Regulation of algal and cyanobacterial auxin production, physiology and application in agriculture: an overview

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Abstract

(220 words)

Algal bioproducts are of growing interest to agriculture because of their biodegradable nature, ability to restore soil fertility, and capacity for plant growth regulation, nitrogen fixation and carbon sequestration. Plants respond to a suite of growth hormones, and auxins present in algal extracts or secreted exogenously by living algae, may be partially responsible for the stimulation of plant growth by algae. Auxins are a major class of phytohormones that influence plant growth and development. The roles of auxins in algae and in plants are well described, but studies on the role of auxins in plant-algae interactions remain scarce. This review summarizes the body of knowledge on the production of auxins and their physiological roles in seaweeds, cyanobacteria and microalgae. Common and differential auxin-associated phenotypes of these algae, including the effect of growth conditions on their auxin production, are also described. Potential mechanisms by which auxins from algae mediate plant development at both phenotypic and molecular levels is also provided. Algal-derived auxins are an environmentally sustainable option for promoting plant growth and yield, but knowledge of their precise mechanisms of action is still rudimentary. Elucidating the pathways by which algal auxins stimulate plant responses, and the means by which key environmental factors influence those pathways, will help to harness the full potential of algal-derived auxins for agricultural development and resource conservation.

Keywords

Auxin, indole-3-acetic acid, auxin production, seaweed, cyanobacteria, microalgae, plant growth promotion

Declarations

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Authors' contributions

C-YT, ICD and SR conceived and designed the structure of the review. C-YT conducted the literature search, data analysis and drafted the entire manuscript. All authors revised and edited the manuscript.

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Introduction

Algae are a group of photosynthetic unicellular or multicellular organisms that lack major structural features such as roots, stems and leaves, thereby distinguishing them from higher plants (Brennan and Owende 2010). There are two main groups of algae: eukaryotic algae comprise macroscopic (seaweeds) and microscopic (microalgae) species, whereas cyanobacteria (or blue-green algae) are photosynthetic prokaryotes (Jaiswal et al. 2018). Algae can contribute to sustainable agriculture by enhancing seed germination rates and promoting plant growth via improved soil fertility and increasing yields (Priyadarshani and Rath 2012). They are especially valuable in increasing soil microbial activities, increasing soil nitrogen and carbon content and reducing soil alkalinity, salinity and electrical conductivity (Renuka et al. 2018a). For example, seaweed products have been used for centuries as soil conditioners (Khan et al. 2009). Live cyanobacterial biofertilizers are widely applied to rice fields to fix atmospheric nitrogen, supplying an additional 15-90 kg N/ha, to enhance grain yield (Mishra et al. 2018). There is increasing commercial interest in developing new resources from algae because of their rapid biomass accumulation and the presence of various metabolites such as carotenoids, polyphenols, tocopherols, vitamins, fatty acids and phytohormones that are valuable to industry, agriculture, human nutrition and medicine. Because bio-products derived from algae, in the form of bio-inoculants and bio-stimulating extracts, can also be easily made available (Renuka et al. 2018a), there has been a recent increase in reported studies on their potential use in agriculture.

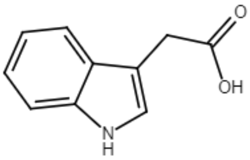
The growth-promoting effects of algae are partly attributed to their secretion of phytohormones, a group of signal molecules essentially involved in physiological growth and stress responses of plants (Stirk and van Staden 2020). Algae, like higher plants, can produce various phytohormones such as auxins, cytokinins, gibberellins, jasmonic acid, abscisic acid and ethylene that are responsible for regulating crop growth and stress-tolerance (Singh et al. 2017). Auxins are one of the most studied phytohormones, particularly because of their key roles in diverse growth and developmental processes (Taiz and Zeiger 1998). Auxins are critically important in plant development: several auxin biosynthesis pathways exist in plants and a fully auxin-deficient mutant has not been isolated, indicating that complete loss of auxin-related genes could be detrimental or even lethal (Teale et al. 2006). The roles of auxin in algae are now better understood and algal-derived auxins can significantly enhance plant growth, including regulation of auxin activities, anther induction, seed germination, regeneration of tissue, stimulation of root and shoot growth, regulation of phytochemical composition and grain yield (Gayathri et al. 2015; Hussain and Hasnain 2011; Jäger et al. 2010; Mazhar et al. 2013; Prasanna et al. 2010; Singh 2014; Rayorath et al. 2008; Stirk & van Staden 1996; Stirk et al. 2013). Information regarding the control of auxin biosynthesis in algae and the physiological effects of algal auxins on plants is still fragmentary. A better understanding of growth conditions that enhance auxin production in algae is needed. In this review, the role of auxins in algae, the internal and external factors affecting auxin production, and the potential for algal auxin to mediate plant development are discussed.

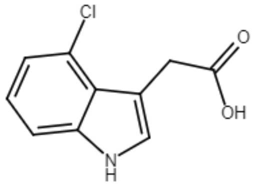
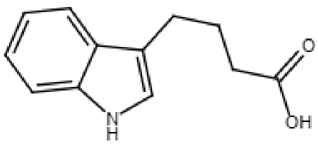
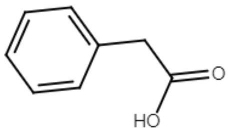
What are auxins?

Auxins are a class of phytohormones (plant hormones) involved in multiple developmental processes *in planta*. Apart from higher plants and algae, auxin is also reported in bacteria, animal tissues, and fungi (Kiseleva et al. 2012). Auxin was the first major phytohormone to be discovered and is a key regulator of cell division and elongation, tissue differentiation, tropisms, apical dominance, senescence, abscission and flowering (Taiz and Zeiger 1998). Because of its versatile influence in a great number of processes, auxin has been long recognized as “the plant growth hormone”. Auxins, either in natural or synthetic forms, are widely applied to root cuttings, obtain seedless fruit, hasten fruit ripening and to prevent premature fruit drop (Serban et al. 2016). Auxin in low concentrations promotes plant growth but is lethal to plants at high concentrations and can be used as a herbicide to control weeds (Grossmann 2007).

Auxins are small organic compounds constituting an aromatic ring and a side chain with a carboxylic acid group. Indole-3-acetic acid (IAA) is the most physiologically active member of the auxin family (Simon and Petrášek 2011). Most knowledge on the influence of auxins on physiological processes in plant cells concerns IAA with the term IAA often used synonymously with auxin. Besides IAA, plants also synthesize other types of auxin (Table 1).

Table 1 Types of auxin and their roles in plant development (adapted from Simon and Petrášek 2011)

Auxin	Abbreviation	Chemical structure	Roles
Indole-3-acetic acid	IAA		The most potent active auxin. Involved in embryogenesis, organogenesis, vascular tissue development, differential growth, senescence, plant-pathogen interactions,

			response to environment and abiotic stress.
Indole-3-butyric acid	IBA		Storage form and source for IAA. More stable than IAA.
4-chloroindole-3-acetic acid	4-Cl-IAA		Specializes in the development of seeds and fruits. Often more active than IAA in root, epinasty, parthenocarpy and pericarp growth.
Phenylacetic acid	PAA		Produced by root symbiotic bacteria for interaction with plant roots.

IAA biosynthesis pathways

Multiple pathways for IAA biosynthesis have been well described. Many studies on IAA biosynthesis use the model plant, *Arabidopsis thaliana*, which has the advantage of being small in size, easy to grow with short generation times and has the ability to reproduce prolifically. Its genome is relatively small and has been completely sequenced (The Arabidopsis Genome 2000), making it useful for mapping and sequencing analyses in molecular research. In addition, *A. thaliana* mutants of various genes are available for molecular-level studies of specific processes and characterization of genes and/or proteins (Somerville and Meyerowitz 2007). In general, IAA can be synthesized from indole through both tryptophan (Trp)-dependent and Trp-independent pathways (Kiseleva et al. 2012; Woodward and Bartel 2005).

Tryptophan-dependent pathway

The Trp-dependent pathways of IAA biosynthesis are distinguished through the production of four major compounds i.e. (i) indole-3-pyruvic acid (IPyA), (ii) tryptamine (TAM), (iii) indole-3-acetaloxime (IAOx), and (iv) indoleacetamide (IAM) which are synthesized from the same precursor, Trp (Fig. 1) (Bogaert et al. 2019; De Smet et al. 2011 ; Le Bail et al. 2010; Mashiguchi et al. 2011). The IPyA pathway is considered the major pathway of IAA production in many plants and bacteria. Another common pathway involves the conversion of TAM to N-hydroxyl-TAM by flavin monooxygenase (YUC) enzyme and finally to IAA. Previous studies have proposed that Trp aminotransferase (TAA) and YUC operate independently in two different pathways. However, both TAA-deficient and YUC-deficient *Arabidopsis* mutants have similar phenotypes and insignificant change in IAA levels, suggesting that both TAA and YUC enzymes could probably function in converting IPyA to IAA via the same pathway (Mashiguchi et al. 2011). The IAOx pathway includes the production of IAOx from Trp under the influence of Trp N-monooxygenase (CYP79B) family and was observed only in relatively few plant species (Mashiguchi et al. 2011). The IAOx pathway is detected exclusively in Brassicaceae plants with the ability to synthesize glucosinolates from IAOx as defense metabolites and it is likely to operate under stresses (Korver et al. 2018; Malka and Cheng 2017). The last pathway, in which IAM is synthesized from Trp by the Trp 2-monooxygenase (IAAM) enzyme, is well known in bacteria and has been also suggested to widely exist in plants and algae due to the presence of IAM; however, the enzyme that catalyses IAM synthesis is still unclear (Gao et al. 2020; Kasahara 2016; Lehmann et al. 2010). All the IAA biosynthesis routes are conserved in algae although some enzymes remain to be elucidated (Fig. 1) and these pathways seem to vary between species and tissues (Bogaert et al. 2019; Stirk and van Staden 2020).

Tryptophan-independent pathway

The Trp-independent pathway of IAA biosynthesis likely utilises indole or indole-3-glycerophosphate as the precursor and/or intermediates in the IAM pathway. IAM can be synthesized via indole-3-glycerophosphate. Besides IAM, IAN or IPyA may be produced in this pathway, but the catalytic enzymes remain unclear (Di et al. 2016; Mano and Nemoto 2012). Some experiments have suggested the existence of Trp-independent pathways (but see Nonhebel 2015). For instance, Trp auxotroph mutants of *Arabidopsis* and maize had higher levels of total IAA than the wild type (Müller and Weiler 2000; Normanly et al. 1993; Wright et al. 1991). Isotopic labeling experiments showed that deuterium from ^{2}H-Trp was poorly incorporated into IAA in these mutants, indicating the evidence of a Trp-independent pathway (Normanly et al. 1993; Rapparini et al. 2002; Sztein et al. 2002). This pathway has been proposed for regulation of basal auxin levels (Di et al. 2016; Ribnicky et al. 2002).

Main heading: Algae and auxin

Subheading 1: Production of auxin in algae

The presence of auxin in marine algae traces back to the 1930s when auxin-like substances were detected in extracts of seaweeds such as *Valonia macrophysa* (Van der Wey 1933), *Fucus vesiculosus* (du Buy and Olson 1937), *Bryopsis* and *Macrocystis pyrifera* (Overbeek 1940). Later, it was postulated that auxin was also present in marine diatoms when the algal extract showed bioactivity similar to that of authentic IAA in the *Avena* coleoptile straight-growth bioassay (Bentley 1960). IAA was initially isolated from seawater and marine sediments where sufficient biomass was available to extract the hormone in detectable amounts; thus, the earliest studies on IAA focused on marine species (Bentley 1960; Maruyama et al. 1989; Mazur et al. 2001). The IAA content in the marine environment was the highest in spring, varied regionally and up to 20-fold seasonally, and corresponded to the amount of organic matter present in the sediments (Mazur 1998). It was presumed, therefore, that microbial decomposition of organic matter caused phytoplankton blooms and the subsequent build-up of IAA.

The study of algal auxins was stimulated by reports of other auxins such as IBA, PAA and indole-propionic acid in algae (Bradley 1991; Craigie 2011). Auxins were also discovered in cyanobacteria (Sergeeva et al. 2002; Singh 2014) and microalgae (Lu and Xu 2015; Tarakhovskaya et al. 2007), and additional studies described the roles and transport of auxins within the algal body (De Smet et al. 2011; Khasin et al. 2018; Zhang and van Duijn 2014). Many elements of the canonical auxin response pathway in higher plants exist in the Chlorophyta and Streptophyta, which include the closest algal relatives to land plants, but the role of auxins in these algae is not fully understood (De Smet et al. 2011). Unicellular green algae in the Chlorophyta have simpler auxin-signaling elements and pathways that differ fundamentally from the canonical auxin machinery of higher plants, indicating that complex auxin signaling evolved somewhere between the diversification of the Chlorophyta and Streptophyta and the evolution of early land plants (De Smet et al. 2011). The Charophyceae, in clade Streptophyta, are considered the closest relatives of plants but still lack TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX (TIR1/AFB), Auxin/INDOLE-3-ACETIC ACID (Aux/IAA) and AUXIN RESPONSE FACTOR (ARF) proteins that mediate the canonical TIR1-Aux/IAA-ARF auxin signaling pathway in land plants (Mutte et al. 2018; Ohtaka et al. 2017). The existence of an auxin carrier system in *Chara*, a multicellular alga in the Charophyceae, is considered a function of the evolution of multicellularity rather than the morphological evolution of a plant body (Dibb-Fuller and Morris 1992). The auxin signaling mechanisms in algae seem to expand from unicellular, subsequently to multicellular or filamentous and to more complex thalloid forms (De Smet et al. 2011). The presence of auxins in distant algal relatives of plants, the brown algae, including basal lineages of green algae, suggests that auxins played important functional roles in algae long before the appearance of land plants (Bogaert et al. 2019).

Many studies report the presence of auxin in algae (Table 2). IAA biosynthesis in algae, as in plants and bacteria, is regulated by several internal and external factors (Fig. 2). Understanding the factors that influence algal IAA production can be beneficial should algae-derived IAA become an alternative source to meet industrial or agricultural needs.

Table 2 Comparison of endogenous and exogenous auxin concentrations in various unicellular and multicellular microalgae, cyanobacteria and seaweeds

Algae	**Auxin concentration**				**Remarks**	**References**
	Endo	**Exo***	**unit**			
Seaweeds						
Chlorophyta						
Caulerpa paspaloides	5.5 – 7.5	-	µg/g	DW	Harvested from natural beds	(Jacobs et al. 1985)
Cladophora glomerata	253	-	µg/g	DW	Harvested from natural beds; concentration in dried extract	(Górka and Wieczorek 2017)
Monostroma oxyspermum	22.5	-	nmol/g	FW	Grown in laboratory; thalli sample	(Gupta et al. 2011)
Ulva fasciata	100 – 2600	-	pmol/g	DW	Harvested from natural beds; thalli sample; pool of six bimonthly collections	(Stirk et al. 2009)
	16.7	-	nmol/g	FW	Harvested from natural beds; thalli sample	(Gupta et al. 2011)
Ulva lactuca	49.3	-	ng/g	DW	Concentration in dried extract	(Benítez García et al. 2020)
	32.5	-	nmol/g	FW	Harvested from natural beds; thalli sample	(Gupta et al. 2011)
Ulva linza	31.7	-	nmol/g	FW		
Ulva reticulata	46.4	-	nmol/g	FW		
Ulva taeniata	27.1	-	nmol/g	FW		
Phaeophyta						
Ascophyllum nodosum	6 – 615	-	ng/g	DW	Commercial dried extract	(Wally et al. 2013)
	9.7 – 32.4	-	nmol/L		Commercial liquid extract	(Ertani et al. 2018)
Dictyota humifusa	200 – 900	-	pmol/g	DW	Harvested from natural beds; thalli sample; pool of six bimonthly collections	(Stirk et al. 2009)
Ecklonia maxima	11.7	-	nmol/L		Harvested from natural beds; concentration in liquid extract	(Stirk et al. 2004)
Ecklonia sp.	9.7 – 22.2	-	ng/g	DW	Commercial dried extract	(Wally et al. 2013)
Laminaria japonica	90 – 95	-	µg/kg	FW	Harvested from natural beds	(Li et al. 2007)
Laminaria sp.	14.6	-	nmol/L		Commercial liquid extract	(Ertani et al. 2018)
Macrocystis pyrifera	9.83	-	nmol/L		Harvested from natural beds; concentration in liquid extract	(Stirk et al. 2004)
Macrocystis sp.	14.6	-	ng/g	DW	Commercial dried extract	(Wally et al. 2013)

Padina durvillaei	39.0	-	ng/g	DW	Harvested from natural beds; concentration in dried extract	(Benítez García et al. 2020)
Sargassum sp.	1091	-	ng/g	DW	Commercial dried extract	(Wally et al. 2013)
Rhodophyta						
Chondracanthus teedei	9081	-	pmol/g	DW	Harvested from natural beds except *Hypnea* (grown in laboratory)	(Yokoya et al. 2010)
Gelidium floridanum	575	-	pmol/g	DW		
Gracilaria birdiae	924	-	pmol/g	DW		
Gracilaria cervicornis	122	-	pmol/g	DW		
Gracilariopsis tenuifrons	9.1	-	pmol/g	DW		
Hypnea musciformis	46 – 1984	-	pmol/g	DW		
Hypnea nigrescens	946	-	pmol/g	DW		
Phorphyra acanthophora	225 – 289	-	pmol/g	DW		
Phorphyra perforata	100	-	ng/kg	FW	-	(Zhang et al. 1993)
Microalgae						
Charophyceae						
Klebsormidium flaccidum	18	-	µg/g	DW	Harvested on early stationary phase	(Jäger et al. 2010)
	~1	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Chlorophyceae						
Acutodesmus acuminatus	~2	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Acutodesmus incrassatulus	~9	-	nmol/g	DW		
Acutodesmus obliquus	~6 (200-230)	-	µmol/L (amol/cell)		Harvested on day 7. Concentration increased during growth and maximized with trans-zeatin	(Piotrowska-Niczyporuk et al. 2018)
Chlorococcum ellipsoideum	~10	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Chlamydomonas reinhardtii	~38	-	nmol/g	DW		
Coccomyxa sp.	~4	-	nmol/g	DW		
Coelastrum microporum	~106	-	nmol/g	DW		
Desmodesmus armatus	~12	-	nmol/g	DW		
Gyoerffyana humicola	~5	-	nmol/g	DW		

Haematococcus pluvialis	~1.8	-	nmol/g	DW	-	(Jirásková et al. 2009)
Monoraphidium contortum	~12	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Nautococcus mamillatus	~3	-	nmol/g	DW		
Poloidion didymos	~73	-	nmol/g	DW		
Protococcus viridis	~1	-	nmol/g	DW		
Protosiphon botryoides	~2	-	nmol/g	DW		
Raphidocelis subcapitata	~12	-	nmol/g	DW		
Scenedesmus armatus	-	6.7 – 57.2	nmol/L		Harvested on day 7 (growth phase); concentration increased when supplied with 2% CO_2	(Mazur et al. 2001)
Scenedesmus obliquus	-	1.12 – 4.0	µmol/L		Harvested during exponential growth; varied illuminance, aeration and agitation rates	(Prieto et al. 2011)
Scotiellopsis terrestris	~3	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Spongiochloris excentrica	~5	-	nmol/g	DW		
Stigeoclonium nanum	~3	-	nmol/g	DW		
Prymnesiophyceae						
Emiliania huxleyi	-	~200	µmol/L		Harvested on day 8 (stationary phase) from cocolith bearing strain; supplied with tryptophan	(Labeeuw et al. 2016)
Trebouxiophyceae						
Chlorella minutissima	~1	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
	0.85 – 26.8	-	µg/g	DW	Harvested on synchronous culture; concentration increased gradually in active-growing conditions	(Stirk et al. 2014)
Chlorella pyrenoidosa	0.5 – 1.46	-	µg/g	DW	Synchronous culture of 2 light:dark cycles; concentration increased from autospore to adolescent stage	(Grotbeck and Vance 1972)
	-	4.6	nmol/L		Harvested on day 7 (growth phase)	(Mazur et al. 2001)
	~3	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Chlorella sorokiniana	~0.25	1.0	nmol/L		Harvested on day 2	(Khasin et al. 2018)
Chlorella vulgaris	37	-	ng/g	FW	-	(Lu et al. 2010)
	~29	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Chlorella spp.	0.19 – 14.3	-	nmol/g	DW	Harvested on early stationary phase	(Jirásková et al. 2009)
Myrmecia bisecta	~2	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Stichococcus bacillaris	~1	-	nmol/g	DW		

Ulvophyceae						
Ulothrix sp.	~2	-	nmol/g	DW	Harvested on day 4 (exponential phase)	(Stirk et al. 2013)
Cyanobacteria						
Cyanophyceae						
Anabaena sp.	-	0 – 11.4	µg/mL		Harvested on day 21 (late log phase); concentration increased over time; highest under continuous light	(Prasanna et al. 2010)
	43.4	35.1	pmol/mg Chl-a		Harvested on week 3	(Hussain et al. 2010)
	12	-	µg/g	DW	Harvested on early stationary phase	(Jäger et al. 2010)
Anabaena spp.	-	0.11 – 11.2	µg/mL		Harvested on week 4 & 8 (late log & stationary phase)	(Prasanna et al. 2008)
	-	0.15 – 1.0	µg/mL		Mixed strains isolated from rice rhizospheres; grown in light and dark	(Prasanna et al. 2009)
Anabaena vaginicola	2.43	-	µg/g	DW	Harvested on week 4	(Shariatmadari et al. 2015)
Anabaena variabilis	-	0.5 – 13.5	µg/mL		Harvested from day 0 to day 4; concentration increased with inceasing tryptophan	(Jaiswal et al. 2018)
Aphanothece sp.	-	~8	µg/mL		Harvested on day 15	(Gayathri et al. 2015)
Calothrix sp., *C. membranacea,* *C. ghosei*	-	0.54 – 9.33	µg/mL		Harvested on day 14; concentration decreased in dark but reversed when supplied with tryptophan	(Karthikeyan et al. 2009)
Calothrix elenkinii	-	3.71	µg/mL		Harvested on week 2	(Priya et al. 2015)
Chroococcidiopsis sp.	0.8 – 1.2	2.9 – 4.0	µg/mL		Harvested on day 7; concentration increased in symbiotic condition	(Mazhar et al. 2013)
	15.3	17.5	pmol/mg Chl-a		Harvested on week 3	(Hussain et al. 2010)
	27	45	ng/mg Chl-a		Harvested on week 5; concentration maximized in the presence of tryptophan, light, nitrate and pH 5	(Ahmed et al. 2014)
Cylindrospermum michailovskoense	16.8	-	µg/g	DW	Harvested on week 4	(Shariatmadari et al. 2015)
Cylindrospermum stagnale	-	95.6	µg/mL		Supplied with tryptophan	(Ahmad and Fatma 2017)
Fischerella muscicola	-	287	µg/mL		Harvested on day 19; concentration increased over time and with tryptophan	(Mishra et al. 2019)
Geitlerinema sp.	-	67.9	µg/mL		Harvested on day 14; supplied with tryptophan	(Babu et al. 2013)
Gloeothece sp.	3.3 – 3.5	1.2	pmol/mg Chl-a		Harvested on week 2; concentration increased when supplied with tryptophan	(Sergeeva et al. 2002)
Hapalosiphon sp., *H. intricatus*	-	0.50 – 4.56	µg/mL		Harvested on day 14; concentration decreased in dark but reversed when supplied with tryptophan	(Karthikeyan et al. 2009)

Leptolyngbya sp.	-	51.1	µg/mL		Harvested on day 14; supplied with tryptophan	(Babu et al. 2013)
	40	-	µg/g	DW	Harvested on early stationary phase	(Jäger et al. 2010)
	2.5 – 3.0	1.1 – 1.2	µg/mL		Harvested on day 7; concentration increased in symbiotic condition	(Mazhar et al. 2013)
Neochloris sp.	9	-	µg/g	DW	Harvested on early stationary phase	(Jäger et al. 2010)
Nostoc calcicola	2.72	-	µg/g	DW	Harvested on week 4	(Shariatmadari et al. 2015)
Nostoc muscorum	-	1 – 15	µg/mL		Harvested from day 0 to day 4; concentration increased with inceasing tryptophan	(Jaiswal et al. 2018)
Nostoc sp.	4 – 21	5 – 34	pmol/mg Chl-a		Concentration increased during 3 weeks and maximized with tryptophan; indolepyruvate decarboxylase mutants available	(Hussain et al. 2015)
Nostoc sp., *N. muscorum*	-	0.62 – 2.19	µg/mL		Harvested on day 14; concentration decreased in dark but reversed when supplied with tryptophan	(Karthikeyan et al. 2009)
Nostoc spp.	-	0.15 – 1.0	µg/mL		Mixed strains isolated from rice rhizospheres; grown in light and dark	(Prasanna et al. 2009)
	6.0 – 42.2	5.2 – 34.0	pmol/mg Chl-a		Harvested on week 2; concentration increased when supplied with tryptophan; generally symbiotic strains had higher auxin	(Sergeeva et al. 2002)
Oscillatoria annae	5.2	-	µg/g	DW	Grown for 7 – 15 days; supplied with tryptophan	(Varalakshmi and Malliga 2012)
Oscillatoria sp.	17.3	12.8	pmol/mg Chl-a		Harvested on week 3	(Hussain et al. 2010)
Phormidium sp.	3.5 – 5.0	1.8 – 2.2	µg/mL		Harvested on day 7; concentration increased in symbiotic condition	(Mazhar et al. 2013)
	5.9	5.2	pmol/mg Chl-a		Harvested on week 3	(Hussain et al. 2010)
	-	0.75 – 20	ng/mg Chl-a		Harvested on day 2; concentration increase with increasing tryptophan and decreasing %NaCl	(Boopathi et al. 2013)
Plectonema sp.	12.8 – 14.9	10.5 – 12.6	pmol/mg Chl-a		Harvested on week 2; concentration increased when supplied with tryptophan	(Sergeeva et al. 2002)
Spirulina platensis	18.2 – 211	20.1 – 194	µg/mL		Harvested on week 5; concentration increased with increasing tryptophan and decreasing pH	(Ahmed et al. 2010)
Synechocystis sp.	1.5 – 2.5	4.2 – 6.1	µg/mL		Harvested on day 7; concentration increased in symbiotic condition	(Mazhar et al. 2013)
	12.5	22.3	pmol/mg Chl-a		Harvested on week 3	(Hussain et al. 2010)
	31	60	ng/mg Chl-a		Harvested on week 5; concentration maximized in the presence of tryptophan, light, nitrate and pH 5	(Ahmed et al. 2014)
Westiellopsis prolifica	-	0.17 – 1.97	µg/mL		Harvested on day 14; concentration decreased in dark but reversed when supplied with tryptophan	(Karthikeyan et al. 2009)

Abbreviation: Endo endogenous; Exo exogenous; DW dry weight; FW fresh weight; Chl-a chlorophyll a

* Exogenous auxin concentrations were measured from culture supernatant

Subheading 2: Factors regulating auxin biosynthesis

2.1 Internal factors

a. Tryptophan

Tryptophan is a precursor of IAA biosynthesis and many microorganisms produce IAA via one or more Trp-dependent pathways. Many algae synthesize auxin in the presence of L-tryptophan, with auxin production proportional to the supply of L-tryptophan (Mazhar et al. 2013). Genomic analyses of the presence of several Trp-dependent gene orthologues within various types of algae suggest that algal cells can synthesize IAA from various tryptophan-derived precursors, as do many plants (Cock et al. 2010; De Smet et al. 2011; Labeeuw et al. 2016). Some cyanobacteria contain other homologues of auxin, IAM and Trp-dependent IAA biosynthesis enzymes such as indole-3-pyruvate decarboxylase and nitrilase (Sergeeva et al. 2002; Wenz et al. 2019). Adding 50 – 6000 µg/mL (0.24 – 29.3 mM) of L-tryptophan to the growth media of cyanobacteria such as *Spirulina*, *Nostoc*, *Anabaena*, *Phormidium* and *Fisherella* may enhance IAA production >10-fold (Ahmed et al. 2010; Mazhar et al. 2013; Mishra et al. 2019; Sergeeva et al. 2002). IAA production is more pronounced during the stationary phase of cultivation than in the early stages, possibly because tryptophan is initially used as a source of nitrogen (Sergeeva et al. 2002). Cyanobacterial auxin production also increases when co-cultivated with plants, compared to free-living conditions, presumably because tryptophan excreted by plant roots stimulates microbial release of IAA (Idris et al. 2007; Mazhar et al. 2013). The presence of high concentrations of tryptophan (>0.1 mM) in the rhizosphere of plants supports this explanation (Jaeger et al. 1999; Kravchenko et al. 2004). In the absence of tryptophan, IAA production may be negligible but not impossible for *Anabaena* and *Nostoc*, suggesting the existence of a tryptophan-independent pathway in these cyanobacteria, but this hypothesis is yet to be tested (Hashtroudi et al. 2013; Prasanna et al. 2010).

b. Organic substances

Microbial activity in soils is often limited by the availability of carbon-based substrates, which would consequently influence auxin production by cyanobacteria and other algae. Microbial production of IAA in marine sediments is enhanced when cultures are enriched with glucose and tryptophan, and incubated with algal substrates (Maruyama et al. 1989). Many algae are able to use organic and/or inorganic carbon as alternative energy sources to light. Different concentrations (0-4%) of CO_2 could only enhance the growth rate of *S. obliquus* but not its IAA production (Prieto et al. 2011). In contrast, 5 g/L glucose supplementation of dark-cultivated *Chlorella minutissima* produced 6-fold more total auxins than cultures that were light-cultivated or dark cultivated without supplementation (Stirk et al. 2014). Tryptophan addition could further IAA production in dark cultures (Karthikeyan et al. 2009). Based on similar observations in *Arabidopsis,* it has been suggested that sufficient organic energy reserves, rather than light, was a key requirement for auxin biosynthesis in algae (Sairanen et al. 2012).

Glucose alters the expression of genes in auxin biosynthesis (YUCCA), perception (TIR1), signaling (Aux/IAA) and transport (PIN) (Mishra et al. 2009). Growing *Chlorella sorokiniana* phototrophically with 2 g/L glucose increased IAA content, although higher glucose concentrations decreased IAA content (Do et al. 2020). Thus, glucose has a biphasic effect on IAA production in algae, similar to that observed in *Arabidopsis* studies where low glucose concentrations induce IAA biosynthesis through multiple pathways involving YUCCA and CYP79B genes (Mishra et al. 2009; Sairanen et al. 2012), but high glucose concentrations reduce auxin levels by repressing PIN, TIR1 and many other auxin-inducible genes (Mishra et al. 2009; Yuan et al. 2014). Glucose-mediated attenuation of IAA levels may regulate various common physiological responses in algae *in vitro* (Mishra et al. 2009; Sairanen et al. 2012).

Some algae thrive better when Provasoli's or Pringsheim's media is supplemented with soil extracts (Pringsheim 1946; Provasoli et al. 1957), suggesting the presence of growth substances (10^{-10} – 10^{-6} M) in soil (Maruyama et al. 1989). Algae can consume sugars and other substrates from root exudates or decaying organic matter for survival in dark subsoils and marine sediments, under favorable pH and moisture conditions (Maruyama et al. 1989; Shields and Durrell 1964). Treating highly weathered and nutrient-poor soils with small amounts of glucose-C (10–50 μg C/g soil) stimulates surges in microbial activity (Hoyle et al. 2008). Field trials to test the effects of short-term organic supplementation on IAA-producing algae will establish the efficacy of such treatments, which may be economical if used at crucial stages of crop establishment.

Other organic substances such as phlorotannins and alginates also influence endogenous auxin levels. Phlorotannins in seaweeds serve as protective compounds against viral and microbial infections, UV radiation and metal toxicity; thus, they possess beneficial pharmacological and agricultural potential (Shi et al. 2018; Stirk et al. 2020). Both phloroglucinol and eckol from phlorotannins promote growth in *Eucomis autumnalis* bulbs with increased auxin levels and inhibited IAA oxidase activity (Aremu et al. 2015). Alginates constitute the cell wall of seaweeds and are widely used as gelling, thickening, stabilizing, and emulsifying agents and recently as plant biostimulants (Stirk et al. 2020). Alginate oligosaccharides stimulate root growth in rice (*Oryza sativa*) by increasing expression of YUCCA, IAA and PIN genes while reducing IAA oxidation (Zhang et al. 2014). The effects of phlorotannins and alginates on algae remain to be further elucidated.

c. Other hormones

Many phytohormones regulate physiological responses, with crosstalk between hormones either synergistic or antagonistic (Stirk et al. 2020), whereby one hormone affects the biosynthesis or downstream signaling, of another (Bajguz and Piotrowska-Niczyporuk 2013). For example, other phytohormones such as cytokinins, gibberellins, brassinosteroids and abscisic acid can all affect auxin biosynthesis, as discussed below.

Cytokinins play versatile roles in algae including cell division, cell differentiation and morphogenesis, rhizoid and thallus growth, chloroplast development, regulation of photosynthetic activity, production of metabolites and stress tolerance (Han et al. 2018; Stirk et al. 2020). Total cytokinins were apparently high during early exponential growth (cell division) of the microalga *Scenedesmus obliquus*, decreasing gradually as population growth approached a stationary phase, although auxin levels continued to increase (Žižková et al. 2017). Exogenously supplied cytokinins (0.01 μM trans-zeatin or 0.1 μM kinetin or 1 μM N,N'-diphenylurea) increased IAA level in another microalga, *Acutodesmus obliquus*, accompanied by cell elongation and enhanced growth rate (Piotrowska-Niczyporuk et al. 2018). Adding same amount of these cytokinins to *A. obliquus* cultures also alleviated the inhibitory effect of lead (Pb) toxicity by improving growth and viability associated with auxin biosynthesis (Piotrowska-Niczyporuk et al. 2020). While cytokinin promoted formation of new lateral branches of the seaweed, *Grateloupia dichotoma*, auxin induced elongation of these branches (Yokoya and Handro 1996). These observations demonstrate that cytokinins may serve as synergistic signaling molecules of auxin biosynthesis for cell proliferation under both favourable and unfavourable conditions. Loss or mutation of cytokinin biosynthetic gene(s) could reduce the rate of auxin biosynthesis (Jones et al. 2010). High levels of auxin, however, may inhibit cytokinin biosynthesis via negative feedback, especially in mature algal cells or tissues, similar to higher plants (Jones et al. 2010; Woodward and Bartel 2005; Žižková et al.

2017). The timing and correct ratio of exogenously applied auxins and cytokinins is crucial, therefore, for promoting desired growth responses in algae (Stirk et al. 2013; Yokoya and Handro 1996).

Gibberellins are involved in cold responses and the stimulation of light-regulated processes in plants such as seed germination, shoot elongation, leaf expansion, flowering and fruiting (Stirk and van Staden 2020; Yamaguchi 2008). In algae, gibberellins are associated with cell expansion, activation of cell division, increased metabolism and the accumulation of pigments and lipids (Han et al. 2018; Romanenko et al. 2016; Stirk et al. 2014; Stirk et al. 2019). Although gibberellin (1 – 10 nM GA3) enhanced cell elongation of *Euglena gracilis,* IAA had a greater effect (Noble et al. 2014). In *Chlorella minutissima*, gibberellin levels decreased with increasing auxin levels suggesting that, in algae, gibberellins are utilized for auxin biosynthesis; this hypothesis needs to be verified (Stirk et al. 2014). Increase in gibberellin levels or over-expression in transgenic plants is associated with an increase in DR5:GUS activity (endogenous IAA levels), IAA biosynthesis and polar transport in roots, and significant synergistic effects are evident when gibberellins are combined with exogenous IAA (Li et al. 2020). Co-applications of gibberellins and auxins in microalgae increased biomass and chlorophyll content in *C. sorokiniana,* and growth and lipid accumulation in *A. obliquus* (Hunt et al. 2010; Renuka et al. 2018b). In plants, gibberellins and auxins share many common transcripts encoded for cell-growth (Björklund et al. 2007) and many studies have demonstrated that exogenous IAA enhances the expression of gibberellin biosynthetic and signaling genes (Li et al. 2020). However, the specific mechanisms underlying gibberellin-auxin crosstalk in algae is still unclear.

Brassinosteroids are essential in stress responses and for influencing multiple developmental processes in plants, ranging from cell division, elongation and differentiation to root and shoot growth, reproductive regulation, seed germination and development of flowers and fruits (Bajguz and Piotrowska-Niczyporuk 2013; Stirk et al. 2020). Applying exogenous brassinosteroids increased cell growth, metabolite content, photosynthetic activity and stress tolerance to heavy metals, salt and cold (Bajguz 2011; Bajguz and Piotrowska-Niczyporuk 2014; Kozlova et al., 2017; Stirk et al. 2018). Brassinosteroids act synergistically with auxins to regulate common target genes (Nemhauser et al 2004). Although exogenous brassinosteroids enhanced IAA levels in *C. vulgaris* (Bajguz and Piotrowska-Niczyporuk 2013), they seem to do this through the enhanced expression of PIN genes (auxin transport) rather than through enhanced auxin biosynthesis; brassinosteroids may trigger similar physiological responses in auxin-saturated environment or deactivate IAA conjugation (Arteca and Arteca 2008; Nemhauser et al 2004).

Abscisic acid (ABA) is often referred to as a stress hormone or negative regulator whose concentrations increase under various biotic and abiotic stresses (Nambara and Marion-Poll 2005). It controls embryogenesis, seed dormancy and senescence, and stimulates physiological responses for stress adaptation such as stomatal closure (Gavassi et al. 2020; Kim 2007). Accumulation of endogenous ABA in algae occurs in response to unfavourable environments such as salinity, pH, oxidative, temperature and nitrogen-deficient stresses (Han et al. 2018; Kobayashi et al. 2016; Stirk and van Staden 2020). Exogenous ABA antagonizes auxin biosynthesis by down-regulating auxin signaling (Munguía-Rodríguez et al. 2020); and repressing growth by stimulating the transition from a vegetative phase to a cyst or reproductive phase, as seen in *Haematococcus pluvialis* and *Laminaria japonica* (Kobayashi et al. 1997; Nimura and Mizuta 2002). Conversely, IAA induces ABA biosynthesis in plants and auxin signaling regulates ABA signaling in carotenoid synthesis, and some common transcripts in algae such as *Chlorella* (Alsenani et al. 2019; Khasin et al. 2018). ABA has been successfully used to increase the production of high-valued byproducts such as beta carotene in *Dunaliella salina*, astaxanthin from *H. pluvialis* and lipids from *Chlorella* (Contreras-Pool et al. 2016; Kobayashi et al. 1997; Mousavi et al. 2016; Wu et al. 2018).

2.2 External factors

a. pH

Cellular auxin concentrations are regulated by a molecular process called polar auxin transport (PAT), which is pH- and energy-dependent, and facilitated by a group of plasma membrane proteins known as influx carriers (AUX1/LAX) and efflux carriers (PIN and ABCB/PGP families). These auxin transporters have been described for algae (Zhang and van Duijn 2014). Briefly, when the algal cell exterior is slightly acidic (pH 5.5), IAA readily diffuses across the lipophilic membrane in its undissociated form (IAAH) into the algal cell where most of it dissociates to IAA^-. The near-neutral interior traps the dissociated IAA^- whose exit is coordinated by active efflux carriers, whose spatial distribution determines the direction of auxin transport. This hypothesis of asymmetric, spatial auxin distribution is widely accepted and expected to function in a similar way in plants and algae because of their close evolutionary relationship. PAT is involved in the long-distance nutrient transport as a function of intercellular communication, although its existence in other green algae remains to be investigated (Raven 2013). In *Chara* (Charophyta), the closest algae relative to land plants, PAT is evidenced by pH- dependent transmembrane fluxes in the presence of IAA, and the presence of auxin efflux carriers (Dibb-Fuller and Morris 1992). The unicellular green alga *Chlorella vulgaris* (Chlorophyta) shows no evidence of IAA carriers and auxin transport across its plasma membrane, and seems to depend solely on pH-sensitive diffusion or cytoplasmic streaming. IAA uptake increases as external pH is decreased from 7.0 to 4.5. External pH lower than 4.5 prevented IAA uptake in *C. vulgaris*, presumably because excess intracellular IAA^- exceeds cytoplasmic buffering capacity and could not be transported out of cells without efflux carriers (Dibb-Fuller and Morris 1992).

The effect of pH on auxin biosynthesis in algae has important implications for their agricultural applications. Decreasing pH of culture media from 9 to 6 increases IAA production in *Arthrospira platensis,* a cyanobacterium occurring in rice fields (Ahmed et al. 2010) and *Chroococcidiopsis,* which is associated with the rhizosphere of rice plants (Ahmed et al. 2014). *Synechocystis* (another cyanobacterium of the rice rhizosphere) IAA production peaks at pH 5 (Ahmed et al. 2014). These observations correspond with pH ~5.5, which is the characteristic of most plant rhizospheres, with key auxin synthesis genes highly expressed at low pH (Yuan et al. 2008). Microbial activity also peaks around pH 5.5, as in a typical rhizosphere environment where various microbes including algae proliferate (Sati et al. 2020; Yuan et al. 2008). Generally, low IAA concentrations stimulate plant growth but exert the opposite effects at high concentrations (Kolachevskaya et al. 2019). High levels of IAAH inhibit the growth of *Chlorella fusca* cultures, while decreasing pH further inhibits growth by increasing the uptake of IAAH (Lien et al. 1971). In summary, cells take up IAA passively and produce more IAA under acidic pH, but high levels of undissociated IAA suppress growth. Higher pHs inhibit IAA production but allow active IAA accumulation, with cellular growth suppressed. Maintaining a rhizosphere environment around pH 5.5 enhances algal excretion of IAA, thereby stimulating plant growth.

b. Light

Light is the predominant energy source for almost all photosynthetic algae. As auxin is involved in many developmental processes, light regulates auxin homeostasis during photomorphogenesis by controlling the biosynthesis, transport, distribution and degradation of auxin (Sassi et al. 2013). At cellular level, light-activated phytochrome B enhances the expression of *SUR2* (IAA suppressor) and represses *TAA1* (IAA biosynthesis), thereby decreasing IAA levels, with non-active phytochrome B having the opposite effect (Halliday et al. 2009). Light also localizes the PGP and PIN efflux carriers at the shaded, basal end of the cell, generating an apical-basal auxin gradient that results in polarization of the cell (Belanger and Quatrano 2000). Polar localization of PIN leads to PAT and determines the direction of auxin flow (Wiśniewska et al. 2006). The cell undergoes asymmetric growth and further divides into apical and basal daughter cells, which can be seen in the polar embryonic development of algae that eventually forms thallus and rhizoid tissues, respectively (Belanger and Quatrano 2000; Bogaert et al. 2019; Le Bail et al. 2010).

Algal cultures experiencing light-dark transitions have higher IAA concentrations than those in continuous darkness, indicating that light is involved in algal IAA biosynthesis (Ahmed et al. 2010; Prasanna et al. 2009; Stirk et al. 2014). Light period and intensity were also positively correlated to IAA production in *Anabaena* sp. RP9 and *Scenedesmus obliquus* respectively (Prasanna et al. 2010; Prieto et al. 2011). However, some cyanobacterial strains isolated from rice rhizospheres, predominated by *Nostoc* and *Anabaena*, excreted more IAA in the dark similar to yeasts and fungi (Prasanna et al. 2009). Presumably non-phototrophic or heterotrophic conditions are favored by certain cyanobacteria which might proliferate better in light-limited subsoils and rhizospheres. The effect of light on algal IAA production is therefore species-dependent.

On the other hand, long periods of white light as low as 46 $\mu E/m^2.s$ can degrade IAA, with complete degradation in 4-7 days (Fig. 3); but this can be prevented under yellow light and dark conditions (Dunlap and Robacker 1988; Leasure et al. 2013). The synergistic effect between light with nutrient salts (Fig. 3a), vitamin B6 (Fig. 3b), pH and oxygen of culture medium hastens IAA degradation before effective uptake (Dunlap and Robacker 1988; Leasure et al. 2013). For example, IAA concentration in the culture medium (Bold's basal medium, 80 – 100 $\mu mol/m^2.s$) decreased from 5 to 0.7 nmol/L in the absence of alga (Mazur et al. 2001). Higher energy UV-B radiation can degrade IAA *in vitro* and *in vivo* even faster (Ros and Tevini 1995). Although IAA is susceptible to degradation, cells maintained steady auxin levels by storing auxin in the form of IBA, which is more stable against degradative enzymes and undergoes slow IAA-IBA interconversion (Hashtroudi et al. 2013; Singh 2014). As in plants, increases in hydrogen peroxide and ABA induce IAA-to-IBA conversion, with the reverse conversion balancing cellular IAA levels during development and responses to stresses

(Damodaran & Strader 2019; Ludwig-Müller 2000; Simon and Petrášek 2011; Woodward & Bartel 2005). Non-enzymatic photodegradation of IAA is thus a major concern during the biological production of IAA under long-term light exposure. Outdoor algal cultivation requires high inoculation rates of cultures, to maximize light energy capture for sustained IAA production while minimizing photoinhibition and degradation of IAA (Wenz et al. 2019).

c. Salinity

In highly saline environments, algae require special adaptations for osmoregulation and ionic balance. Salinity is an abiotic stress that suppresses algal growth and development by damaging proteins, DNA, antioxidant and photosynthetic systems (Ji et al. 2018). Salt inhibits PIN and AUX1 protein expression and alters PIN localization (Kazan 2013). Reactive oxygen species (ROS) accumulated under salt stress could trigger degradation of auxins, thereby attenuating gene transcription and downstream cellular processes (Astier et al. 2017; Huang et al. 2020). In *Chlorella sorokiniana*, a freshwater microalga with enhanced lipid production under salinity stress, auxin levels decreased to 75% when grown in 5-20 g/L (86-340 mM) NaCl (Do et al. 2020). IAA production in a mangrove root-associated cyanobacterium (*Phormidium* sp.) decreased from 0 to 4% NaCl but this reduction could be offset by supplementation with tryptophan (Boopathi et al. 2013). The ability of some algae to produce IAA at different salinity levels indicates their potential use as biofertilizers for halophytes.

Subheading 3: Role of IAA in algae

The important roles of auxins in various aspects of growth and development in algae were recorded as early as the 1940s (Overbeek 1940). Algae produce IAA and with IAA signaling pathways similar to those of higher plants (Cock et al. 2010; De Smet et al. 2011; Labeeuw et al. 2016; Sergeeva et al. 2002). Cell-cell communication is achieved through the classical PAT mechanism via PIN and AUX1/LAX proteins, which trace back to basal lineages of land plants such as bryophytes (Paponov et al. 2009). However, only a partial sequence of these proteins could be retrieved from Charophyta, implying that complete auxin machinery is not essential for multicellular filamentous or mat-forming algae (De Smet et al. 2011). This is also supported by only the subdomains of auxin-response proteins present in red algae and chlorophytes. However, Charophyta contains multi-domains of such proteins, reflecting evolutionary pressure to combine these subdomains (Mutte et al. 2018). PIN or auxin response proteins have not been identified in many basal algae (Labeeuw et al. 2016; Mutte et al. 2018; Viaene et al. 2013) but appear in highly differentiated algae, suggesting these proteins play important roles in multicellular activities (De Smet et al. 2011; Khasin et al. 2018). However, PIN-like (PILS) homologues, which have a similar topology to PIN, are found in all algae and have been conserved throughout land plant evolution (Bogaert et al. 2019; De Smet et al. 2011; Viaene et al. 2013).

IAA signaling may have evolved early in algal evolution. IAA plays a signaling role between different *Emiliana huxleyi* cell types, a unicellular marine microalga where specific cell types produce auxin and other cell types respond to auxin. This implies an early role for intercellular auxin-mediated signaling within populations of unicellular organisms that predated multicellularity (Labeeuw et al. 2016). Most of the algae secreting exogenous auxin are multicellular cyanobacteria and colony-forming microalgae, but not seaweeds (Table 2). It has been suggested that IAA might be released extracellularly as a quorum sensing molecule that regulates intraspecies population density and biofilm development, or interspecies communication within biofilm communities (Khasin et al. 2018; Lu and Xu 2015).

The existence of simple auxin-signaling machineries in algae implies that algal responses to auxins are similar to those of land plants, at least at a primitive, cellular level. Complex multicellular algae such as Charophyta, Rhodophyta and Phaeophyta share characteristics with basal plants such as bryophytes (mosses, liverworts, hornworts), including rhizoids, a thallus-like body and the absence of vascular elements (Cooke et al. 2002; Zhang and van Duijn 2014). Cytoskeletal and rhizoid responses to auxin in the moss, *Physcomitrella patens,* are similar to those of *Chara* (Jin et al. 2008; Klämbt et al. 1992; Sakakibara et al. 2003). Treating *P. patens* and the charophyte *Klebsormidium nitens* with 100 µM exogenous auxin inhibited cell division and cell elongation (Ohtaka et al. 2017). Auxin-induced callus growth and regeneration in seaweeds such as *Grateloupia* and *Kappaphycus* resembles that of many bryophytes and angiosperms (Fadel et al. 2013; Muñoz et al. 2006; Yokoya and Handro 1996). Both auxin and auxin transport inhibitors such as naphthylphthalamic acid (NPA), 2-[4-(diethylamino)-2-hydroxybenzoyl] benzoic acid (BUM) and 2,3,5-triiodobenzoic acid (TIBA) alter embryonic polarity and rhizoid development in algae such as *Chara*, *Fucus*, and *Dictyota* in much the same way as in the moss *Funaria* and the liverwort *Marchantia polymorpha* (Basu et al. 2002; Bogaert et al. 2019; Klämbt et al. 1992; Ohtaka et al. 2017). These observations suggest that primitive auxin responses of algae were conserved in bryophytes and have continued to evolve into the more complex, canonical auxin system in higher plants (Ohtaka et al. 2017).

The physiological responses of algae to exogenous auxins depend on the types and concentration of auxin (Table 3). Both algae and the shoots of higher plants have optimal growth responses at a concentration of 10^{-5} M of exogenous auxin, but growth is inhibited at 10^{-4} M (Fig. 4a). In summary, at a cellular level, auxins induce cell enlargement, cell division, photosynthetic activities and synthesis of biochemical compounds contributing to biomass increment in all types of algae (Fig. 4b), although the response to specific auxins may vary among species of algae. Auxin further stimulates cellular differentiation such as polarity, rhizoid and thallus development, embryogenesis and tropism as well as the production of several bioactive compounds. Lower than threshold auxin levels, which are typically higher in vegetative tissues, can stimulate transition to reproductive phases (Kai et al. 2006). Recently, auxins have been used to enhance the agricultural capacity of algae, such as nitrogen fixing efficiency, or to produce algal organic compounds of industrial value, such as phycobiliproteins, antioxidants, lipids and fatty acids (Anahas and Muralitharan 2019; Dao et al. 2018; Mansouri and Talebizadeh 2017; Piotrowska-Niczyporuk et al. 2018; Tiwari et al. 2020; Udayan and Arumugam 2017; Zhang et al. 2020). Differential growth responses to auxins in different algae are therefore attributable to variation in auxin receptor content and combination, cell permeability to auxin, and rates of metabolic turnover (Kolachevskaya et al. 2019).

Table 3 Physiological and growth responses of a variety of algal species to supplementation with different concentrations of auxin

Algae	Type of auxin	Supplemented auxin (µmol L^{-1})	Responses	References
Seaweeds				
Charophyta				
Chara contraria	IAA, NAA	10	High cytoskeletal response	(Jin et al. 2008)
Chara globulis	IAA	0 – 1.0	Stimulated rhizoid growth	(Klämbt et al. 1992)
		10	Decreased rhizoid growth	
Chlorophyta				
Caulerpa prolifera	IAA	0.1 – 10	Increased blade proliferation	(Dawes 1971)
	IAA, IBA, IPA	100 – 1000	Inhibition of rhizomes	
Ulva fasciata	IAA	0.57 – 5.7 (0.1 – 1.0 mg/L)	Increased biomass and amino acid but reduced sugar and fat contents.	(Mohsen et al. 1974)
Phaeophyta				
Alaria esculenta	NAA, 2,4-D	1000	Inhibited photosynthetic activity; altered chlorophyll structure.	(Buggeln and Bal 1977)
Ascophyllum nodosum	IAA	0.033 – 0.33	Increased biomass.	(Fries 1988)
Dictyota dichotoma	NAA	100	Stimulated zygote polarization and rhizoid outgrowth	(Bogaert et al. 2019)
	IAA	100	Inhibited zygote growth	
Fucus distichus	IAA	5 – 100	Induced formation of multiple rhizoids	(Basu et al. 2002)
Fucus spiralis	PAA, IAA, *p*-hydroxyPAA	0.1 – 10	Restored morphology and induced growth	(Fries 1977; Fries 1984)
Fucus vesiculosus	IAA	5.7	Stimulated embryo growth and apical hair formation; inhibited photosynthetic activities	(Tarakhovskaya et al. 2013)
Laminaria japonica	IAA	0.01 – 10	Induced elongation of sporophytes; delayed sorus formation	(Kai et al. 2006)
		100	Inhibited elongation of sporophytes and sorus formation	

Sargassum muticum	PAA	100	Inhibited growth of primary lateral segments	(Gorham 1979)
Rhodophyta				
Chondracanthus chamissoi	IAA, 2,4-D	0.5 – 50	Stimulated thallus and callus growth	(Yokoya et al. 2014)
Gracilaria vermiculophylla	IAA	0.57 – 5.7 (0.1 – 1.0 mg/L)	Stimulated thallus and callus growth	(Yokoya et al. 1999)
		57 (10 mg/L)	Inhibited growth	
Grateloupia dichotoma	IAA, 2,4-D	2.86 – 28.6 (0.5 – 5.0 mg/L)	Stimulated cell division, elongated apical and intercalary segments; induced elongation but inhibited formation of lateral branches	(Yokoya and Handro 1996)
Kappaphycus alvarezii	IAA, NAA	2.3 – 5.7 (0.4 – 1.0 mg/L)	Induced callus regeneration	(Fadel et al. 2013; Muñoz et al. 2006)
Microalgae				
Bacillariophyceae				
Chaetoceros muelleri	IAA	25 – 75	Increased cell number, chlorophyll and soluble polysaccharide content	(Li et al. 2007)
		100	Inhibited growth	
Phaeodactylum tricornutum	2,4-D	2.3 – 13.6 (0.5 – 3.0 mg/L)	Increased biomass and lipid production	(Zhang et al. 2020)
Skeletonema costatum	IAA	0.057 – 0.57 (0.01 – 0.1 mg/L)	Increased cell number	(Bentley-Mowat 1967)
Charophyceae				
Klebsormidium flaccidum	IAA	0.1 – 100	Inhibited cell growth and cell elongation	(Ohtaka et al. 2017)
Chlorophyceae				
Acutodesmus obliquus	IAA, IBA, PAA	0.01 – 0.1	Increased cell size and number, photosynthetic pigments, and soluble proteins; stimulated enzymatic and non-enzymatic antioxidant	(Piotrowska-Niczyporuk et al. 2018)

Chlamydomonas reinhardtii	IAA	0.57 – 57 (0.1 – 10 mg/L)	Increased biomass, cell size, cell division, chlorophyll contents and fatty acid methyl esters yield	(Park et al. 2013)
Desmodesmus opoliensis, Desmodesmus komarekii	IAA	100 – 200	Increased number of unicells, cell size and lipid production	(Chung et al. 2018)
		300 – 500	Reduced growth and chlorophyll a/b ratio (photosynthetic activity)	
Desmodesmus komarekii	IAA, 2,4-D, NAA	>100	Reduced growth	(Lin et al. 2020)
Dunaliella salina	IAA	25 – 100	Increased cell number and chlorophyll content	(Li et al. 2007)
Scenedesmus armatus	IAA	1 – 10	Stimulated cell division	(Mazur et al. 2001)
Scenedesmus obliquus	IAA	28 – 114	Stimulated growth and formation of four-celled colonies	(Prasad 1982)
	IAA	0.01 – 10	Increased biomass and PUFA content	(Salama et al. 2014)
Scenedesmus quadricauda	IAA, IPA, IBA, NAA	28.6 – 343 (5 – 60 mg/L)	Increased biomass and lipid production	(Liu et al. 2016)
	IAA	0.001 – 1.0	Increased biomass, chlorophyll-a, carotenoid and lipid production	(Kozlova et al. 2017)
Scenedesmus sp.	IAA, 2,4-D	0.057 – 5.7 (0.01 – 1.0 mg/L)	Increased cell size and number, photosynthetic rate and efficiency, chlorophyll, FAME and MUFA content	(Dao et al. 2018)
	2,4-D	5.7 – 57 (1.0 – 10 mg/L)	Reduced growth	
	IAA	28.6 – 114 (5 – 20 mg/L)	Increased biomass, cell size, N- and P-uptakes, lipid and carbohydrate productivities, pigments and dehydrogenase activity	(Yu et al. 2017)
		286 (50 mg/L)	Inhibited growth	
Eustigmatophyceae				
Nannochloropsis oceanica	IAA	57 – 286 (10 – 50 mg/L)	Decreased biomass but increased lipid and EPA production	(Udayan and Arumugam 2017)
Nannochloropsis oculata	IAA	0.57 – 5.7	Increased cell numbers and chlorophyll a content	(Trinh et al. 2017)

Porphyridiophyceae				
Porphyridium cruentum	IAA	25 – 100	Increased cell number and soluble polysaccharide content but decreased soluble protein content	(Li et al. 2007)
Trebouxiophyceae				
Chlorella pyrenoidosa	IAA	0.57 – 57 (0.1 – 10 mg/L)	Stimulated cell division	(Vance 1987)
	IAA	50 – 100	Stimulated excretion of protein and polysaccharides	(Czerpak and Bajguz 1993)
	IAA, IBA, ILA, NAA, 2,4-D, tryptamine	10 – 100	Increased biomass, total carotenoids, carotenes and xanthophylls	(Czerpak and Bajguz 1997)
	IAA, IPA, IBA, NAA	28.6 – 343 (5 – 60 mg/L)	Increased growth and lipid production	(Liu et al. 2016)
Chlorella sorokiniana	IAA	28.6 – 114 (5 – 20 mg/L)	Increased biomass, cell size, N- and P-uptakes, lipid and carbohydrate productivities, pigments and dehydrogenase activity	(Yu et al. 2017)
		286 (50 mg/L)	Inhibited growth	
Chlorella vulgaris	IAA, IBA, PAA, NAA	0.1 – 10	Increased cell number, photosynthetic pigments, monosaccharides and soluble proteins; stimulated enzymatic and non-enzymatic antioxidant; suppressed lipid peroxidation and H_2O_2 accumulation	(Piotrowska-Niczyporuk and Bajguz 2014)
		100	Inhibited growth	
Chlorella sp.	IAA	25 – 100	Increased cell number	(Li et al. 2007)
		75 – 100	Decreased chlorophyll and soluble protein content	
Ulvophyceae				
Ulothrix subtillisma	IAA	0.017	Increased biomass	(Conrad et al. 1959)
Cyanobacteria				
Cyanophyceae				
Anabaena cylindrical, *Anacystis nidulans,*	IAA	< 10	Increased biomass	(Ahmad and Winter 1968)

Chlorogloea fritschii, *Nostoc muscorum,* *Phormidium foveolarum,* *Tolypothrix tenuis*		>100	Inhibited growth	
Anabaena doliolum	IAA	11.4 – 285 (2 – 50 mg/L)	Increased biomass, nitrogen fixation, chlorophyll content and heterocyst frequency	(Kapoor and Sharma 1981)
Anabaena sphaerica	indole-3-carboxaldehyde	68.9	Increased biomass and lipid production	(Anahas and Muralitharan 2019)
Anabaena sp., *Nostoc muscorum*	IAA	0.29	Increased growth, photosynthetic pigments, nitrogen metabolism, exopolysaccharides, carbohydrate and protein contents under Cr stress	(Tiwari et al. 2020)
Aulosira laxa, *Nostoc muscorum,* *Tolypothrix lanata*	2,4-D	22.6 – 226 (5 – 50 mg/L)	Increased biomass and chlorophyll content but decreased nitrogen fixation activities	(Kobbia and El-Sharouny 1985)
		>226	Inhibited growth	
Nostoc linckia	2,4-D	452 (100 mg/L)	Increased specific growth rate and heterocyst frequency	(Mishra and Tiwari 1986; Tiwari et al. 1981)
	IBA	0.01 – 1.0	Increased heterocyst frequency, chlorophyll, carotenoid, and amino acid but reduced sugar contents	(Mansouri and Talebizadeh 2017)
		10 – 100	Increased biomass, heterocyst frequency, phycocyanin, allophycocyanin, and phycoerythrin contents	
Nostoc sp.	NAA	13.4 – 53.7 (2.5 – 10 mg/L)	Increased biomass productivity	(Hunt et al. 2011)
Spirulina platensis	2,4-D	0.09 – 0.9	Increased biomass, chlorophyll and protein contents	(Saygideger and Okkay 2008)
		9 – 90	Inhibited growth	
Synechococcus aeruginosus	2,4-D	905 (200 mg/L)	Increased chlorophyll, protein, carbohydrate and allophycocyanin contents	(Jyothi 2016)
		>905	Inhibited growth	

Abbrevations: IAA indole-3-acetic acid; IBA indole-3-butyric acid; ILA indole-3-lactic acid; IPA indole-3-propionic acid; NAA 1-naphthaleneacetic acid; PAA phenylacetic acid; 2,4-D 2,4-dichlorophenoxyacetic acid

Application of algae-derived IAA

In modern sustainable agriculture, the use of natural algae products such as biostimulants and biofertilizers as alternatives to conventional inorganic fertilizers has slowly gained market share owing to their biodegradability, capacity to improve the physical and chemical properties of soil and greatly reduced environmental impacts compared to chemical fertilizers (Craigie 2011; Renuka et al. 2018a). In nature, some living algae colonize the rhizosphere (10^2 - 10^7 cells/g soil at a depth of 0-40 cm) and stimulate plant growth by releasing growth substances (including auxins) and other extracellular products that enhance the surrounding microbial activities (Abinandan et al. 2019; Ahmed et al. 2014; Florenzano et al. 1978; Prasanna et al. 2009; Sati et al. 2020). Agricultural products from algal extracts contain various macro-nutrients, trace elements, metabolites, amino acids and phytohormones that could improve the nutrient status, vegetative growth and yield of crops (Renuka et al. 2018a).

The growth stimulatory effects of algae products are sometimes related to their auxin-like bioactivity and the production of substances that foster endogenous synthesis of IAA in plants (Mógor et al. 2018). The presence of auxin and auxin-like compounds in various algae are also well documented in seaweeds, cyanobacteria and other microalgae (Table 2). Undoubtedly, algae do produce auxin endogenously and secrete it exogenously at concentrations well within the optimal physiological response range for plant roots (10^{-9} M) and shoots (10^{-5} M; Fig. 4a) (Kolachevskaya et al. 2019). These critical effects of auxin are highly dependent on the dosage and types of auxin as well as the plant genera and tissues (Dodd et al. 2010; Kolachevskaya et al. 2019). Auxin-producing algae can stimulate seed germination, tissue regeneration, shoot and root growth, endogenous auxin level, yield, and changes in biochemical composition such as increased protein, carbohydrate, and lipid content (Table 4). The most prominent growth responses of plants treated with algae bioproducts is a change in root physiology, whereas plant-growth-promoting bacteria (PGPB) are often used to stimulate shoot growth (Dodd et al. 2010). Auxin-mediated root growth is usually associated with primary root elongation and lateral root development (Raheem et al. 2018; Singh 2014). Overall, plant growth responses including those within the rhizosphere, are highly correlated with the IAA concentrations of the algae they are treated with (Ahmed et al. 2014; Hussain and Hasnain 2011; Jäger et al. 2010); and algal strain-dependent when considering factors such as extracellular products and stress tolerance (Shariatmadari et al. 2015; Singh et al. 2011). Studies of growth responses and plant-algae interactions (discussed below) further confirm the plant growth-promoting capabilities of algal-derived auxins.

Seaweed extracts

Seaweed extract was first commercially produced 70 years ago, after which the number of research articles on seaweed use in agriculture increased exponentially (Craigie 2011). Various seaweed extracts are manufactured from brown seaweeds, especially *Ascophyllum nodosum* and *Ecklonia maxima,* and their applications are associated with improved crop growth and yields and increased resistance to biotic and abiotic stresses (Khan et al. 2009; Stirk and van Staden 1996). Seaweed extracts are often applied only in small amounts, thus, their growth promoting effects are thought to be caused by growth-stimulating substances such as auxins, which are typically present in low concentrations, rather than their nutrient content (Stirk and van Staden 1996). All six tested commercial seaweed extracts possessed auxin-like activity in mung bean rooting bioassays, but reduced rooting at higher concentrations (Stirk and van Staden 1996), similar to a previous study which used *E. maxima* extract (Crouch and van Staden 1991). *A. nodosum* extracts altered auxin-responsive promoter DR5-driven GUS activity and expression of auxin biosynthesis genes in *Arabidopsis* plants (Rayorath et al. 2008; Wally et al. 2013). Contrary findings were observed in root DR5:GUS activity (Table 4), possibly due to their use of different concentrations and types of extracts, which might alter plant cytokinin and ABA levels, potentially antagonising auxin activity. Seaweed extracts can inhibit primary root elongation and lateral root formation at concentrations higher than 1%, but green seaweed *Ulva intestinalis* extract (at similar concentration) applied to *A. thaliana* signaling mutants revealed that ABA, and elements such as Al^{3+}, Cu^{2+} and Na^{+} may inhibit root growth instead of auxin (Ghaderiardakani et al. 2019; Khan et al. 2009). Applying seaweed extracts to soil increased plant resistance to nematode infestation, presumably by altering plant auxin and cytokinin content (Khan et al. 2009). In summary, the growth-stimulating potential of seaweed extracts is unlikely to be attributed to a single hormonal (auxin) alone, but to a complex interplay between the diverse constituents, and should be applied with care at low concentrations due to auxin’s biphasic effects.

Table 4 Auxin-like bioactivities in different algae products and their effect on plant growth

Type of plant	Effect	Product from algae			References
		Type	**Concentration**	**Auxin content**	
Mung bean rooting bioassay	10-100 µM IBA equivalent.	Commercial seaweed extracts	20%	-	(Stirk and van Staden 1996)
	1-2.5 fold of 100 µM IBA equivalent.	*Ecklonia maxima* extract (Kelpak)	10%	-	(Crouch and van Staden 1991)
	0.1-0.5 mg/L of IBA equivalent.	Inoculants of *Calothrix*, *Chlorella*, *Coenochloris*, *Tetracystis*, *Chlamydomonas*	2 g/L	-	(Stirk et al. 2002)
	10 µM or less IBA equivalent.	*Calothrix* and *Scenedesmus* extracts (from 1 g dried biomass)	50-100%	-	(Stirk et al. 2002)
Excised cucumber cotyledon rooting bioassay	0.3-0.6 mg/L IBA equivalent.	Dried biomass of *Anabaena, Klebsormidium flaccidum*, *Leptolyngbya*, *Neochloris*	2 g/L	9 – 40 µg/g DW (endo)	(Jäger et al. 2010)
Zea mays (maize)	43-100% and 40-96% increase in frequency of anther induction and embryo-like structures respectively compared to 2 mg L^{-1} of auxin 2,4-dichlorophenoxy-acetic acid				
Arabidopsis bioassays	High DR5:GUS activity in root.	*Ascophyllum nodosum* extract	1 g/L	-	(Rayorath et al. 2008)
	Reduction in root DR5:GUS activity, IAA content (33-42%), expression of key auxin biosynthetic genes (0.4-0.7 fold)	*Ascophyllum nodosum* extract	0.1 g/L	95 – 110 ng/g DW (endo)	(Wally et al. 2013)
Arachis hypogaea (peanut)	2-fold increase in shoot and root length compared to medium supplemented with 1-2 mg/L IBA.	Extracellular product from *Aphanothece*	0.5 – 1.0 mL per 10 mL	8 µg/mL (exo)	(Gayathri et al. 2015)
Moringa oleifera (drumstick tree)	Increase in average shoot and root length compared to medium supplemented with 1-2 mg/L IBA.				
Triticum aestivum (wheat)	Up to, 40% increase in fresh weight, 52% increase in shoot length, 26% decline in root length, 52% increase in lateral root number, 43% increase in grain yield, 4-fold and 2-fold increase of IAA in root and shoot respectively.	Inoculant of *Anabaena, Oscillatoria, Phormidium, Chroococcidiopsis, Synechocystis*	0.1 µg/mL chlorophyll-a	3.8 – 28.3 pmol/mg chlorophyll-a (exo)	(Hussain and Hasnain 2011)

	Up to, 53% increase in shoot length, 43% reduction in root length, 50% increase in root number, 75% and 98% increase in shoot and root auxin contents, respectively.	Inoculants of *Chroococcidiopsis, Synechocystis, Leptolyngbya, Phormidium*	1.0 µg/mL chlorophyll-a	1 – 6 µg/mL (exo)	(Mazhar et al. 2013)
	Induced seed germination - up to 40% and 100% increase in radicle and coleoptile length, respectively.	Inoculants of *Nostoc* and *Anabaena* isolates	Evenly spread on petriplates	0.15 – 1.0 µg/mL (exo)	(Prasanna et al. 2009)
	Induced seed germination - up to 81% and 105% increase in radicle and coleoptile length, respectively.	Supernatant containing IAA from *Anabaena* isolates	Seed soaking for 36h	1.4 – 11.4 µg/mL (exo)	(Prasanna et al. 2010)
Pisum sativum (pea)	Up to, 166% increase in lateral root number, 50% decrease in root length.	Supernatant containing IAA from *Spirulina platensis*	1 – 5 mL per 10 mL per petri dish	0.5 – 22 µg/mL (exo)	(Ahmed et al. 2010)
	Up to, 192% increase in lateral root number, 81% increase in root length (1 mL supernatant), 40% decrease in root length (5 mL supernatant).	Supernatant containing IAA from *Chroococcidiopsis* and *Synechocystis*	1 – 5 mL per 10 mL per petri dish	1.0 – 20 µg/mL (exo)	(Ahmed et al. 2014)
Nicotiana tabacum (tobacco)	90% seed germination, 100% and 60% increase in root and shoot length, respectively.	Supernatant containing IAA from *Phormidium*	5 mL of 100 µg/mL per petri dish	0.75 – 20 µg/mg chlorophyll-a (exo)	(Boopathi et al. 2013)
Oryza sativa (rice)	Induced seed germination - up to 838% and 122% increase in radicle and coleoptile length, respectively.	Supernatant containing IAA from *Fisherella muscicola*	Seed soaking for 36h	287 µg/mL	(Mishra et al. 2019)
	Root length are corresponded with the level of phytohormones in the rhizospheric soil.	Inoculants of *Anabaena oryzae, A. doliolum, Phormidium fragile, Calothrix geitonos, Hapalosiphon intricatus, Aulosira fertilissima, Tolypothrix tenuis, Oscillatoria acuta and Plectonema boryanum.*	Seed soaking (with culture at 0.67 OD_{663}) for 4h	0 – 15 µg/g soil	(Singh et al. 2011)
	Increase in IAA content (32% in root, 7.8-fold in leaves), nitrogenase activity (3.8-fold), peroxidase activity (3.5-fold in root, 4.5-fold in shoot), polyphenol peroxidase activity (1.5-fold in root, 2.9-fold in shoot), population density (10-fold) of culturable bacteria from root and shoot.	Inoculant of *Calothrix elenkinii*	5.0 µg/mL chlorophyll-a	0.08 – 3.71 µg/mL (exo)	(Priya et al. 2015)
Helianthus annus L.	Increase by, 100% leaf weight, 20% root weight, up to 46% total protein, carbohydrate and lipid, 20% yield, compared to chemical	*Oscillatoria annae* extract	0.01% foliar spray	5.2 µg/g DW (endo)	(Varalakshmi and Malliga 2012)

	fertilizer control. 0.01% IAA equivalent in rooting bioassay.				
Mentha piperita L.	Increase up to, 103% shoot length, 75% root length, 175% root biomass, 170% shoot biomass, 60% essential oil content. Growth impacts correlated with IAA contents in algae.	*Anabaena vaginicola, Nostoc calcicole, Trichormus ellipsosporus, Cylindrospermum michailovskoense* extracts	1% foliar spray	2.43 – 16.8 µg/g DW (endo)	(Shariatmadari et al. 2015)
Triticum aestivum (wheat) & *Oryza sativa* (rice)	5-fold increase in algal *ipdC* gene expression during root colonization. Decrease root colonization, plant weight, root and shoot length for *ipdC* knockout mutant. Restored and enhanced growth for IAA supplementation or *ipdC*-complemented mutant.	Inoculant of *Nostoc* sp. and its *ipdC* mutants.	1 µg mL^{-1} chlorophyll-a	5 – 34 (exo), 4 – 21 (endo), pmol/mg chlorophyll-a	(Hussain et al. 2015)

Abbreviation: Endo endogenous; Exo exogenous; DW dry weight; IAA indole-3-acetic acid; IBA indole-3-butyric acid; *ipd*C indole-3-pyruvic acid decarboxylase

Cyanobacteria

Besides playing a key role in N_2 fixation, cyanobacteria excrete numerous organic and inorganic plant growth-promoting compounds (Jaiswal et al. 2018). Formerly diazotrophic cyanobacteria were explored mainly for N-fertilization in rice fields due to their ability to colonize the rhizosphere. Since then, a number of algae with other biofertilizing potentials such as carbon accumulation, phytohormone production, nutrient mobilization, wasteland reclamation and biocidal control have been successfully demonstrated on other crops besides rice including wheat, maize, chickpea, and tomato (Renuka et al. 2018a). The presence of different phytohormones including auxin and auxin-like bioactivities have been detected in many cyanobacteria (endogenously and exogenously) using various bioassays (Table 4). Auxin might be released freely to the surroundings by free-living cyanobacteria or to the plant-cyanobacteria symbiotic sites that might promote physiological development of both the symbionts; as observed between *Nostoc* spp. and hosts such as lichenized fungus *Peltigera*, the angiosperm *Gunnera* and the water-fern *Azolla* (Sergeeva et al. 2002). *Anabaena* induces auxin-like effects and enhances anther induction and regeneration frequency in maize, possibly by changing endogenous auxin levels of microspores that affect androgenic fate and embryogenic development (Jäger et al. 2010). The extracellular products of *Aphanothece* containing IAA induced root and shoot growth in peanuts (*Arachis hypogaea*) and reduced the accumulation of phenolic compounds that cause browning and blackening of plants (Gayathri et al. 2015), which were crucial issues in commercial *in vitro* culture. Exogenous IAA secretion of various cyanobacteria (*Anabaena, Oscillatoria, Phormidium, Chroococcidiopsis,* and *Synechocystis)* were positively correlated with the endogenous IAA of roots and shoots of wheat (*Triticum aestivum)* inoculated with these cyanobacteria, and with shoot and spike length and with seed biomass (Hussain and Hasnain 2011). Wheat grown hydroponically with *Chroococcidiopsis, Synechocystis, Leptolyngbya* and *Phormidium* showed similar responses (Mazhar et al. 2013). These cyanobacteria enhanced lateral root production, but inhibited root elongation, according to excreted IAA levels. Enhanced expression of the *ipdC* IAA biosynthesis in *Nostoc* demonstrated the involvement of IAA in regulating growth of rice and wheat (Hussain et al. 2015). The *ipdC* knockout *Nostoc* mutant had lower IAA production, lower root colonization and reduced plant growth-promoting efficiency (i.e., length and mass of roots and shoots) than the wild-type strain. The phenotypes were later restored and enhanced when the mutant was complemented with the *ipdC* gene. Co-cultivation of plants with cyanobacteria seems a viable growth-promoting strategy, with simultaneously enhanced IAA production in both the host and symbiont.

A potentially important observation is that cytokinin (zeatin and zeatin riboside) levels in wheat seedlings did not correlate with IAA released by cyanobacteria, possibly because auxin and cytokinin have antagonistic effects (Hussain and Hasnain 2011). For example, auxins might suppress cytokinin content by repressing the *ipt* gene responsible for *de novo* cytokinin synthesis, and inducing cytokinin oxidase to breakdown or convert cytokinins to inactive conjugates (Jones and Schreiber 1997; Nordström et al. 2004). In a field study, the hydrolysate of *Arthospira platensis* demonstrated auxin-like activity by increasing root number and biomass in lettuce (*Lactuca sativa*), which was subsequently attributed to its increased polyamine content, a well-known family of growth promoting compounds (Mógor et al. 2018). Thus, apart from their nitrogen-fixing capability, cyanobacteria are potentially good candidates for exploring phytostimulation by auxins and other phytohormones.

Microalgae

Microalgae are generally referred to as a group of eukaryotic microorganisms with photosynthetic chloroplasts. Their high growth rates and ability to survive extreme conditions, especially in non-arable soils, have attracted commercial interest in producing agricultural bio-products from microalgae. The ability of *Chlorella* extracts to induce chlorophyll production, and stimulate growth and rooting of fruit-trees, vegetables and rice plants is attributed to their IAA content (Mazur et al. 2001; Yamaguchi 1996). Among seven Chlorophyta strains tested, extracts from *Chlamydomonas, Coenochloris* and *Tetracystis* had the highest auxin-like activity (Stirk et al. 2002). The auxin-like activity of microalgal strains *Klebsormidium flaccidum* and *Neochloris* was tested on anther cultures of maize using excised cucumber cotyledon bioassay. Activity was positively correlated with high endogenous IAA content of the algae and improved androgenic response (Jäger et al. 2010). Other microalgae such as *Chlorella pyrenoidosa* and *Scenedesmus* spp. also secrete IAA exogenously (Mazur et al. 2001; Prieto et al. 2011), indicating that these microalgae may act as alternative sources of auxin to stimulate plant growth.

Challenges and future development in application of algal auxin

Integrating modern molecular biotechnologies for mechanistic studies

Despite a long history of research, current understanding of the precise mechanism of auxin action in algae is still incomplete. Demonstrating that a specific response does not occur in the absence of IAA and that the response can be restored with the addition of the compound is necessary (Bradley 1991; Mazur et al. 2001). Advances in new technologies for genetic and molecular studies have confirmed the importance of algal auxins in plant-algae interactions by studying algal mutants with altered IAA production and auxin-resistant plant mutants (Ghaderiardakani et al. 2019; Hussain et al. 2015). Phytohormone-mediated quorum sensing, another new opportunity in microalgae biotechnology (Khasin et al. 2018; Lu and Xu 2015), is worth exploring to understand the underlying mechanisms of the extracellular production of IAA. When coupled with next-generation sequencing techniques, more novel genes could be discovered to confirm putative pathways and further improve IAA production in a gene-targeted manner.

Algae-derived extracts have gained increasing interest in crop production because of their physiological stimulatory effects that are similar to those evoked by plant growth-promoting hormones. However, the mechanism of action of these extracts, whether it is via phytohormone action, other beneficial substances or the synergistic effect of both, is still unclear (Ghaderiardakani et al. 2019; Khan et al. 2009). In view of the beneficial action by algal auxins, more field-scale studies of their activity on crops merit investigation to evaluate their contribution in agriculture. Multi- or meta-omics analyses may help evaluate molecular mechanisms of plant-algae interactions. A combination of isotope labelling and IAA degradation investigations might further reveal the auxin effects of these extracts, either directly or indirectly, on the growth of different plant tissues mediated by long-distance auxin signaling (Dodd et al. 2010).

Potential of algal auxins in other applications

To improve and generate new crop varieties, anther cultures in rice, maize and wheat often suffer from low response frequencies and regeneration difficulties. Thus, much work has been done to optimize cultivar selection, pretreatment, culture media and growth conditions (Tripathy et al. 2019). Auxins such as IAA, NAA and 2,4-D have successfully promoted androgenesis, androgenic embryo induction, callus induction, cell proliferation and root formation (Mukherjee et al. 2015; Sohn 2001; Xa and Lang 2011). Algal extracts containing high auxins and other hormones could be used as universal induction media to enhance the cultivability of anthers for producing more homozygous lines (Jäger et al. 2010). Although salts can induce salinity stress in algae, indigenous cyanobacterial strains isolated from mangroves can produce auxins under different conditions of salinity and may help future reforestation and rehabilitation of valuable mangrove ecosystems, which are being rapidly depleted (Bashan et al. 1998).

Wastewater as a nutrient source for growing auxin-producing algae

The agricultural potential of microalgae will depend largely on the costs of production, which may require large amounts of synthetic chemicals and freshwater. Low-cost sources of nutrients and water, for example, wastewater may help counter these economic constraints. Algae have a proven track record of nutrient recovery from an assortment of industrial effluents from the textile (Lim et al. 2010), palm oil (Tan et al. 2016) and rubber industries (Phang et al. 2001), landfills (Mustafa et al. 2012) and pig farms (Vadiveloo et al. 2019). Nonetheless, the sources used for producing algal biomass for agricultural soil applications need to be limited to agro-industrial and agricultural wastes that are free from heavy metals and hazardous compounds (Phang et al. 2015). Several valuable products derived from algae have been produced using wastewater as a nutrient source to generate valuable algal biomass that can be used as feedstock for biofuel, lipids, proteins, pigments, biopesticides and other phycochemicals, including biofertilizers (Chu 2017; Mahapatra et al. 2016; Marella et al. 2020; Phang et al. 2015; Ranglová et al. 2021; Shah 2019; Van Den Hende et al. 2016). However, auxin accumulation from algae in wastewaters remains to be explored. The emerging use of waste-grown algae could be a sustainable alternative to improve agricultural productivity, while simultaneously remediating waste streams.

Merits of auxin-producing algal biofertilizers and their relationship with other soil microbes

The use of algae as biofertilizers on crops has been extensively reported with most studies in rice (35%), followed by wheat (26%), tomato (11%), maize (9%), cotton (6%) and others (Renuka et al. 2018a). Microalgae and cyanobacteria are primary colonizers, comprising 27% of total biomass in agricultural lands, and thus play a potentially crucial role in soil fertility (Abinandan et al. 2019). In eroded and degraded lands including deteriorated agricultural soils, these algae aggregate loose soil particles by forming sheaths and filaments to help retain moisture and nutrients. They also establish a favorable growth environment for other microbes such as PGPB, fungi, lichens, and actinomycetes. These microorganisms constitute the biological soil crust (BSC), which is a key indicator of soil health, fertility and agricultural productivity (Belnap 2006). In addition to the development of BSC, cyanobacteria possess nitrogen-fixing and nutrient mineralization capabilities, including the extracellular production of useful metabolites and antimicrobial compounds. Chlorophyta have the advantages of high growth rates and thus the potential to improve soil biomass and carbon accumulation (Stirk et al. 2002). Algae-microbe interactions are initiated by algal fixation of inorganic carbon and nitrogen, releasing phytohormones, enzymes and allelochemicals that are utilised by PGPB, which then solubilize phosphate and produce plant growth-promoting substances, whereas fungi assist in increasing soil nutrient availability by decomposing the dead organic matter (Abinandan et al. 2019). Biofertilizers of consortia inoculants between cyanobacteria, PGPB, and fungi such as *Anabaena–Serratia, Anabaena–Pseudomonas, Anabaena–Rhizobium* and *Anabaena–Trichoderma* can increase crop yields and micronutrient contents, soil nitrogenase and phosphatase activities, and soil organic carbon (Bidyarani et al. 2016; Prasanna et al. 2015; Rana et al. 2015; Swarnalakshmi et al. 2013). Potential savings of nitrogen fertilizers, sequestration of greenhouse gases and restoration of soil fertility justify the potential of microalgae and cyanobacteria in modern sustainable agriculture (Abinandan et al. 2019).

Conclusion

Among the auxins, the most well-known is IAA for which several biosynthetic pathways have been described in plants and to a lesser extent in algae. Auxin biosynthesis seems to have evolved early in algal evolution and several internal and external factors influence its production in algae. Algae are the closest ancestors of vascular plants and appear to have more elementary auxin biosynthesis and signaling pathways that require further elucidation. Manipulating these factors influencing auxin biosynthesis would help to maximize and sustain auxin accumulation in algae exposed to environmental fluctuations, especially during outdoor cultivation. Using wastewaters may alleviate the costs of mass production of algal auxin. Apart from the contribution of auxins, auxin-producing algae have promising agricultural potential via carbon sequestration, nitrogen fixation and nutrient mineralization for improving soil fertility.

Numerous studies have established the potential of algal bioproducts in agriculture with regard to the growth-promoting effect of algal auxins for their vital roles in all stages of plant development. As algal biofertilizers and biostimulants are increasingly applied globally, the precise mechanisms of auxin action merit future investigation to enhance agricultural sustainability. Understanding auxin physiology, the factors affecting auxin production, and the synergistic nature of plant-algae interactions will be crucial steps towards validating and enhancing the commercial value of these algal bioproducts.

Figure caption

Fig. 1 Tryptophan-dependent and -independent pathways for indole-3-acetic acid biosynthesis. Blue letters stand for gene abbreviation of enzymes involved. Green arrows represent the putative orthologs found in algae. Question marks indicate where genes are not well-defined. Graphics adapted from Le Bail et al. (2010), De Smet et al. (2011), Mashiguchi et al. (2011) and Bogaert et al. (2019)

Fig. 2 Major internal and external factors influencing auxin production in algae

Fig. 3 Schematic diagram of indole-acetic acid (IAA) degradation in the Murashige-Skoog liquid medium (**a**) with all salts present (S+) or absent (S-) under light (L) and dark (D) conditions (modified from Dunlap and Robacker 1988); and (**b**) with vitamin B6 present under white light (modified from Leasure et al 2013). Spectral shift after 48 hours indicates enhanced IAA degradation by B6

Fig. 4 (a) Typical dose-dependent growth effects of exogenous auxin (lines) applied to algae with comparison to plant roots and shoots (adapted from Kolachevskaya et al. 2019). Bars represent the auxin content of different algae that lies within the range of growth-response concentrations for roots and shoots. (*) indicates the values are expressed in weight-to-weight ratio with no exogenous auxin is reported. **(b)** Summary of common and differential growth effects observed in algae (color code: mixture of red, green and brown - seaweeds species; cyan/blue green – cyanobacteria species; green – microalgae species; blue – algal cultures) after applying exogenous auxin. Growth responses and auxin content, including other information of algae in the figure were compiled from the literature reviewed in this paper

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