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Research article

Hormone profiles in microalgae: Gibberellins and brassinosteroids

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ABSTRACT

Endogenous gibberellins and brassinosteroids were quantified in 24 axenic microalgae strains from the Chlorophyceae, Trebouxiophyceae, Ulvophyceae and Charophyceae microalgae strains after 4 days in culture. This is the first report of endogenous gibberellins being successfully detected in microalgae. Between 18 and 20 gibberellins were quantified in all strains with concentrations ranging from 342.7 pg mg⁻¹ DW in *Raphidocelis subcapitata* MACC 317–4746.1 pg mg⁻¹ DW in *Scotiellopsis terrestris* MACC 44. Slower growing strains (*S. terrestris* MACC 44, *Gyoeffiana humicola* MACC 334, *Nautococcus mamillatus* MACC 716 and *Chlorococcum ellipsoideum* MACC 712) exhibited the highest gibberellin contents while lowest levels of gibberellins were found in faster growing strains (*R. subcapitata* MACC 317 and *Coelastrum excentrica* MACC 504). In all strains, the active gibberellin detected in the highest concentration was GA₆, the predominant intermediates were GA₁₅ and GA₅₃ and the main biosynthetic end products were GA₁₃ and GA₅₁. Gibberellin profiles were similar in all strains except for the presence/absence of GA₁₂ and GA₁₂ald. To date this is the second report of endogenous brassinosteroids in microalgae. Brassinosteroids were detected in all 24 strains with concentrations ranging from 117.3 pg mg⁻¹ DW in *R. subcapitata* MACC 317–977.8 pg mg⁻¹ DW in *Klebsormidium flaccidum* MACC 692. Two brassinosteroids, brassinolide and castasterone were determined in all the strains. Generally, brassinolide occurred in higher concentrations than castasterone.

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1. Introduction

Plant hormones are ubiquitous and essential in regulating growth and development in multicellular plants as well as controlling their responses to environmental cues and stresses [1]. Although research on the occurrence and function of plant hormones in microalgae is lagging far behind that of the more complex multicellular plants, there is increasing evidence that plant hormones are present in microalgae [2]. We recently quantified endogenous auxins and cytokinins in 24 axenic microalgae strains [3]. These strains included the more closely related Chlorophyceae (17 strains), Trebouxiophyceae (5 strains) and Ulvophyceae (1

strain) within the Chlorophyta clade and one strain from the divergent Streptophyta clade from which land plants evolved [4]. Two auxins, i.e. indole-3-acetic acid (IAA) and indole-3-acetamide (IAM), were present in all 24 strains. Nineteen cytokinins were also detected in these 24 strains with *cis*-zeatin (*cZ*) forms being the most abundant. Moderate amounts of isopentenyladenine (*iP*) forms and low concentrations of *trans*-zeatin (*tZ*) and dihydrozeatin (*DHZ*) forms were measured [3]. Considering the other classes of plant hormones, abscisic acid (ABA) has been detected and quantified in microalgae [5,6]. To date, gibberellins (GAs) have not been found in microalgae [2] and there is only one report of brassinosteroids (BRs) identified in the microalga *Chlorella vulgaris* [7].

Gibberellins control various aspects of plant growth such as seed germination, stem elongation, leaf expansion and flower and seed development [8]. Over 130 GAs have been identified in plants and other organisms. The first gibberellin was isolated from *Gibberella fujikuroi*, a fungal rice pathogen and more GAs have since been isolated from other fungi and bacteria. However, the biosynthetic pathway differs a bit from that in plants [8]. Gibberellins have also been identified in some tree ferns while functional homologs that

Abbreviations: ABA, abscisic acid; BL, brassinolide; BRs, brassinosteroids; CS, castasterone; *cZ*, *cis*-zeatin; *DHZ*, dihydrozeatin; GAs, gibberellins; IAA, indole-3-acetic acid; IAM, indole-3-acetamide; *iP*, isopentenyladenine; LOD, limit of detection; MACC, Mosonmagyaróvár Algal Culture Collection; *tZ*, *trans*-zeatin; UPLC-MS/MS, ultraperformance tandem mass spectrometry.

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form complexes with GAs have been identified in Lycophytes, e.g. *Selaginella moellendorffii* and *Selaginella kraussiana* [8]. Recently 18 GAs were detected in the stipe and frond of the kelp *Ecklonia maxima* (Phaeophyceae) [9].

Brassinosteroids are now recognized as a relatively new class of plant hormones. They have a dual function, acting as growth-promoting hormones and playing a role in protection against environmental stresses [10]. Brassinosteroids are widely distributed in the plant kingdom [10] with over 70 BRs isolated from plants [11] including angiosperms (both dicotyledons and monocotyledons), gymnosperms as well as from a few lower order plants such as *Equisetum arvense* (Pteridophyte) [12], *Marchantia polymorpha* (Bryophyte) [13], the freshwater alga *Hydrodictyon reticulatum* (Chlorophyceae) [14], the seaweed *E. maxima* (Phaeophyceae) [9] and the microalgae *C. vulgaris* (Trebouxiophyceae) [7].

There is evidence for cross-talk between plant hormones [1]. Gibberellins and auxins act synergistically with GA levels positively regulated by auxin. There are antagonistic effects between GAs and ABA as well as GAs and cytokinins [8,15]. Brassinosteroids have a synergistic effect with auxins and interact with ABA, have an additive effect with GAs and increase ethylene production [11]. Thus, it is important to have an overview of the total hormone complement in microalgae in order to improve their growth and responses to external factors when grown in culture. We previously reported on the endogenous auxin and cytokinin profiles in 24 microalgae strains [3]. The aim of the present study was to quantify endogenous GAs and BRs in the same 24 strains to confirm their presence in microalgae.

2. Results

2.1. Growth in culture

As the starting density was 10 mg L⁻¹ DW for all the cultures, biomass accumulation measured on day 4 was used as a measure of growth rates. The fastest growing strain with the highest biomass accumulation was *Raphidocelis subcapitata* MACC 317 and the

slowest growing strain with the lowest biomass accumulation was *Gyoeffiana humicola* MACC 334 (Table 1).

2.2. Gibberellins

Between 18 and 20 GAs were detected in the 24 microalgal strains analyzed after 4 days growth in culture. Total GA concentrations ranged from 342.7 pg mg⁻¹ DW in *R. subcapitata* MACC 317 to 4746.1 pg mg⁻¹ DW in *Scotiellopsis terrestris* MACC 44. When plotted against biomass which was used as a measure of growth, slower growing strains exhibited the highest GA contents, e.g. *S. terrestris* MACC 44, *G. humicola* MACC 334 and *Nautococcus mamillatus* MACC 716, while faster growing strains, e.g. *R. subcapitata* MACC 317 and *Coelastrum excentrica* MACC 504, showed the lowest GA levels (Fig. 1).

Gibberellin profiles were similar in all strains except for the presence/absence of GA₁₂ and GA_{12ald}. While these two GAs were both present in high concentrations in 16 strains, five strains contained high concentrations of GA₁₂ but with GA_{12ald} being below the limit of detection (LOD), 1 strain had only GA_{12ald} that occurred in a high concentration with GA₁₂ below the LOD and both GA₁₂ and GA_{12ald} were below the LOD in two strains (Table 2). Biologically active GAs (GA₁, GA₃, GA₄, GA₅, GA₆ and GA₇) contributed between 5 and 33% of the total GA content, the metabolic end products (GA₁₃ and GA₅₁) contributed between 7 and 40% and the intermediates made up the biggest proportion (between 36 and 91%) of the total GA content (Table 2; Fig. 1). In all 24 strains, the active GA detected in the highest concentration was GA₆, the predominant intermediates were GA₁₅ and GA₅₃ and the biosynthetic end products (GA₁₃ and GA₅₁) occurred in relatively high amounts (Table 2).

2.3. Brassinosteroids

Using the recently developed sensitive mass spectrometry based method for simultaneous profiling of many of the known brassinosteroid precursors and metabolites in small amounts of

Table 1
Taxonomic details, culture origin and biomass accumulation in the 24 microalgal strains analyzed after 4 days in culture.

Class	Genus and species	MACC	Origin	DW mg L ⁻¹	
Chlorophyceae	<i>Stigeoclonium nanum</i> (Dillwyn) Kütz.	790	Czech Republic, soil	635	
	<i>Chlorococcum ellipsoideum</i> Deason et Bold	712	Czech Republic, soil	320	
	<i>Gyoeffiana humicola</i> Kol et Chodat	334	Brazil, soil	239	
	<i>Monoraphidium contortum</i> (Thur.) Komárková-Legnerová	700	Czech Republic, soil	470	
	<i>Nautococcus mamillatus</i> Korschikov	716	Czech Republic, soil	277	
	<i>Ploidion didymos</i> Pascher	545	Brazil, soil	427	
	<i>Protosiphon botryoides</i> G.A. Klebs	32	Czech Republic, soil	461	
	<i>Acutodesmus acuminatus</i> ^a (Lagerh.) Tsarenko	41	Czech Republic, soil	630	
	<i>Acutodesmus incrassatus</i> ^b (Bohlin) Tsarenko	730	Brazil, soil	430	
	<i>Desmodesmus armatus</i> ^c (R. Chodat) E. Hegewald	59	Czech Republic, soil	657	
	<i>Scotiellopsis terrestris</i> (Reisigl) Punčoch. et Kalina	44	Czech Republic, soil	385	
	<i>Raphidocelis subcapitata</i> (Korshikov) G. Nygaard, J. Komárek, Kristiansen et Skulberg	317	Czech Republic, soil	1020	
	<i>Chlamydomonas reinhardtii</i> P.A. Dang.	772	Brazil, soil	559	
	<i>Protococcus viridis</i> C. Agardh	219	Brazil, soil	765	
	<i>Coelastrum microporum</i> Nägeli	51	Czech Republic, soil	525	
	<i>Spongiochloris excentrica</i> Starr	504	Czech Republic, soil	884	
	<i>Coccomyxa</i> sp.	535	Brazil, soil	429	
	Trebouxiophyceae	<i>Chlorella pyrenoidosa</i> Chick	3	Russia, soil	559
		<i>Chlorella vulgaris</i> Beyerinck	755	Czech Republic, soil	681
<i>Chlorella minutissima</i> Fott et Nováková		361	Brazil, soil	594	
<i>Myrmecia bisecta</i> Reisigl		594	Czech Republic, soil	284	
<i>Stichococcus bacillaris</i> Nägeli		505	Czech Republic, soil	376	
Ulvophyceae	<i>Ulothrix</i> sp.	777	Brazil, soil	413	
Charophyceae	<i>Klebsormidium flaccidum</i> (Kütz.) P.C. Silva, K.R. Mattox et W.H. Blackw.	692	Ukraine, soil	443	

^a Formerly *Scenedesmus acuminatus*.

^b Formerly *Scenedesmus incrassatulus*.

^c Formerly *Scenedesmus armatus*.

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