APC contents under red light (Assunção et al., 2022). *Phormidium* sp. showed better PC production under green light, PE production under blue light, and APC production under coloured light (blue, green, and red) (Hotos and Antoniadis, 2022). In contrast, blue light negatively affected the production of PC and APC by *A. platensis* (Zittelli et al., 2022). The ratio of the two light colours (red:blue) had a positive effect on C-PC production by *Potamosiphon* sp. UFPS008 (Contreras-Ropero et al., 2024).

Photoperiod also affects pigment production. For *Ankistrodesmus falcatus*, the highest Chl content was obtained under 12:12 h and 18:6 h light/dark photoperiod, and the lowest content was found in total darkness (George et al., 2014). Several studies have reported that a light/dark photoperiod of 16:8 h enhances the production of β -carotene and PC by *Synechocystis* sp., *Anabaena* sp., *Gloeocapsa* sp., *Lyngbya* sp., *Synechococcus* sp. PCC6715 and *C. vulgaris* (Hemlata and Fatma, 2009; Johnson et al., 2014; Klepacz-Smólka et al., 2020; Maurya et al., 2014; Seyfabadi et al., 2011). During PBP production by *Oscillatoria* sp. KJ652541, the maximum yield was found at a photoperiod of 14:10 h (Tiwari et al., 2019), which was the same with highest PE production by *Anabaena* sp. BTA 903 (Nath et al., 2024).

Although not so focussed on this study, some studies also address the effect of other radiation spectra on pigment production by M&C, such as Dwivedi and Ahmad's (2023) study analysing the effect of UV-B radiation on the production of photosynthetic pigments by cyanobacteria (Dwivedi and Ahmad, 2023).

4.1.2. Temperature

Temperature, known to be one of the main abiotic factors affecting the proliferation of microorganisms (Gupta et al., 2017; Sun et al., 2023), also exerts an important effect on pigment production. Chl content is affected by temperature. However, the best growth temperature varies between species, for example, *Euryhalinema* sp. produce high Chl content at 28 °C (Khazi et al., 2021). A lower temperature (18 °C) combined with 60 $\mu\text{mol}\cdot\text{photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ is the optimum condition for Chl a production by *P. lutheri* (Carvalho et al., 2009). For *Aphanizomenon* sp. ULC602, the optimal temperature range for higher Chl a production was between 18 and 23 °C (Pham et al., 2023). In contrast, the production of Chl a by *Anabaena* sp. VKB01 and *Nostoc* sp. VKB02 was optimum at 25 and 35 °C, respectively (Amin et al., 2024).

Higher temperatures also inhibit Chl production by *M. aeruginosa* (Huang et al., 2023). Lower temperatures are optimum for higher total carotenoid content, such as 30 °C for *A. quadricellulare* PUMCC 5.1.1 (Singh et al., 2019), 25 °C for *S. salina* LEGE 06115 (Assunção et al.,

2023), and 23 °C for *Anabaena* PCC 7120 (Kłodawska et al., 2019). Specific carotenoids such as lutein, astaxanthin and β -carotene have higher production at lower temperatures (25 °C–30 °C) by *Muriellopsis* sp., *Chlorella protothecoides*, *Neosporangiococcus gelatinosum* and *D. salina* (Del Campo et al., 2001; García-González et al., 2005; Wei et al., 2008). *M. aeruginosa* appears to produce more astaxanthin at higher temperatures (30 °C and 35 °C) but less β -carotene and zeaxanthin at the same temperatures (Huang et al., 2023). The greater production of carotenoids by *Nostoc* sp. VKB02 and *Anabaena* sp. VKB01 is associated with higher temperatures (Amin et al., 2024).

Analysing the production of PBPs, the literature reports an enhanced production at temperatures higher than 30 °C (Chaneva et al., 2007; Hemlata and Fatma, 2009; Hifney et al., 2013; Johnson et al., 2014; Khazi et al., 2021; Kumar et al., 2011; Maurya et al., 2014); for some species, the optimal temperature for increasing PBP content is higher than 35 °C (Chaneva et al., 2007; Maurya et al., 2014). Khazi et al. (2021) found that the optimum PBP production occurred at 28 °C for *Euryhalinema* sp. (Khazi et al., 2021). Furthermore, the production of PBPs by *S. salina* LEGE 06115 was higher at 23 °C, combined with high pH and low NaCl concentrations (Assunção et al., 2023). In *S. subsalsa*, higher temperatures led to an increase in C-PC content (Jiang et al., 2023). Higher PE and PC production was obtained when *P. raciborskii* PMC 877.14 was grown below 30 °C (Touceda et al., 2024). The production of total carotenoids by *D. salina* and *Nannochloropsis gaditana* is enhanced at temperatures between 55 and 60 °C (Macías-Sánchez et al., 2009). The optimal temperature for the production of different PBPs by *Nostoc* sp. VKB02 and *Anabaena* sp. VKB01 is not uniform and ranges between 25 and 35 °C (Amin et al., 2024).

4.1.3. pH

In the case of the abiotic factor pH, most strains produce higher pigment contents at roughly neutral to alkaline pH (Assunção et al., 2023; Sun et al., 2023). Regarding Chl a, a previous study showed that *Nostoc* sp. UAM206 is not affected by a pH increase (Poza-Carrión et al., 2001). Patel et al. (2022) concluded that the highest levels of Chl a produced by *S. platensis* were obtained at pH 8.5 (Patel et al., 2022). A neutral pH was optimal for higher Chl a production by *Phanizomenon* sp. ULC602 (Pham et al., 2023). For *Nostoc* sp., the optimum Chl production was observed at pH 9 (Hemlata and Fatma, 2009).

The optimum production of total carotenoids was attained at a pH between 7 and 8.5 for *Scenedesmus almeriensis*, *Chlorococcum citriforme*, *N. gelatinosum*, *A. quadricellulare* PUMCC 5.1.1 and *S. platensis* (Del Campo et al., 2000; Patel et al., 2022; Singh et al., 2019). The production of β -carotene by *D. salina* was optimal at pH 7.5 (Del Campo et al., 2000;

Table 5
– Effect of temperature on the production of pigments by M&C species.

Abiotic Factor	Pigment	Cyanobacteria/ Microalgae	Effect on the production	Condition	References	
Temperature	Chl	<i>Euryhalinema</i> sp.	↓	28 °C	Khazi et al., 2021	
		<i>M. aeruginosa</i>	↑	30 and 35 °C	Huang et al., 2023	
Total Carotenoids	Chl α	<i>P. lutheri</i>	↓	18 °C and 60 $\mu\text{mol}_{\text{photon}}\text{S}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Carvalho et al., 2009	
		<i>Anabaena</i> sp. VKB01	↓	25 °C	Amin et al., 2024	
		<i>Nostoc</i> sp. VKB02	↓	35 °C	Amin et al., 2024	
		<i>Aphanizomenon</i> sp. ULC602	↓	18 and 23 °C	Pham et al., 2023	
		<i>N. gaditana</i> <i>D. salina</i>	↓	55 and 60 °C	Macías-Sánchez et al., 2009	
	Total Carotenoids	Total Carotenoids	<i>S. salina</i> LEGE 06115	↓	25 °C, combined with pH 8 or low NaCl concentrations	Assunção et al., 2023
			<i>Anabaena</i> sp. VKB01	↓	40 °C	Amin et al., 2024
			<i>Nostoc</i> sp. VKB02	↓	45 °C	Amin et al., 2024
			<i>A. quadricellulare</i> PUMCC 5.1.1	↓	30 °C	Singh et al., 2019
			<i>Anabaena</i> PCC 7120	↓	23 °C	Klodawska et al., 2019
β -carotene	β -carotene	<i>D. salina</i>	↓	25 °C	García-González et al., 2005	
		<i>M. aeruginosa</i>	↑	30 and 35 °C	Huang et al., 2023	
Astaxanthin	Astaxanthin	<i>M. aeruginosa</i>	↓	25–35 °C	Huang et al., 2023	
Zeaxanthin	Zeaxanthin	<i>M. aeruginosa</i>	↑	30 and 35 °C	Huang et al., 2023	
Lutein	Lutein	<i>Muriellopsis</i> sp. <i>C. protothecoides</i> <i>N. gelatinosum</i>	↓	28 °C	Del Campo et al., 2001; Wei et al., 2008	
PBPs	PBPs	<i>Synechocystis</i> sp. <i>Anabaena</i> sp. <i>Gloeocapsa</i> sp. <i>Lyngbya</i> sp. <i>S. salina</i> LEGE 06115	↓	35 °C	Maurya et al., 2014	
		<i>S. salina</i> LEGE 06115	↓	23 °C, combined with high pH and low NaCl concentration	Assunção et al., 2023	
		<i>Anabaena</i> sp.	↓	30 °C	Chaneva et al., 2007; Hemlata and Fatma, 2009	
		<i>Synechococcus</i> sp. <i>A. africanum</i>	↓	36 °C	Chaneva et al., 2007	
		<i>Spirulina</i> sp. <i>Nostoc</i> sp. <i>S. platensis</i>	↓	Higher than 30 °C	Kumar et al., 2011; Hifney et al., 2013; Johnson et al., 2014	
		<i>Euryhalinema</i> sp.	↓	28 °C	Khazi et al., 2021	
		<i>Desertifilum</i> sp.	↓	32 °C	Khazi et al., 2021	
		PBPs (PC)	PBPs (PC)	<i>S. subsalsa</i>	↓	25–40 °C
<i>Anabaena</i> sp. VKB01	↓			25 °C	Amin et al., 2024	
<i>Nostoc</i> sp. VKB02	↓			35 °C	Amin et al., 2024	

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Table 7
– Effect of nutrient availability on the production of pigments by M&C species.

Abiotic Factor	Pigment	Cyanobacteria/ Microalgae	Effect on the production	Condition	References		
Nutrients Availability	Nitrogen	Chl	<i>C. vulgaris</i> <i>Chlorella fusca</i> <i>S. platensis</i> <i>Scenedesmus dimorphus</i>	↓	Nitrogen starvation	Lv et al., 2010; Cakmak et al., 2012; Ferreira et al., 2016; Jerez et al., 2016	
		Chl a and Chl b	<i>C. minutissima</i>	↓	Nitrogen addition to a nitrogen-stressed inoculum	Ördög et al., 2012	
	Total Carotenoids	Chl a	<i>Anabaena</i> sp.	↓	100 % nitrogen surplus medium	Issa et al., 2020	
			<i>A. platensis</i>	↓	Sodium nitrate as nitrogen source	Khazi et al., 2021	
		β-carotene	<i>Aphanizomenon</i> sp. ULC602	↑	Sodium nitrate or urea as nitrogen source	Pham et al., 2023	
			<i>Phormidium</i> sp. <i>Pseudoscillatoria</i> sp.	↓	Ammonium chloride as nitrogen source	Khazi et al., 2021	
		Lutein	<i>A. quadricellulare</i> <i>PUMCC 5.1.1</i>	↓	Medium supplementation with 10 mM of nitrate	Singh et al., 2019	
			<i>H. pluvialis</i> <i>D. salina</i>	↓	Nitrogen starvation	Kang et al., 2006; Mojaat et al., 2008	
		PBPs	β-carotene	<i>S. almeriensis</i>	↓	Nitrogen concentration	Sánchez et al., 2008
				<i>C. protothecoides</i>	↓	Urea as nitrogen source	Shi et al., 2000
			PBPs (PC)	<i>A. fertilissima</i> PUPCCC 410.5	↓	Nitrites concentration of 2 mmol L ⁻¹	Khattar et al., 2015
				<i>Anabaena</i> NCCU-9	↓	Nitrogen-free environment	Hemlata and Fatma, 2009
	<i>Fischerella</i> sp.			↓	Nitrate grown cells	Hemlata and Fatma, 2009	
	<i>N. sphaerocarpa</i>			↓	Sodium nitrite concentrations of 10 mM	Kaushal et al., 2017	
	<i>Euryhalinema</i> sp. <i>Desertifilum</i> sp.			↓	Sodium nitrate (3 g/L) as the nitrogen source	Khazi et al., 2021	
	<i>A. platensis</i>			↓	Sodium nitrate as nitrogen source	Khazi et al., 2021	
	<i>Phormidium</i> sp. <i>Pseudoscillatoria</i> sp.			↓	Ammonium chloride as nitrogen source	Khazi et al., 2021	
	Chl			<i>A. variabilis</i> ATCC 29413	↓	Medium supplementation with 0.5 g/L of glucose and 2 mM of nitrate	Cottas et al., 2020
		<i>Phormidium</i> sp.	↓	Medium supplementation with 1 g/L of glucose	Mastropetros et al., 2023		
	Carbon	β-carotene	<i>Phormidium</i> sp.	↓	Medium supplementation with anaerobic digestion effluent at 10 %	Mastropetros et al., 2023	
Chl			<i>Chlorella</i> sp. <i>Nannochloropsis</i> sp. <i>I. galbana</i> <i>D. salina</i>	↓	Heterotrophic cultivation	Cheirsilp and Torpee, 2012; Gim et al., 2016	
PBPs		<i>D. salina</i>	↑	Photoheterotrophic cultivation	Mojaat et al., 2008		
		<i>A. fertilissima</i> PUPCCC 410.5 <i>N. sphaerocarpa</i>	↓	0.5 % fructose and 0.5 % sucrose	Khattar et al., 2015; Kaushal et al., 2017		
PBPs (PC)		<i>A. variabilis</i> ATCC 29413	↓	Medium supplementation with 1 g/L of glucose or 0.5 g/L of glucose and 2 mM of nitrate	Cottas et al., 2020		
		Chl	<i>C. pyrenoidosa</i>	↑	Iron restriction	Fan et al., 2014	
β-carotene			<i>D. salina</i>	↓	Iron (II) sulphate concentration of 450 mM	Mojaat et al., 2008	

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Table 7 (continued)

Abiotic Factor	Pigment	Cyanobacteria/ Microalgae	Effect on the production	Condition	References
	Astaxanthin	<i>H. pluvialis</i>	↓	Medium supplementation with iron	Fábregas et al., 2003; Kang et al., 2006
		<i>Chlorococcum</i> sp.	↓	Medium supplementation with iron	Ma and Chen, 2001
Copper	PBPs	<i>Euryhalinema</i> sp. <i>Desertifilum</i> sp.	↓	Ferric ammonium citrate concentration of 12 mg L ⁻¹	Khazi et al., 2021
	Chl	<i>I. galbana</i> <i>Pavlova viridis</i> <i>P. tricornutum</i>	↑	Copper concentrations of 1 and 3 mg L ⁻¹	Li et al., 2006
Zinc	Chl	<i>P. viridis</i>	↑	Zinc concentrations of 3.25 and 6.5 mg L ⁻¹	Li et al., 2006
Sulphur	Chl	<i>C. reinhardtii</i> <i>C. fusca</i>	↑	Sulphur deprivation	Cakmak et al., 2012; Jerez et al., 2016
	Carotenoids	<i>C. reinhardtii</i> <i>C. fusca</i>	↓	Sulphur deprivation	Cakmak et al., 2012; Jerez et al., 2016
Phosphorus	Astaxanthin	<i>H. pluvialis</i> <i>C. reinhardtii</i> <i>Parachlorella kessleri</i>	↓	Sulphur restriction	Cakmak et al., 2012; Yamazaki et al., 2018
	Chl	<i>S. obliquus</i> <i>Isochrysis galbana</i> <i>C. pyrenoidosa</i>	↓	Phosphorus concentration higher than 10 mg L ⁻¹	Chen et al., 2011; Fan et al., 2014; Roopnarain et al., 2014
	Carotenoids	<i>A. quadricellulare</i> PUMCC 5.1.1	↓	Phosphate concentration of 3.5 mM	Singh et al., 2019
	Astaxanthin	<i>H. pluvialis</i>	↓	Phosphate deficient medium	Brinda et al., 2004

Table 8

– Effect of salinity on the production of pigments by M&C species.

Abiotic Factor	Pigment	Cyanobacteria/Microalgae	Effect on the production	Condition	References
Salinity	Carotenoids	<i>H. pluvialis</i>	↓	NaCl concentration of 2.5 %	Tam et al., 2012
		<i>A. carterae</i> Dn241EHAU <i>C. rostralis</i> BMCC18	↓	Sea salt concentration of 30 g/L	Macías-de la Rosa et al., 2024
		<i>H. akashiwo</i> BMCC75	↓	Sea salt concentration of 25 g/L	Macías-de la Rosa et al., 2024
		<i>A. quadricellulare</i> PUMCC 5.1.1	↓	NaCl concentration of 0.17 mM	Singh et al., 2019
	Astaxanthin and Canthaxanthin	<i>C. zofingiensis</i>	↓	Salt stress and low light quality	Pelah et al., 2004
	Fucoaxanthin	<i>P. tricornutum</i> <i>C. muelleri</i> <i>T. lutea</i>	↓	Salinity of 45 ppt	Ishika et al., 2017
	PBPs	<i>Anabaena</i> NCCU-9	↓	NaCl concentration of 0.01 M	Hemlata and Fatma, 2009
		<i>Anabaena</i> NCCU-9	↓	NaCl concentration of 0.25 M	Hemlata and Fatma, 2009
		<i>Phormidium</i> sp.	↓	Sea salt concentration of 0.5 M	Jonte et al., 2013
		<i>S. maxima</i>	↓	NaCl concentration of 0.2 M	Abd El-Baky and El-Baroty, 2012
Scy	<i>S. platensis</i>	↓	NaCl concentrations of 0.8 M	Sharma et al., 2014	
	<i>Anabaena</i> sp. <i>Oscillatoria</i> sp.	↓	NaCl concentrations of 10–15 ppt	Hemlata and Fatma, 2009	
	<i>Chroococidiopsis</i> sp. UAM571	↓	NaCl concentration of 20 g/L	Casero et al., 2024	

García-González et al., 2005; Patel et al., 2022).

For *Nostoc* sp., *Synechocystis* sp., *Anabaena* sp., *Gloeocapsa* sp., *Lyngbya* sp., and *N. sphaerocarpa*, pH 8 was found to be optimal for highPBP production (Hemlata and Fatma, 2009; Johnson et al., 2014; Kaushal et al., 2017; Keithellakpam et al., 2015; Maurya et al., 2014). *Nostoc* sp. and *Spirulina* sp. produce high concentrations of PBPs at pH 9

(Hemlata and Fatma, 2009; Hifney et al., 2013; Ismaiel et al., 2016; Mohite and Wakte, 2011; Patel et al., 2022; Poza-Carrión et al., 2001). *Anabaena fertilissima* produces high concentrations of PBPs at pH 9.5 (Khattar et al., 2015). Some studies have reported no significant differences in the production of PBPs by *A. fertilissima* PUPCCC 410.5 and *Anabaena* NCCU-9 (Hemlata and Fatma, 2009; Khattar et al., 2015). Poza-Carrión et al. (2001) studied the effect of pH on PBP production by *Nostoc* sp. UAM206 and concluded that the production increased with higher pH values (Poza-Carrión et al., 2001). Higher PBP productivity was achieved at a neutral pH for strains belonging to the genera *Spirulina*, *Phormidium*, *Nostoc*, *Calothrix* and *Anabaena* (Keithellakpam et al., 2015; Sharma et al., 2014).

4.1.4. Nutrient availability

The availability of certain nutrients is a core factor that affects the production of bioactive compounds by microorganisms, with carbon and nitrogen being the most important (Khazi et al., 2021; Sun et al., 2023). Several studies have investigated the effects of nitrogen concentration on the production of Chl, carotenoids and PBP.

Research on the effect of nitrogen on the production of Chl has led to the conclusion that the concentration of nitrogen is directly related to Chl concentration in *S. platensis*, *C. vulgaris*, *Scenedesmus subspicatus*, *C. fusca*, *C. reinhardtii* and *S. dimorphus* (Cakmak et al., 2012; Ferreira et al., 2016; Jerez et al., 2016; Lv et al., 2010). In the specific case of Chl a and b, an increased content of these pigments was produced by *Chlorella minutissima* when nitrogen was added to a nitrogen-starved inoculum (Ördög et al., 2012). Chl a concentrations were higher when 100 % nitrogen surplus medium was added to *Anabaena* sp. (Issa et al., 2020), when NH₄Cl was added as the nitrogen source for *Phormidium* sp. and *Pseudoscillatoria* sp. (Khazi et al., 2018), and when the medium was supplemented with NaNO₃ for *S. platensis* (Khazi et al., 2018). In contrast, in *Aphanizomenon* sp. ULC602, nitrogen supplementation with urea or NaNO₃ decreased Chl a production (Pham et al., 2023).

Higher total carotenoids production was obtained with nitrate supplementation in *A. quadricellulare* PUMCC 5.1.1 (Singh et al., 2019). High lutein content was related to the use of urea as a nitrogen source for *C. protothecoides* (Shi et al., 2000). However, in *S. almeriensis*, a study found that nitrogen concentration did not affect the production of this carotenoid (Sánchez et al., 2008). β -carotene content increased after nitrogen starvation, as detailed in the studies published by Kang et al. (2006) and Mojaat et al. (2008).

A nitrogen-free environment has been reported to lead to a greater production of PBPs by *Anabaena* NCCU-9 (Hemlata and Fatma, 2009). In *Fischerella* sp. and *A. fertilissima* PUPCCC 410.5, nitrate and nitrite addition to the grown cells, respectively, resulted in a higher production of PBPs (Hemlata and Fatma, 2009; Khattar et al., 2015). Kaushal et al. (2017), Khazi et al. (2018), and Khazi et al. (2021) studied the effect of different nitrogen sources on the production of PBPs by cyanobacteria and found that *Euryhalinema* sp., *A. platensis*, and *Desertifilum* sp. produced high PBP content with sodium nitrate as the nitrogen source; *Phormidium* sp. and *Pseudoscillatoria* sp. with ammonium chloride; and *N. sphaerocarpa* with sodium nitrite (Kaushal et al., 2017; Khazi et al., 2018, 2021). Supplementation of BG-11 medium with glucose led to high PC content in *A. variabilis* ATCC 29413 and *Phormidium* sp. (Cottas et al., 2020; Mastropetros et al., 2023).

Based on the nutrition of microorganisms and, therefore, the carbon source, researchers have suggested that photoautotrophic cultivation results in higher Chl accumulation than heterotrophic cultivation of *Chlorella* sp., *Nannochloropsis* sp., *I. galbana* and *D. salina*. In mixotrophic cultivation, an increase in carbon reduces the Chl content (Cheirsilp and Torpee, 2012; Gim et al., 2016). The amount of β -carotene produced by *D. salina* markedly increased when photoheterotrophically cultivated (Mojaat et al., 2008). PBP production doubled when *A. fertilissima* PUPCCC 410.5 and *N. sphaerocarpa* were grown under culture conditions of 0.5 % sucrose or 0.5 % fructose (Kaushal et al., 2017; Khattar et al., 2015). The PC content of *A. variabilis* ATCC 29413 was highest

when the medium was supplemented either with 1 g/L of glucose or 0.5 g/L and 2 mM of nitrate (Cottas et al., 2020).

Other nutrients, such as iron (Fábregas et al., 2003; Fan et al., 2014; Kang et al., 2006; Khazi et al., 2021; Ma et al., 2015; Ma and Chen, 2001; Mojaat et al., 2008), copper (Li et al., 2006), zinc (Li et al., 2006), sulphur (Cakmak et al., 2012; Jerez et al., 2016; Yamazaki et al., 2018), and phosphorus (Brinda et al., 2004; Chen et al., 2011; Fan et al., 2014; Roopnarain et al., 2014; Singh et al., 2019) affect the production of several pigments produced by numerous M&C species.

4.1.5. Salinity

Medium salinity is an additional abiotic factor that influences pigment production by microorganisms (Sun et al., 2023). Higher concentrations of NaCl also caused an increase in the carotenoid content per cell in *H. pluvialis* (Tam et al., 2012), and in *A. quadricellulare* PUMCC 5.1.1, higher amounts were obtained under 0.17 mM of NaCl (Singh et al., 2019). The ideal sea salt concentration for high carotenoid production is between 25 and 30 g/L for the microalgae *Heterosigma akashiwo* BMCC75, *Chrysochromulina rostralis* BMCC18, and *Amphidinium carterae* Dn241EHAU (Macías-de la Rosa et al., 2024). Other carotenes, such as astaxanthin and canthaxanthin, show increased accumulation in *C. zofingiensis* under salt stress conditions (Pelah et al., 2004). Fucoxanthin is produced by *P. tricornutum*, *C. muelleri*, and *Tisochrysis lutea* at a salinity of 45 ppt (Ishika et al., 2017).

Previous studies have reported that high salt concentrations inhibit the production of PBPs by organisms such as *S. platensis* and *Anabaena* NCCU-9 (Hemlata and Fatma, 2009; Sharma et al., 2014). Despite these findings, the opposite has been observed in other microorganisms such as *Phormidium* sp., *Oscillatoria* sp., *Anabaena* sp., and *Spirulina maxima*, where higher salt concentrations enhance PBP production (Abd El-Baky and El-Baroty, 2012; Hemlata and Fatma, 2009; Jonte et al., 2013). The production of Scy by *Chroococcidiopsis* sp. UAM571 increased in a medium supplemented with 20 g/L NaCl (Casero et al., 2024).

The information shared in the quoted research is relevant for a greater yield of pigments by M&C species. The variety of strains and conditions to study makes it challenging to optimise a cross-cutting methodology to produce these bioactive compounds. Other abiotic factors, such as aeration, must be investigated to understand their influence and impact on these organisms and their compounds. Nevertheless, several scaling up strategies can be implemented to achieve a higher pigment production.

4.2. Scaling up strategies for the production of microalgae and cyanobacteria pigments

The transition from laboratory-scale cultivation to large-scale production presents significant challenges that require the optimisation of biological, technological and economic factors (Fig. 3). Overcoming these challenges will enable the industrial application of M&C pigments and guarantee their complete acceptance by markets and consumers.

Algal biorefinery emerges as a suitable solution for an optimized, sustainable and harnessing production of M&C products. The concept focuses on the exploitation of algae biomass to produce a variety of high value bioproducts, such as biofuels, chemicals and other compounds (Ferreira and Gouveia, 2020). This optimisation strategy makes it feasible the parallel extraction of several products from the same biomass, as well the remnant uses for other purposes, as agriculture, which can maximize resource use and profitability, demonstrating its viability and sustainable approach (Massa et al., 2024).

Nevertheless, other challenges in scaling up pigment production include high investment and operation costs, large contamination risks and regulatory barriers (Ferreira and Gouveia, 2020). Hence, research to optimise production methods is required to ensure the industrial production of M&C pigments and viable application of these bioproducts.

Selecting the appropriate strain is as fundamental as optimising the cultivation conditions. Different strains exhibit diverse capacities for

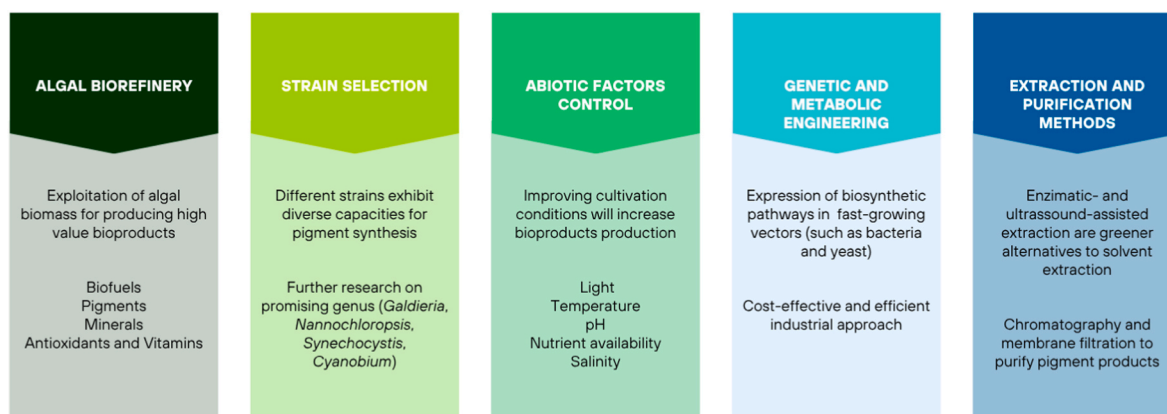


Fig. 3. Elements to consider in the up-scale production of M&C pigments.

pigment synthesis, growth rates and tolerance to environmental conditions. Therefore, strain selection should prioritise high pigment yields, rapid growth rates and robustness in large-scale systems (Assunção et al., 2023; Pagels et al., 2019; Sandybayeva et al., 2022). The use and study of species/genus derived from inhospitable environments may represent an interesting solution for an efficient choice of suitable strains, given the resistance and adaptability of these microorganisms to adverse conditions. The search for new strains with high yields of M&C pigments is necessary to strengthen the implementation of these pigments at an industrial level. Currently, large-scale production is carried out with a small number of strains, which may not represent the real potential of M&C for pigment production. Further research should be performed in the genus *Galdieria*, *Nannochloropsis*, *Synechocystis* and *Cyanobium*, that already proven to be great pigment producers by several authors (Assunção et al., 2023; Pagels et al., 2020; Portillo et al., 2022; Vadiveloo et al., 2017). In the same sense, the high level of experience in the production of certain M&C species, such as *Dunaliella* sp., *Haematococcus* sp., *Spirulina* sp. and *Chlorella* sp., can provide expertise for new production processes with different genus.

The main abiotic factors such as light, temperature, pH and nutrient availability can significantly affect pigment production. Increasing pigment yields should begin by improving the cultivation conditions (Assunção et al., 2023; Pagels et al., 2019; Sandybayeva et al., 2022). Several cultivation systems can be used to scale up the production of pigments. Open pond systems, such as raceways and ponds, offer cost-effective solutions but are vulnerable to contamination and weather fluctuations. Photobioreactors, including vertical columns and flat panels, provide higher productivity under controlled conditions (Sandybayeva et al., 2022).

Genetic and metabolic engineering are powerful tools to enhance pigment production. Overexpression of key biosynthetic pathway genes can significantly increase yields. Synthetic biological approaches, including the construction of heterologous expression systems, can enhance pigment production by expressing biosynthetic pathways in bacterial or yeast vectors with higher growth rates, resulting in a more cost-effective and efficient industrial manufacturing procedure (Assunção et al., 2023; Pagels et al., 2019; Saini et al., 2018; Sandybayeva et al., 2022). Several ongoing studies have already succeeded, on a laboratory scale, in developing heterologous expression systems with *E. coli* to produce carotenoids (Lee et al., 2024; Xinrui et al., 2023) and PBPs (Wu et al., 2018; Liu et al., 2023). Other approaches are also being explored by some researchers, such as overexpressing genes related to the heme synthetic pathway in *Synechocystis* sp. for producing PC (Cao et al., 2023), or the production of carotenoids through genes overexpression in *Aurantiochytrium* sp. (Shao et al., 2025).

Efficient extraction methods are essential for large-scale recovery of pigments. Solvent extraction is the most common technique; however, it often requires toxic solvents. Enzymatic- and ultrasound-assisted

extraction offer greener alternatives. Supercritical fluid extraction provides high purity and yield but involves high operational costs. Downstream purification steps, including chromatography and membrane filtration, further refine pigment products for commercial applications but imply higher costs to the production system (Pagels et al., 2021a; Sandybayeva et al., 2022).

In line with environmental regulations, the sustainable and eco-friendly characteristics of these pigments must be prioritised over the economic aspects of their production. Despite the necessity to secure sufficient production for the industrial application of these pigments, it is also important to raise consumers' and the industrial sector's awareness of the aspects associated with this production and application.

5. Market acceptance of microalgae and cyanobacteria pigments as sustainable alternatives

The significance of sustainable consumption is linked to the re-emergence of public consciousness regarding environmentally friendly solutions to major pollution problems. Consumers and businesses are becoming increasingly aware of environmental issues, climate change and the profound impact of human activities on the planet. This heightened awareness has led to a growing demand for eco-friendly and sustainable products (Hartmann and Apaolaza-Ibáñez, 2012). Nevertheless, changes in consumption patterns are required to ensure sustainable consumption.

Developed countries have attempted to alter their consumption patterns by implementing environmental taxes, eco-labels, process and product standards, and other strategies. Recently, these countries have introduced new regulations, legislation and policies to achieve a greater state of sustainability by targeting all phases of the product life cycle (Commission, 2019, 2020, 2021a), including the European Green Deal (EGD). The EGD is a pact between 27 European Union member states that aims to make the European Union climate-neutral by 2050, by employing a comprehensive set of policy initiatives. It involves various sectors, including energy, transport, industry and agriculture, with the goal of advancing the circular economy (Commission, 2019).

Market acceptance of sustainable products has been a requirement for improving several industries and sectors, which is also related to the wide range of regulations and standards enforcing companies' green transition and circular economy implementation in their products, processes and facilities (e.g. consumption, waste management and environmental footprint) (Commission, 2021a, 2021b). Regulatory approval from organisations such as the Food and Drug Administration and European Food Safety Authority for the use of microalgal pigments in food and cosmetics further strengthens their credibility and market acceptance (Enzing et al., 2014; Mendes et al., 2022).

Green marketing is an active strategy implemented by brands and enterprises that sums environmental sustainability as the third aim

beyond consumer satisfaction and company profitability (Dangelico and Vocalelli, 2017). Public demand for green/natural products and environmentally friendly processes is evident and studies have been conducted to assess the market approval of these products. Despite being used interchangeably, the concept of green products has a different meaning from that of natural products. A green product is defined as “a product whose design and/or attributes, production, and/or strategy use recycling (renewable/toxic-free/biodegradable) resources, thereby enhancing its environmental impact or reducing environmental damage throughout its entire life cycle” (Durif et al., 2010). In contrast, a natural product is a chemical compound or substance produced by living organisms (Ige et al., 2012).

The WTP can be defined as the maximum amount of money an individual consumer is willing to spend or invest in a particular product, service, or attribute (Le Gall-Ely, 2009). This value has been analysed for sustainable goods and services, usually called green products. The range of WTP values for green products differs significantly among studies.

Li and Kallas (2021) developed a meta-analysis of consumers' WTP for sustainable food products, and their results suggested that an average of 29.5 % of consumers are willing to pay a premium for these products (Li and Kallas, 2021). U.S. consumers are reported to have a WTP of approximately 51 % more for a green product, with higher values observed in Europe (Xia et al., 2022). Despite this, the same study found that although consumers' WTP as a premium for green products increases retail prices and the market share of such products, it does not necessarily make the supply chain greener or improve environmental quality. Instead, it incentivises retailers and manufacturers to invest in green technology (Xia et al., 2022).

Consumers are increasingly demanding clean labels and plant-based ingredients in the food, cosmetics and textile industries. In a study conducted in the East, consumers' WTP premiums for green products was strongly influenced by their trust in these products, highlighting the importance of innovation in the development of these products (Biswas, 2016). Gomes et al. (2023) verified that Generation Z (the generation born between 1997 and 2012) was willing to pay extra for green products because of environmental concerns (Gomes et al., 2023).

Concerning natural and organic products, organic food items have the highest estimated WTP (Li and Kallas, 2021). Morone et al. (2021) found compelling evidence of a higher WTP for bio-based products; however, consumers with a lower WTP were less prone to choosing

bio-based products than conventional alternatives (Morone et al., 2021). In an analysis of the WTP for natural food products, Migliore et al. (2018) obtained interesting results, as approximately 68 % of Italian chewing gum consumers had an extra WTP for the natural attribute of chewing gum (Migliore et al., 2018). Moreover, in a study conducted in Spain, the unlikely consumers' WTP premium for organic food products was almost zero, in contrast to likely or actual organic food consumers, who were willing to pay more for these characteristics (Gil et al., 2000). This study also found that organic attributes were more important in fresh or perishable products for increasing consumers' WTP. Consumers from the production regions of these natural products exhibited a higher WTP than those from the consumption regions (Gil et al., 2000). Ratajczak et al. (2023) found that 61 % of Poland consumers are willing to pay a higher price for natural cosmetic products (Ratajczak et al., 2023).

In a report presented by Tuovila (2024), the WTP premium for a sustainably manufactured garment was evenly divided among age groups. In the same study, the main barrier described by consumers for purchasing circular garments was the price and own financial situation. Nevertheless, consumers have a very positive attitude towards such garments, proving consumers acceptance (Tuovila, 2024).

The literature reports several factors that affect consumers' WTP for green/natural products (Fig. 4). Migliore et al. (2018) reported that personal characteristics are less relevant for consumers' choice for purchasing natural products compared with altruistic motivations (Migliore et al., 2018). Age (younger groups related to higher WTP premium), sex (females have higher WTP values), region (Asian and European WTP value higher than North American WTP) and literacy (higher-educated consumers have lower WTP premium) are as the main factors that influence the WTP for green products (Gomes et al., 2023; Li and Kallas, 2021; Petrescu-Mag et al., 2019; Wei et al., 2018).

The opposite finding has been described in other studies (Morone et al., 2021; Xia et al., 2022), where consumers' sense of guilt and personal reasons were the most relevant to an increased WTP premium for green/natural products. Some investigations have described the motivations behind the higher WTP for these products, such as the presence of fewer chemical substances and the sustainable attributes of the products (Gomes et al., 2023; Li and Kallas, 2021; Petrescu-Mag et al., 2019; Ratajczak et al., 2023). The main reasons presented in the literature are related to environmental awareness and care (Li and



Fig. 4. Main influences leading to increased market acceptance of natural/green products. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Kallas, 2021; Ratajczak et al., 2023; Shi and Jiang, 2023; Wei et al., 2018).

Overall, these studies indicated that consumers are willing to pay premiums for green products, particularly when trust and innovation are strengthened. Accordingly, the market acceptance of natural and sustainable alternatives, such as M&C pigments, aligns with increasing consumer awareness of environmental sustainability, coupled with regulatory advancements and corporate green initiatives, which have driven a growing demand for eco-friendly products.

However, substantive industrial implementation of M&C pigments is limited to a narrow range of products in particular sectors, as outlined above. Large-scale production of natural M&C pigments is insufficient to meet demand, which leads to a loss of interest by the market and, consequently, to low business volumes. In addition, the cost of the conventional/synthetic product is generally lower than the more sustainable alternative, leading to reduced interest from industries. Nevertheless, despite slower industrial acceptance, there is a growing need for these products to fulfil consumer concerns and regulatory obligations. This leads to large adverts from companies, even to attract investors and to pursue research, that end up failing to satisfy public demand. It is essential to recognise the limitations of large-scale production of M&C pigments and the primary approach should focus in raising awareness and changing the paradigm.

6. Conclusion and future prospects

This study explores the potential of M&C pigments across diverse industrial sectors, including food and feed, cosmetics and textiles. These naturally derived colourants boast vibrant colours, safety assurance, functional advantages and eco-friendly attributes, perfectly aligning with the growing demand for sustainable solutions, proving the heightened demand for these pigments, represented by their high market values.

However, significant challenges persist in scaling up production, driven by concerns regarding cost-effectiveness, yield optimisation, purity enhancement and stability maintenance. Overcoming these obstacles is paramount to unlock the full transformative capacity of M&C pigments, enabling them to drive sustainable consumption practices and effectively mitigate environmental repercussions. Several approaches can be applied to overcome the hurdles of large-scale production of M&C pigments, passing through an optimisation of culture conditions, strain selection, genetic and metabolic engineering and purification methods. Algal biorefinery can be considered a more effective strategy for achieving a sustainable industrial application of these pigments. The study of new genus, or even species, with promising attributes is necessary to ensure continuity industrial applicability.

Furthermore, the crucial role of market acceptance cannot be overstated, highlighting the need to address these challenges promptly. Large-scale production processes are scarce, leading to resistance from numerous industrial sectors to a more regular and widespread application of these pigments. In the near future, the application of M&C pigments will probably lie in small industrial niches, in which smaller quantities and less pure products are used, prospecting the challenge in transitioning to an all-natural colouring process.

In the author's perspective, sustained efforts in research, innovation and collaboration requires to be done so that these pigments have a proper application at an industrial level. A change in mindset is fundamental for industrial sectors, such as textile and clothing industry, are to enable greater inclusion of these pigments in their colouring processes. This is essential to pave the way for a sustainable future in which natural resources are responsibly utilised to meet the needs of both current and future generations.

CRedit authorship contribution statement

Mariana Reimão: Writing – review & editing, Writing – original

draft, Conceptualization. **Liliana Almeida:** Writing – original draft, Conceptualization. **Cristiana Ramos:** Writing – review & editing. **Nádya Eusébio:** Writing – review & editing. **Rosário Martins:** Writing – review & editing. **Manuela Vieira da Silva:** Writing – review & editing. **Vitor Vasconcelos:** Writing – review & editing. **Marisa Freitas:** Writing – review & editing, Validation, Supervision, Conceptualization.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jclepro.2025.146071>.

Data availability

No data was used for the research described in the article.

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