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Complementary chromatic adaptation of cyanobacteria-bryophytes symbionts to environment

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ABSTRACT

By means of column (CC), thin- layer (TLC), high-performance liquid (HPLC) and ion exchange chromatography (IEC) the authors investigated the photosynthesizing pigments (chlorophylls, carotenoids, phycobiliproteins). The phytochromes were also studied in the cyanobacteria- bryophytes (*Anthoceros punctatus*, *Blasia pusilla*) and photobiont (*nostocacean cyanobacteria*). Three groups of pigments absorbing rays of PAR beams from the environment are present in this bryophytes and chromatic adaptation can exist in the conditions of the woods and is characterized by relatively different solar energy.

KEYWORDS: hornworts, liverworts, cyanobacteria, chlorophylls, carotenoids, phycobiliproteins, phytochromes, chromatic adaptation, environment

INTRODUCTION

The representatives of Cyanoprokaryota live in symbiosis with some other species of lower and higher plants [1], between which are also some species of bryophytes [2].

Cyanobacterium which live in symbiosis with bryophytes are the representatives of *Nostoc* genus which are also symbiotic partners of other plant species such as lichens [3]. Our lichen studies showed that, in the adaptation to the light conditions in environment, the phycobiliprotein pigments which occur in the cells of cyanobacterium play a significant role.

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As a result of this we were interested in the process taken part by the cyanobacteria *Nostoc* - bryophytes symbiont- in chromatic adaptation of bryophytes.

MATERIAL AND METHODS

Anthoceros punctatus L. (hornwort) and *Blasia pusilla* L. (liverworts) thalli were both collected in late summer (20 August 2007) from the Knyszynska Forest in north- eastern part of Poland. The plants glued to the small pieces of cardboards which were put into the containers with the conditions of the natural environment of those species. The experimental beakers were stored in boxes equipped with appropriate glass filters [4]. Four basic colours were used: red (λ=700 nm), yellow (λ=590 nm), green (λ=500 nm) and blue (λ=450 nm). The boxes were placed in growth cabinet and were exposed to the light of 2.9 W m^{-2} (sun) and 1.2 W m^{-2} (shade). The detailed method is described in Czeczuga *et al*. [5].

The total amount of chlorophylls and carotenoids in the extract was calculated using the formulas proposed by Jeffrey and Humphrey [6]. The presence of the respective carotenoids in the specimens of two species of bryophytes assayed was identified by column (CC), thin- layer (TLC) and high- performance liquid chromatography (HPLC). This methods are described in detail in Czeczuga *et al*. [7].

The phycobiliproteins were separated from cyanobacteria according to the earlier methods with ammonium sulphate [8]. Relative amounts of particular phycobiliproteins were determined by the method of Bennett and Bogorad [9, 10].

The phytochrome proteins were isolated using ion exchange chromatography (IEC) method according to Tokuhisa *et al*. [11] described by López-Figueroa *et al*. [12]. The details of this method were described in the paper of the authors [5].

RESULTS

The gametophytes of the 2 investigated species of bryophytes contained chlorophyll *a* and *b*, 16 carotenoids (Table 1) and 3 phycobiliprotein pigments types: C-phycoerythrin, C-phycocyanin and allophycocyanin (Table 2). Of particular interest is the presence of such carotenoids as lycoxanthin, adonixanthin, astaxanthin and β-apo-8'-carotenal. The total chlorophyll *a* content ranged from 232.86 (*Anthoceros punctatus*) to 315.24 μg g^{-1} dry weight (*Blasia pusilla*) and chlorophyll *b* ranged from 220.84 (*Blasia pusilla*) to 235.48 μg g^{-1} dry weight (Anthoceros *punctatus*). The total content of carotenoids ranged from 118.5 (*Anthoceros punctatus*) to 136.4 μg g^{-1} dry weight (*Blasia pusilla*). In the *Nostoc* phycobiont we have found the presence of three phycobiliprotein pigments- allophycocyanin was the major pigment is both the investigated species. The total content of phycobiliproteins ranged from 0.118 (*Anthoceros punctatus*) to 0.224 mg g^{-1} dry weight (*Blasia pusilla*). The investigation revealed that both- the part of gametophytes (tissues of bryophytes) and phycobiont (cyanobacterium *Nostoc*) contained phytochromes. The highest concentration of chlorophylls and carotenoids were included in the gametophytes of both species with the green light and smallest in the case of the blue (chlorophylls) and yellow light (carotenoids). The C-phycocyanin increased in the phycobiont of both investigated bryophytes species when using the red light and in shade whereas the C-phycoerythrin increased while using the blue light and in the sun. Total content of phycobiliprotein pigments increased in shade and in the red light (Table 3).

Table 1. List of the carotenoids from the investigated bryophyte species.

Carotenoid		Summary formula	Semisystematic name
1.	Lycopene	$C_{40}H_{56}$	ψ,ψ -Carotene
2.	α-Carotene	$C_{40}H_{56}$	β,ε-Carotene
3.	β-Carotene	$C_{40}H_{56}$	β,β-Carotene
4.	Lycoxanthin	$C_{40}H_{56}O$	ψ,ψ-Caroten-16-ol
5.	α-Cryptoxanthin	$C_{40}H_{56}O$	β,ε-Caroten-3-ol
6.	β-Cryptoxanthin	$C_{40}H_{56}O$	β, β-Caroten-3-ol
7.	Lutein	$C_{40}H_{56}O_2$	β,ε -Carotene-3,3'-diol
8.	Lutein epoxide	$C_{40}H_{56}O_3$	5,6-Epoxy-5,6-dihydro- β,ε -carotene-3,3'-diol
9.	Zeaxanthin	$C_{40}H_{56}O_2$	β,β-Carotene-3,3'-diol
10.	Antheraxanthin	$C_{40}H_{56}O_3$	5,6-Epoxy-5,6-dihydro- β,β-carotene-3,3'-diol
11.	Violaxanthin	$C_{40}H_{56}O_4$	5,6,5',6'-Diepoxy-5,6,5',6'-tetrahydro- β,β-carotene-3,3'-diol
12.	Mutatochrome	$C_{40}H_{56}O$	5,8-Epoxy-5,8-dihydro- β,β-carotene
13.	Adonixanthin	$C_{40}H_{54}O_3$	3,3'-Dihydroxy- β,β-caroten-4-one
14.	Canthaxanthin	$C_{40}H_{52}O_2$	β,β-Carotene-4,4'-dione
15.	Astaxanthin	$C_{40}H_{52}O_4$	3,3'-Dihydroxy- β,β-carotene-4,4'-dione
16.	β-Apo-8'-carotenal	$C_{30}H_{40}O$	8'-Apo- β-caroten-8'-al

Table 2. Pigments content in investigated bryophyte species.

Specification	*Anthoceros punctatus*	*Blasia pusilla*
Chlorophylls		
Chlorophyll *α* µg g^{-1} dry weight	232.86	315.24
Chlorophyll *b* µg g^{-1} dry weight	235.48	220.84
Chl. *a* / chl. *b* ratio	0.99	1.43
Carotenoids		
Carotenoid presence (see Table 1)	1-4,6-12,13,16	1-11,14,15
Major carotenoid %	8(32.16)	11(28.42)
Total content µg g^{-1} dry weight	118.52	136.46
Phycobiliproteins		
C-phycocyanin (CPC) in %	25.8	26.8
C-phycoerythrin (CPE) in %	32.8	30.6
Allophycocyanin (APC) in %	41.4	42.6
CPC/CPE ratio	0.8	0.9
Total content mg g^{-1} dry weight	0.118	0.224
Phytochromes		
In cyanobiont		
Pg form - induces by 650 nm	+	+
Pr form - induces by 540 nm	+	+
In host (bryophyte)		
Pr form - induces by 670 nm	+	+
Pfr form - induces by 710 nm	+	+

DISCUSSION

In both the investigated species of bryophytes there are associations of the cyanobacterium colonies which are situated in the mucilaginous cavities on the undersurface of the gametophytes [13]. In *Anthoceros* species, the presence of cyanobacterium was first described by Askenazy [14] who wrote:.. “in addition to chlorophyll- a water soluble substance related to the blue- green colour of this moss reminiscent of *Oscillatoria*” [15]. Whereas, Essenbeck [16] was credited as the first to notice that phycobiliproteins were released from a colour substance during autolysis of the cells of cyanobacterium *Oscillatoria* sp. The presence of *Nostoc* cells in *Anthoceros* was noted by Leitgeb [17] and in *Blasia* by Waldner [18]. The observations of Leitgeb was confirmed in light microscope by Campbell [19] and by Ridgway [20]. Prantl [21], Pierce [22] and Garjeanne [23] made simple physiological studies. Bond and Scott [24] for the first time showed that the symbiosis of those bryophytes fixed the nitrogen and this finding was confirmed by the Watanabe and Kiyohara [25]. The cyanobacterium isolated from *Anthoceros punctatus* and *Blasia pusilla* appeared to be identical [13]. Now it is known that this photobiont has been identified as strains of *Nostoc sphaericum* by Vaucher [13, 25, 26]. At present, taxonomy of the bryophytes cyanobiont remains

Table 3. Pigments content in investigated bryophyte species in dependence on light quality.

Pigments	Sun ($6.72\ Wm^{-2}$)	Shade ($3.76\ Wm^{-2}$)	Light				
			White	Red	Yellow	Green	Blue
Anthoceros punctatus							
Chlorophyll *a* μg g^{-1} dry weight	320.8	407.4	315.4	320.2	272.6	348.2	220.8
Chlorophyll *b* μg g^{-1} dry weight	226.4	314.8	217.1	228.4	198.8	308.6	270.3
Chl. *a* / chl. *b* ratio	1.42	1.29	1.45	1.40	1.37	1.13	0.82
Carotenoids μg g^{-1} dry weight	76.5	102.2	72.8	98.2	91.7	120.4	108.2
Phycobiliproteins mg g^{-1} dry weight	0.086	0.133	0.128	0.148	0.109	0.098	0.110
C-phycocyanin (CPC) in %			61.8	62.8	61.2	49.6	47.8
C-phycoerythrin (CPE) in %			38.2	37.2	38.8	50.4	52.2
CPC/CPE ratio			1.51	1.69	1.58	0.98	0.92
Blasia pusilla							
Chlorophyll *a* μg g^{-1} dry weight	252.3	306.2	240.8	258.2	204.6	298.6	188.4
Chlorophyll *b* μg g^{-1} dry weight	220.7	294.4	228.2	237.6	184.7	282.2	170.9
Chl. *a* / chl. *b* ratio	1.14	1.04	1.06	1.09	1.11	1.06	1.10
Carotenoids μg g^{-1} dry weight	90.5	152.7	86.6	109.7	98.8	145.4	124.8
Phycobiliproteins mg g^{-1} dry weight	0.168	0.225	0.194	0.240	0.209	0.142	0.26
C-phycocyanin (CPC) in %			64.5	68.3	59.8	38.4	35.2
C-phycoerythrin (CPE) in %			35.5	31.7	40.2	61.6	64.8

undefined. All investigators accept that this cyanobiont belongs to the genus *Nostoc*- called nostacean cyanobacteria.

Both of the examined bryophytes species, independently of the light type, showed a relatively high level of chlorophyll *b* in comparison to chlorophyll *a*. This changes were observed by us during examining the specimens of *Marchantia polymorpha* (liverworts) and 13 species of mosses (Musci) [5]. Chlorophyll *b* content increases and leaves absorb more blue rays [27, 28] both in lower and higher plants [29, 30]. In woodland-shade this is bluish or bluish- grey radiation while in any habitat, early and late during the day [31]. To such light conditions, bryophytes adapt as all other mosses [5] and plants on both- the morphological [32] and physiological level [33]. Not only the total content of chlorophylls but also one of the carotenoids increases. We observed those changes already during the examination of other species of mosses and plants in different environmental conditions [34-39]. A number of carotenoids which occurred in the investigated bryophytes especially including β-carotene, β-cryptoxanthin, lutein, zeaxanthin, antheraxanthin and violaxanthin absorb shorter- wave radiations [40-44]. The presence of four xanthophylls in the investigated materials was an interesting finding. Lycoxanthin, a derivative of lycopene is a common xanthophyll in lichens [45, 46]. The presence of adonixanthin was found in the vascular plants [47] and in some species of fishes [48]. The asthaxanthin was reported in animal species also, especially in water animals [49]. In plants, the asthaxanthin occurred mostly in the cryptogams [45, 46, 50], whereas in the vascular plants this xanthophyll occurred sporadically [5]. B-apo-8'-carotenal, on the other hand, is its derivative [51]. The apocarotenals groups are formed in mosses [52], in the leaves of the ferns [53], and in higher plants at the end of the growing season [54].

In both the investigated species of bryophytes it was shown that the phycobiliproteins pigment content in the phycobilisomes of the photobiont *Nostoc* sp. is not constantly depending as it does on the intensity and the spectral composition of the light. Where the intensity of light is less, the phycobiliprotein pigments content increases and vice versa. This kind of chromatic adaptation also takes place in lichens of the *Peltigera* and *Stereocaulon* genus [4, 45, 55].

The structure of phycobilisome, content of phycobiliprotein pigments and transfer of energy in species of *Nostoc* genus were studies by some investigators. In free- living species of *Nostoc corneum* and *Nostoc pruniforme* the content of phycobiliprotein pigments was examined by Czeczuga *et al*. [56]. In the cells of *Nostoc commune*, the photomorphogenesis was investigated [57], and in *Nostoc muscorum*, the action spectrum for developmental photoinduction of this species was studied [58]. The actions of several denaturants of C-phycocyanin in the cells of *Nostoc punctiforme* have been investigated [59, 60]. In cells of *Nostoc* sp., phycobiliprotein pigments and phycobilisome complexes were investigated [61-63]. In phycobilisomes also such forms of allophycocyanin as allophycocyanin I, II, III, B and 680 were investigated [64-66]. Some authors [67-70] have examined the phycobilisomes and phycobiliprotein pigments of chromatically adapted cells of *Nostoc* sp. to light conditions, and energy transfer in the light harvesting antenna system [71, 72].

The content of particular phycobiliprotein pigments [73-80] and complementary chromatic adaptation of *Nostoc* sp. as photobiont of lichens [74, 79, 81, 82] was also investigated. This investigations have shown that the occurrence of particular phycobiliprotein pigments in plant, plays the role of additional antennae which absorbs the light rays of an appropriate wave length. The energy absorbed by the C-phycoerythrin is transferred to C-phycocyanin which, in turn, transfers it to allophycocyanin and in the final stage into chlorophyll *a*.

The biosynthesis of antennae pigments is controlled by the phytochromes. The phytochromes occurred in the cells of the tissues of bryophytes induced the biosynthesis of chlorophylls and carotenoids [83] and phytochromes of cells of *Nostoc* sp.- biosynthesis of phycobiliprotein pigments [84]. With complementary chromatic adaptation are connected the studies, which running for some time already, on *Anthoceros punctatus* [85] and *Blasia pusilla* [86], on differentiation of chloroplasts [87] and genetic diversity of bryophytes species [88, 89] and their symbionts [90-94]. This studies show the evoluational changes in symbiont [95, 96] and in those two species of bryophytes [97, 98] according to the conditions in which they occur. The content of antenna pigments depends also on season [5], age of the representatives of the plant or on its part [99, 100]. Those changes are connected with complementary chromatic adaptation.

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