STIMULATORY EFFECT OF AUXINS AND CYTOKININS ON CAROTENES, WITH DIFFERENTIAL EFFECTS ON XANTHOPHYLLS IN THE GREEN ALGA *CHLORELLA PYRENOIDOSA* CHICK.

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ABSTRACT

Research concerning the influence of auxins and cytokinins on the content of carotenoids in *Chlorella pyrenoidosa* (*Chlorophyceae*) has been conducted. The strongest stimulating effect on carotenoids content in *Ch. pyrenoidosa* biomass was exerted by cytokinins (N-6-benzylaminopurine and N-6-furfurylaminopurine) and allantoin, weaker by auxins and their chemical analogues, and the weakest by tryptamine and 2,4-dichlorophenoxyacetic acid compared to the control. Under the influence of cytokinins the content of α- and β-carotene have been stimulated several times stronger than by auxins, and especially 2,4- dichlorophenoxyacetic acid and tryptamine. However, oxygen-rich xanthophylls content was most strongly reduced by cytokinins (60-70% in relation to the control) in the 20 day lasting of *Ch. pyrenoidosa* cultivation, similarly to auxins: 1-naphthaleneacetic acid, indole-3-butyric acid, 2,4- dichlorophenoxyacetic acid.

KEY WORDS: *Chlorella pyrenoidosa*, carotenoids, carotenes, xanthophylls, auxins, cytokinins.

INTRODUCTION

Carotenoids are polyen pigments that widely occur in animal and plant kingdom in the free form or as esters of fatty acids. Carotenoids are indispensable components of photosynthetic pigment-protein complexes. They serve as light-harvesting pigments and play an important role in protecting the photosynthetic apparatus against the damaging effects of singlet state oxygen. Singlet state oxygen in the photosynthetic apparatus can be formed by energy transfer from triplet-state chlorophyll to ground-state oxygen (Foppen 1971, Isler et al. 1971, Goodwin 1976, 1980, Young 1991).

Carotenoids present in algae are characterized by great heterogeneity and chemical variability that are mainly caused by environmental and genetic factors. Each taxonomic group of algae contains characteristic carotenoid pigments. Carotenoids content in algae cells fluctuates between 0.5-1.7 %, while in vascular plants it can amount to the maximum 0.3 % of dry weight. In *Chlorella* genus commonly occur: α- and β -carotene, canthaxanthin, β-cryptoxanthin, echinenon, lutein, violaxanthin, neoxanthin and zeaxanthin (Iwata et al. 1961, Jensen 1977, Czygan 1980).

Abbreviations:
IAA, indole-3-acetic acid; IBA, indole-3-butyric acid; ILA, indole-3-lactic acid; Trp-NH_2, tryptamine; 2,4-D, 2,4-dichlorophenoxyacetic acid; NAA, 1-naphthaleneacetic acid; BAP, N-6-benzylaminopurine; FAP, N-6-furfurylaminopurine; AT, allantoin.

Carotenoid pigments, along with chlorophylls, play an important role in photosynthesis, especially in algae existing in deeper water strata. They perform a role of direct light energy absorbents. Carotenoids prevent chlorophyll from photooxidation and perform essential role as a constituent element of photoreceptors in a phototaxis and sexual chemotaxis of algaes mobile cells. They also perform a very important role in oxidation-reduction connected with oxygen, hydrogen and electron transport. Some of carotenoids are precursors of plant hormones, for example abscisic acid (ABA) (Lewin 1962, Stewart 1974).

Some research showed that auxins, especially IAA, can be stimulated by biosynthesis, cumulation and durability of photosynthetic pigments, mainly chlorophylls, α-, β-carotene and lutein (Pilet and Phipps 1968, Szirajewa and Gamburg 1973, Gamburg 1978, Adhikary and Pattnaik 1979, Volfova et al. 1979). Also the effect of cytokinin on the content of photosynthetic pigments increases in vascular plants and algae. The majority of publications concerning those problems concern vascular plants, while few research studies have been performed on algae (Augier 1976, 1977, Czerpak 1979, 1983 1990, Burkiewicz 1987, Czerpak et al. 1994). Due to the lack of comparative analyses of metabolic activity of auxins and cytokinins in algae, attempts were made to evaluate their stimulative effect on the biomass dry weight, photosynthetic pigments in *Ch. pyrenoidosa* with respect to their chemical structure. In addition the optimum concentration range and the effective action period of auxins and cytokinins were studied.

MATERIALS AND METHODS

Organisms and culture conditions

Ch. pyrenoidosa Chick was grown under controlled conditions at 25 (± 1) C. Illumination was supplied 16 h photoperiod (8 h dark period) by a bank of fluorescent lights yielding a photon flux of 50 μmol m^{-2} s^{-1} at the surface of the tubes. Permanent synchronous growth was established according to the method of Pirson and Lorenzen (1966), in the conditions developed by Sayegh and Greppin (1973). The culture medium used was modified Knops medium. The pH of the medium was adjusted to 6.5 with 1 N NaOH. The *Chlorella* cells were cultured in an Erlenmeyer flask (500 mL) containing 250 mL of medium, and shaken at 50 rpm in rotary shaker. The algae were grown in medium supplemented with additional following substances: auxins: indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), indole-3-lactic acid (ILA) (auxins); tryptamine (Trp-NH_2) (auxin precursor); 2,4-dichlorophenoxyacetic acid (2,4-D), 1-naphthaleneacetic acid (NAA) (chemical analogues of auxin); N-6-benzylaminopurine (BAP), N-6-furfurylaminopurine (FAP) (cytokinins), allantoin (AT). The hormones were dissolved in 50 % ethanol, and 10 μL of the solution was applied to the cultures. To the control, 10 μL of 50 % ethanol was applied.

Determination of dry weight

To determine the biomass dry weight, two 10-mL algal cultures were filtered through preweighed glass microfiber filters (Whatman, Maidstone, UK), washed with 0.5 N HCl and distilled water to remove mineral salt precipitates, dried overnight at 105°C, and then weighed (Lee and Low 1993).

Determination of carotenoids

In the course of the experiments samples of material were collected from particular trophic links in the amount 0.1-0.2 g of weight for the qualitative-quantitative analysis of carotenoid pigments, the methods used being absorption column chromatography and spectrophotometry. Carotenoid pigments were identified in visible light and UV. Most operations involved in chemical analysis of carotenoids were performed under nitrogen and semi-darkness.

The ester and complex compounds of carotenoids contained in extracts were hydrolysed with 10% KOH solution in methanol in the volume ratio 1:1, at room temperature in the presence of nitrogen during 6 or 12 hrs. After completing hydrolysis the extract was neutralized with 15% acetic acid to weakly basic reaction of pH value 8-9 and diluted with water. The total content of carotenoids was determined in the petroleum ether extract calculated into β-carotene (max. absorption 450 nm). In order to isolate the fraction of carotenes and oxygen rich xanthophylls chromatographic distribution was used on the column filled with adsorbent – activated Al_2O_3. The fraction of carotenes was extracted from the columns by a mixture of 1% acetone in the petroleum ether. The fraction of oxygen-rich xanthophylls was extracted with methanol. Earlier, small amounts of oxygen-poor xanthophylls were extracted with acetone in petroleum ether, whose content under the influence of egxogennously used phytohormones was not changed in a statistically significant way. The identification of carotenoids was conducted on the basis of maximum absorption, while the quantitative measurements of the above mentioned carotenoids fractions were done using coefficients of mole extinction (2600 for carotenoids and 2270 for xanthophylls) according to the formulae by Foppen (1971), Czygan (1980) Goodwin (1980), Lichtenthaler and Wellburn (1983).

RESULTS

Maximum stimulatory effect of exogenous hormones on the growth was observed at concentrations $5x10^{-5}$-10^{-4} M (Table 1). Changes of analyzed carotenoids in *Ch. pyrenoidosa* are presented in tables 2-3 (SE – less than 5%).

Total content of carotenoids, under the influence of auxins, was most strongly stimulated after 20 days of *Ch. pyrenoidosa* culturing, at the concentrations: 10^{-4} M IAA about 109.7%, $5x10^{-5}$ M IBA about 103.1% and 10^{-4} M ILA about 85.6% in relation to the control (100%) (Table 2).

Total content of carotenes were most intensively stimulated by IAA after 10 days of algae cultivation in $5x10^{-5}$ M by about 87.3% and after 15 days in 10^{-4} M by about 85.6%. Carotenoids content was slightly less stimulated by IBA than ILA. Carotenoids accumulation in *Ch. pyrenoidosa* under the influence of auxins was the greatest between 10th and 15th day of cultivation (Table 2).

Oxygen-rich xanthophylls content was most intensively stimulated after 10 days by 10^{-5} M IBA and ILA, the least by $5x10^{-5}$ M IAA when compared to the control. However, after 20 days of algae cultivation. The decrease of oxygen-rich xanthophylls content in 10^{-5} M IAA and ILA was shown (Table 3).

Auxins chemical analogues application showed the greatest general carotenoid content stimulation after 20 days of algae cultivation in 10^{-4} M NAA, slightly weaker in $5x10^{-5}$ M Trp-NH_2 and significantly weaker in 10^{-4} M 2,4-D on the control. Carotenoids content was most intensively stimulated after 10 days of algae cultivation under the influence of 2,4-D between the 10th and the 15th day of the culturing in the range of $5x10^{-5}$-10^{-4} M.

In the period between the 5th and the 10th day of algae cultivation increase of oxygen-rich xanthophylls content was intensively stimulated by $5x10^{-5}$ M concentration, the most intensively by NAA in a range of 58.5-62.5% and slightly less under the influence of Trp-NH_2 about 44.7-45.2 % and 2,4-D about 38.2-40.4% on the control. However, in the case of Trp-NH_2 after 20 days of cultivation in 10^{-4} M concentration, minimum xanthophylls content (about 2.9%) decrease is shown.

Under the influence of cytokinins used general carotenoid content was most strongly stimulated after 20 days of algae cultivation in $5x10^{-5}$ M FAP about 185.2% and less after 10 days in 10^{-3} M AT about 89.1% on the control.

α- and β-carotene content was most intensively stimulated after 10 days of algae culturing under the effect of 10^{-4} M BAP (194.3%), slightly less after 15 days in $5x10^{-5}$ M FAP (168.1%) and least after 10 days in 10^{-3} M AT (107.5%).

Oxygen-rich xanthophylls content intensively decreases during 20 day period of *Ch. pyrenoidosa* cultivation under the influence of cytokinin used and AT. Decrease of their content was most intensive between the 5th and the 10th day of cultivation in 10^{-5} M BAP in the range of 66.3-70.7%, slightly weaker after 15 days of cultivation and it appears the least under the influence of AT in 10^{-4} M about 58.2% after 20 days in relation to the control.

DISCUSSION

General content of carotenoids was stimulated in a maximum degree by the application of growth substances between the 15th and the 20th day of algae cultivation. The greatest stimulating effect on carotenoids content had cytokinin (BAP and FAP), which after 20 days of algae cultivation caused their growth by about 185-190% when compared to the con-

TABLE 1. Effects of hormones on the growth of *Ch. pyrenoidosa*. SE less than 5%.

Hormones	Molar concentration	Biomass (g/l)			
		5 d	10 d	15 d	20 d
IAA	10^{-4}	2.16	3.52	7.85	9.25
	5×10^{-5}	2.51	3.98	7.31	8.01
	10^{-5}	2.11	3.37	5.53	6.21
IBA	10^{-4}	1.41	1.88	3.92	5.57
	5×10^{-5}	1.67	2.98	6.15	7.13
	10^{-5}	1.82	3.18	4.02	5.12
ILA	10^{-4}	1.60	2.91	6.80	8.52
	5×10^{-5}	1.98	3.63	5.99	7.53
	10^{-5}	1.79	2.81	4.51	5.75
NAA	10^{-4}	2.93	6.21	12.27	14.61
	5×10^{-5}	3.56	8.28	11.51	13.69
	10^{-5}	3.11	6.45	10.12	11.58
Trp-NH_2	10^{-4}	2.76	6.63	9.29	10.72
	5×10^{-5}	3.89	9.04	11.81	13.51
	10^{-5}	3.35	8.30	10.52	12.13
2,4-D	10^{-4}	1.56	3.58	7.06	11.03
	5×10^{-5}	2.01	5.40	6.51	9.46
	10^{-5}	1.72	3.95	5.49	7.33
BAP	10^{-4}	4.66	8.12	10.21	12.75
	5×10^{-5}	3.32	6.27	7.50	8.81
	10^{-5}	2.35	3.28	4.60	5.52
FAP	10^{-4}	3.78	8.89	11.50	13.80
	5×10^{-5}	5.43	10.29	13.41	15.90
	10^{-5}	3.49	6.20	7.97	9.83
AT	10^{-3}	5.19	11.84	16.03	18.22
	5×10^{-4}	4.24	11.01	14.28	16.03
	10^{-4}	3.17	7.82	10.49	12.05
Control	0	1.29	1.71	2.23	2.71

trol. Considerably less stimulating effect on their content had AT in 124% and IAA, IBA, NAA about 103-110%, and the least stimulating effect on general carotenoids content had 2,4-D in the range of 76-94% on the control.

Among carotenoids, carotene content increases most intensively under the influence of applied cytokinins between 10th and 15th day of algae cultivation in the range of 168-194%, which was confirmed by research on *Scenedesmus acuminatus* (Sykut 1987). Less intensive stimulation of carotene content was under the influence of 2,4-D and ILA only about 36-62% about the control.

Those oxygen-rich xanthophylls are known to appear most plentifully in ageing and pathological condition of plant cells. Under the influence of cytokinin applied during 20 days of *Ch. pyrenoidosa* cultivation considerable decrease of oxygen-rich xanthophylls content was observed from 58 to 71%, while under the influence of auxins, their chemical analogues and Trp-NH_2 application between the 5th and the 10th day of algae cultivation content of oxygen-rich xanthophylls increases considerably in the range of 38-74%, between the 15th and the 20th day of *Ch. pyrenoidosa* cultivation, under the influence of ILA and Trp-NH_2 a slight decrease in the range 2-25% occurs.

The results of the research showed that cytokinins and AT considerably delays oxidation process of photosynthetic pigments, especially chlorophylls and carotenoids. Mechanisms of that action is probably based on inhibition of oxidases and dehydrogenases activity – enzymes responsible for oxidation process and following degradation of chlorophylls and carotenoids. Such action has not been found in auxins, their precursors and chemical analogues (Pilet and Phipps 1968, Szirajewa and Gamburg 1973).

After 20 days of algae cultivation carotenes and oxygen-rich xanthophylls content increases most, which means they can be precursors in producing ABA. Those results showed algae's cells progressing process of ageing, which was manifested by carotenoids oxidation increase. Carotenoids content increase in algae under the influence of auxins used on correlated with their cell proliferation, which has been shown in research on *Ch. pyrenoidosa* and *Sc. quadricauda*. Generally growth regulators stimulating algae and vascular plants growth start anabolic reactions and reduce catabolic reactions of carotenoids. Cytokinins were more active in action than auxins. They cause greater effect of stimulation in a shorter period time in eucaryota organisms cells rather than procaryota (Czerpak 1979, 1990, Tatkowska and Buczek 1980, Czerpak et al. 1994).

TABLE 2. Effect of hormones on the content of total carotenoids and carotenes. SE less than 5%.

Hormones	Molar concentration	Total carotenoids (mg/g dry wt.)				Carotenes (mg/g dry wt.)			
		5 d	10 d	15 d	20 d	5 d	10 d	15 d	20 d
IAA	10^{-4}	0.942	1.411	2.253	2.604	0.281	0.405	0.722	0.832
	5×10^{-5}	1.011	1.504	1.990	2.320	0.303	0.427	0.686	0.787
	10^{-5}	0.903	1.301	4.597	1.823	0.274	0.382	0.638	0.706
IBA	10^{-4}	0.743	1.064	1.965	2.101	0.239	0.351	0.614	0.690
	5×10^{-5}	0.802	1.112	2.173	2.523	0.258	0.372	0.659	0.744
	10^{-5}	0.941	1.330	1.696	1.872	0.280	0.394	0.575	0.663
ILA	10^{-4}	0.861	1.232	1.905	2.305	0.275	0.349	0.583	0.712
	5×10^{-5}	0.912	1.349	1.634	1.934	0.282	0.369	0.542	0.639
	10^{-5}	0.823	1.194	1.404	1.628	0.270	0.340	0.506	0.586
NAA	10^{-4}	0.842	1.212	2.073	2.562	0.261	0.383	0.605	0.830
	5×10^{-5}	0.971	1.364	1.902	2.368	0.286	0.413	0.579	0.788
	10^{-5}	0.900	1.268	1.701	2.187	0.272	0.398	0.538	0.731
Trp-NH_2	10^{-4}	0.785	1.127	1.523	1.810	0.268	0.400	0.521	0.681
	5×10^{-5}	0.902	1.273	1.869	2.414	0.280	0.429	0.587	0.776
	10^{-5}	0.861	1.221	1.808	2.162	0.275	0.417	0.572	0.714
2,4-D	10^{-4}	0.752	0.980	1.782	2.183	0.203	0.271	0.529	0.728
	5×10^{-5}	0.841	1.221	1.727	2.026	0.214	0.307	0.508	0.678
	10^{-5}	0.820	1.165	1.542	1.843	0.267	0.292	0.449	0.620
BAP	10^{-4}	1.232	2.180	2.963	3.601	0.432	0.671	1.021	1.264
	5×10^{-5}	0.936	1.781	2.592	3.206	0.417	0.638	0.937	1.242
	10^{-5}	0.828	1.287	1.978	2.509	0.374	0.587	0.804	0.949
FAP	10^{-4}	0.842	1.684	2.278	3.008	0.343	0.542	0.896	1.128
	5×10^{-5}	1.009	1.882	2.803	3.542	0.351	0.576	1.043	1.311
	10^{-5}	0.858	1.604	2.306	2.900	0.317	0.521	0.914	1.074
AT	10^{-4}	1.087	1.634	2.251	2.778	0.321	0.473	0.638	0.891
	5×10^{-5}	0.992	1.510	2.003	2.421	0.302	0.449	0.582	0.787
	10^{-5}	0.915	1.356	1.751	2.043	0.281	0.415	0.528	0.692
Control	0	0.710	0.864	1.113	1.242	0.196	0.228	0.389	0.536

The majority of the growth substances studied induce to the maximum the growth and the general content of carotenoids and carotenes at the concentration 5×10^{-5} M, with the exception of the allantoin at the concentration 10^{-3} M, and IBA in *Ch. pyrenoidoisa* at the concentration 10^{-5} M. Also the content of oxygen-rich xanthophylls is most intensively stimulated at the same concentrations of the regulators of the growth of these plants. Compared to the control algae cultivation (100%), the auxins studied, their direct precursors and chemical analogues stimulate the content of oxygen rich xanthophylls within the range of 50%, while IBA and NAA much more over 50%. This activity was most obviously visible between the 5th and 10th day of the algae cultivation. Cytokinins (BAP and FAP) and allantoin (the product of their partial degradation) have reverse influence, i.e. they inhibit the content of oxygen rich xanthophylls by 40% to 70%, compared to the control (100%), throughout the entire period of the 20-day cultivation of *Ch. pyrenoidosa*. Such influence of cytokinins upon the content of carotenoids and their level of oxygenation in *Ch. pyrenoidosa* demonstrates that they slow down the processes of oxidation and degeneration of carotenoids and chlorophylls (Augier 1977, Czerpak 1979, 1983, 1990, Tatkowska and Buczek 1980, Czerpak et al. 1994) and the processes of ageing of plants. Hence it appears that while *Ch. pyrenoidosa* undergo the process of ageing, the auxins increase the oxidation of carotenoids, which weakens their biological activity, especially photosynthesis, while cytokinins and allantoin slow down their oxidation, especially towards oxygen rich xanthophylls.

The substances studied, which promote the growth of *Ch. pyrenoidosa*, act probably in higher concentrations, from 10^{-4} M, when compared to vascular plants, possibly due to their use in the Knop mineral solution. Under the influence of intensive lighting, excess of oxygen and, possibly, some of the mineral elements in the solution, during 20 day algae cultivation, either degradation or inactivation of small amounts of plant regulators occurs. That is probably why auxins and cytokinins, and their precursors and chemical analogues, demonstrate stimulating influence upon algae, starting at the concentration 10^{-5} M, and allantoin even at the concentration 10^{-3} M. Higher concentrations have toxic influence, causing the death of algae after 3 to 4 days of cultivation.

TABLE 3. Effect of hormones on the content of oxygen-rich xanthophylls. SE less than 5%.

Hormones	Molar concentration	Oxygen-rich xanthophylls (mg/g dry wt.)			
		5 d	10 d	15 d	20 d
IAA	10^{-4}	0.139	0.161	0.197	0.231
	5×10^{-5}	0.145	0.172	0.172	0.206
	10^{-5}	0.127	0.148	0.141	0.157
IBA	10^{-4}	0.141	0.167	0.210	0.235
	5×10^{-5}	0.152	0.183	0.249	0.276
	10^{-5}	0.170	0.214	0.188	0.211
ILA	10^{-4}	0.154	0.186	0.252	0.265
	5×10^{-5}	0.168	0.208	0.283	0.238
	10^{-5}	0.149	0.172	0.161	0.203
NAA	10^{-4}	0.144	0.162	0.216	0.270
	5×10^{-5}	0.169	0.195	0.194	0.253
	10^{-5}	0.157	0.181	0.178	0.238
Trp-NH_2	10^{-4}	0.130	0.147	0.162	0.202
	5×10^{-5}	0.151	0.178	0.202	0.232
	10^{-5}	0.144	0.169	0.196	0.210
2,4-D	10^{-4}	0.128	0.146	0.207	0.247
	5×10^{-5}	0.146	0.170	0.202	0.235
	10^{-5}	0.140	0.158	0.177	0.213
BAP	10^{-4}	0.047	0.050	0.086	0.133
	5×10^{-5}	0.038	0.041	0.077	0.106
	10^{-5}	0.035	0.036	0.061	0.074
FAP	10^{-4}	0.046	0.051	0.050	0.089
	5×10^{-5}	0.048	0.053	0.074	0.124
	10^{-5}	0.043	0.048	0.052	0.081
AT	10^{-3}	0.078	0.096	0.122	0.144
	5×10^{-4}	0.071	0.083	0.103	0.113
	10^{-4}	0.056	0.061	0.082	0.087
Control	0	0.104	0.123	0.157	0.208

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STYMULUJĄCY WPŁYW AUKSYN I CYTOKININ NA ZAWARTOŚĆ KAROTENOIDÓW, ZE ZRÓŻNICOWANYM WPŁYWEM NA KSANTOFILE W ZIELONYM GLONIE *CHLORELLA PYRENOIDOSA* CHICK.

STRESZCZENIE

Przeprowadzono badania dotyczące wpływu auksyn i cytokinin na zawartość karotenoidów w *Chlorella pyrenoidosa* (*Chlorophyceae*). Największy stymulujący wpływ na zawartość karotenoidów, a zwłaszcza karotenów w biomasie *Ch. pyrenoidosa* był wywierany przez cytokininy (BAP i FAP) i AT, nieco mniejszy przez auksyny i ich analogi chemiczne, zaś najmniejszy przez Trp-NH_2 i 2,4-D w porównaniu do kontroli. Pod wpływem użytych cytokinin zawartość karotenów była stymulowana kilka razy silniej aniżeli pod działaniem auksyn i ich analogów, a zwłaszcza 2,4-D i Trp-NH_2. Natomiast zawartość ksantofili bogato utlenionych była intensywnie hamowana przez cytokininy w 60-70% w porównaniu z kontrolą (100%), dość równomiernie podczas 20-dniowej hodowli *Ch. pyrenoidosa*. Z kolei auksyny oraz stosowane ich prekursory i analogi chemiczne działają stymulująco na zawartość bogatych w tlen ksantofili w granicach 20-60% w odniesieniu do hodowli kontrolnej glonów. Z przeprowadzonych badań wynika, że auksyny i związki pokrewne podczas starzenie się glonów wzmagają oksydację karotenoidów, osłabiają ich aktywność metaboliczną. Cytokininy i alantoina posiadają, w przeciwieństwie do auksyn, hamujące działanie na utlenianie karotenoidów, opóźniając ich degradację i wydłużając w czasie wzrostu glonów ich aktywność biologiczną.

SŁOWA KLUCZOWE: *Chlorella pyrenoidosa*, karotenoidy, karoteny, ksantofile, auksyny, cytokininy.