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COMPARATIVE ANALYSIS OF D1 PROTEIN SEQUENCES IN CYANOBACTERIA

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SUMMARY. The D1 protein of Photosystem II (PSII), encoded by the *psbA* genes, is an indispensable component of oxygenic photosynthesis. Due to strongly oxidative chemistry of PSII water splitting, the D1 protein is prone to constant damage and requires its replacement by a new copy every 5 h under low light conditions and every 20 minutes under intense illumination, whereas most of the other PSII subunits remain ordinarily undamaged. In cyanobacteria the D1 protein is encoded by a *psbA* gene family, ranging from 1 to 6 members. The presence of multiple *psbA* genes encoding different D1 isoforms is an indication of their importance in regulatory mechanisms responsible for maintaining a functional PSII upon changing environmental conditions in natural habitats of cyanobacteria. Herewith, we present a comparative analysis of the protein sequences encoded by *psbA* gene family in model cyanobacteria strains with sequenced genomes, highlighting their characteristic features that give indication of their putative function.

Keywords: cyanobacteria, D1 protein, Photosystem II, photosynthesis;

Introduction

Photosynthesis is one of the most important processes responsible for the maintenance of the oxygen level in the atmosphere and the reduction of CO_2 to carbohydrates (Loll et. al., 2005). It creates organic matter out of inorganic compounds. In plants, as well as in algae and cyanobacteria, photosynthesis is initiated in Photosystem II (PSII) using light energy to drive two distinct chemical reactions - the photo-oxidation of water and the reduction of plastoquinone (Singhal *et. al*., 1999). PSII is a large homo-dimeric protein-cofactor complex consisting of 20 protein subunits and more than 77 co-factors. Two proteins form the reaction center core of PSII: the D1 and D2 proteins. While higher plants have one *psbA* gene encoding the D1 protein, cyanobacteria generally display a small *psbA* gene family, consisting of 1 to 6 members, differentially expressed, according

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to environmental conditions (Mulo *et. al*., 2009). The D1 protein of PSII is an indispensable component of oxygenic photosynthesis. The aminoacid structure of the *PsbA* peptide gives clues about the hydrophobic nature for D1 protein with five membrane spanning helices (Dwivedi and Bhardwaj, 1995). The D1 protein is photodamaged because of the strongly oxidative chemistry of the Photosystem II, requiring its replacement, whereas most of the other subunits of PSII remain undamaged. The D1 protein is the primary component damaged and replaced in all organisms that perform oxygenic photosynthesis. In normal growth conditions a D1 protein is replaced in the PSII every 5 h, and under different stress conditions the replacement occurs every 20 minutes (Mulo *et. al*., 2009). When the D1 protein is damaged, the Photosystem II is inactivated; the dimers separate, followed by the partial disassembly of the Photosystem II. The damaged D1 protein is removed by an FtsH type protease and degraded. Subsequently a new copy of D1 protein is translated, and the new D1 protein is co-translational inserted into the membrane. The C-terminus of the D1 protein is post-translational processed. The monomers are assembled, then the functional dimers are formed and the PSII is active again (Mulo *et. al*., 2009).

Due to the advance of sequencing techniques, new genomes of cyanobacteria are being sequenced and annotated all the time (http://genome.microbedb.jp/cyanobase/), so periodically new *psbA* gene sequences and of the proteins they encode become available. These sequences allow for putative functional identification of the D1 isoforms and offer clues about their role. The studies of gene expression showed that under stress conditions, cyanobacterial cells adopt different strategies to cope with the changes. One strategy involves the production of larger amount of the same D1 protein, compensating for the higher rate of damage under stress, behavior best characterized in *Synechocystis* sp. PCC 6803, where one type of D1 protein is encoded by two *psbA* genes (Mate *et. al*., 1998). Another strategy involves the replacement of a D1 protein isoform present in normal growth conditions with another one under stress conditions, this strategy was first described at *Synechococcus* sp. PCC 7942 (Sane *et. al*., 2002). The D1 protein isoforms exchange occurs helping the cell to resist better in stress conditions and increases the adaptability to different environmental conditions (Clarke *et. al.*, 1993). A parallel strategy involves the induction of another *psbA* gene, considered silent for a long time (Sicora *et. al*., 2009, Summerfield *et. al*., 2008). It was shown that during the microaerobic conditions, a distinct D1 protein isoform is induced, the D1' isoform, hence its postulated role in adaptation of the cells to low oxygen conditions (Sicora *et. al*., 2009; Summerfield *et. al*., 2008). Recently, a new class of D1 protein termed 'D1 rogue' (D1r), present in diazotrophic cyanobacteria, was postulated by Murray (2012). Based on its structural characteristics, the protein D1 rogue impairs the PSII function during night allowing for nitrogen fixation.

In conclusion, five, functionally different, D1 protein isoforms are known to date (Mulo *et. al*., 2009):

D1m or D1major is an isoform present in PSII in normal growth conditions, and induced in most stress conditions.

D1:1 is expressed in PSII under normal growth conditions, repressed under stress conditions.

D1:2 are repressed in PSII under normal growth conditions, induced under stress conditions. The D1:1 and D1:2 proteins differ at 25 of 360 amino-acid positions, with a conserved change of Gln with Glu at position 130 (Campbell *et. al*., 1998).

D1' protein is induced in microaerobic conditions. The sequence of amino-acid shows three conserved mutations at positions 80, 158 and 286; these changes are characteristic to the D1' isoform: position 80 is a Gly to Ala mutation, at position 158 is a Phe to Leu mutation and at position 286 is a Thr to Ala mutation (Sicora *et. al*., 2009).

D1r protein is a hypothetical protein, which blocks the Photosystem II during night and has 8 characteristic amino-acids differences; the most relevant from them are at positions: 61 Asp to Glu, 170 Asp to Glu/Ser, 189 Glu to Asp/Ala/Arg, 333 Glu to Ala/Ser, 342 Asp to Thr/Leu/Val, 344 Ala to Ala/Ser (Murray, 2012).

While functional characterization is needed for proper D1 isoform identification, in this article we identify possible D1 protein isoforms inferred from the existing sequencing data available fitting them in the proposed functional classes. We also propose models for the gene family development in the studied cyanobacteria strains.

Materials and methods

All the cyanobacterial *psbA* gene sequences were obtained from CyanoBase (http://genome.microbedb.jp/cyanobase/) and imported in the CLC Sequence Viewer 6.9.1 software (freeware http://www.clcbio.com). Using the aminoacid sequences, we made an accurate multiple alignment of all 91 sequences, bassed on progressive alignment algorithm. The alignment was manual edited, the non-informative regions were deleted resulting a number of approximative 360 positions. This made possible the comparison of the aminoacids conserved at all D1 protein isoforms. Based on the alignment, we summarized the amino-acid changes in tables 2, 3 and 4. The next step was the construction of phylogenetic trees by Neighbour Joining method, 1000 replicates, made with CLC Sequence Viewer 6.9.1 program. A Venn diagram, showing the grouping and distribution of the studied D1 protein isoforms was constructed.

Results and discussion

In this study we analyzed a number of 30 cyanobacterial strains with sequenced genomes, from Cyanobase and identified a total of 91 *psbA* genes which encode different isoforms of the D1 protein (Table 1). There are cases when

several genes encode one D1 protein isoform and other cases when each gene encodes a different D1 protein.

As the functional data accumulated it had become evident that all D1 protein isoforms have specific changes in the peptide structure. Based on this experimental observations it has been concluded that the presence at position in the position 130 of a glutamic acid (Glu), instead of glutamine (Gln) suggests the presence of the D1:2 isoform of the D1 protein strongly induced under stress conditions (Table 2).

Table 1.

Cyanobacterial strains analyzed in this study and the proposed number of *psbA* genes within.

Nr. Crt	**Cyanobacterial strain**	**Number of *psbA* genes**
1	*Synechocystis* sp. PCC 6803	3
2	*Anabaena* sp. PCC 7120	5
3	*Thermosynechococcus elongatus* BP-1	3
4	*Gloeobacter violaceus* PCC 7421	5
5	*Mycrocystis aeruginosa* NIES-843	5
6	*Prochlorococcus marinus* SS120	1
7	*Prochlorococcus marinus* MED4	1
8	*Prochlorococcus marinus* MIT9313	2
9	*Synechococcus sp*. WH8102	4
10	*Synechococcus elongatus* PCC 6301	3
11	*Synechococcus sp*. CC9311	2
12	*Synechococcus sp*. PCC 7002	3
13	*Acaryochloris marina* MBIC11017	3
14	*Prochlorococcus marinus* str. NATL2A	3
15	*Anabaena variabilis* ATCC 29413	6
16	*Synechococcus sp*. CC 9902	4
17	*Synechococcus elongatus* PCC 7942	3
18	*Synechococcus sp*. JA-2-3B'a(2-13)	3
19	*Synechococcus sp*. JA-3-3Ab	4
20	*Prochlorococcus marinus* str. AS9601	1
21	*Prochlorococcus marinus* str. MIT9515	1
22	*Prochlorococcus marinus* str. MIT9303	1
23	*Prochlorococcus marinus* str.	2

	NATL21A	
24	*Prochlorococcus marinus* str. MIT 9301	1
25	*Synechococcus sp*. RCC307	4
26	*Synechococcus sp*. WH7803	4
27	*Prochlorococcus marinus* str. MIT9215	1
28	*Cyanothece sp*. ATCC 51142	5
29	*Nostoc punctiforme* ATCC 29133	4
30	*Arthrospira platensis* NIES-39	4
TOTAL	30	91

Usually, one cyanobacterial strain posessing the D1:2 isoform also has the D1:1 isoform of the D1 protein expressed under optimal growth conditions, so we can see that from the total of 30 cyanobacterial strains studied, 17 strains have 45 *psbA* genes which encode the D1:2 isoform of the D1 protein.

Table 2.

List of proteins (emphasized by bold characters below strain's name) from studied cyanobacterial strains exhibiting aminoacid changes characteristic to D1:1 and D1:2 isoforms.

D1:2		
130 Gln to Glu		
Synechococcus sp. PCC 7002 **SynPCC7002_A1418**	*Synechococcus sp.* PCC 7002 **SynPCC7002_A0157**	*Anabaena sp.* PCC 7120 **Alr_4592**
Synechococcus elongatus PCC 7942 **Synpcc7942_1389**	*Synechococcus elongatus* PCC 7942 **Synpcc7942_0893**	Anabaena sp. PCC 7120 **Alr_3727**
Synechococcus elongatus PCC 6301 **Syc0166_d**	*Synechococcus elongatus* PCC 6301 **Syc0647_d**	*Anabaena sp*. PCC 7120 **All_3572**
Anabaena variabilis ATCC 29413 **Ava_1597**	*Anabaena variabilis* ATCC 29413 **Ava_2460**	*Anabaena variabilis* ATCC 29413 **Ava_3553**
Nostoc punctiforme ATCC 29133 **Npun_F3544**	*Nostoc punctiforme* ATCC 29133 **Npun_R5188**	*Nostoc punctiforme* ATCC 29133 **Npun_R2273**
Synechococcus sp. WH8102 **SYNW0983**	*Synechococcus sp.* WH8102 **SYNW1919**	*Synechococcus sp.* WH8102 **SYNW2151**
Synechococcus sp. CC9902 **Syncc9902_1814**	*Synechococcus sp.* CC9902 **Syncc9902_2036**	*Synechococcus sp.* CC9902 **Syncc9902_1817**

Synechococcus sp. CC9311 **Sync_2384**	*Synechococcus sp.* WH 7803 **SynWH7803_0366**	*Synechococcus sp.* WH 7803 **SynWH7803_0790**
Synechococcus sp. WH 7803 **SynWH7803_2084**	*Synechococcus sp.* RCC307 **SynRCC307_1440**	*Synechococcus sp.* RCC307 **SynRCC307_2009**
Synechococcus sp. RCC307 **SynRCC307_2183**	*Arthrospira platensis* NIES-39 **NIES39_K03030**	*Arthrospira platensis* NIES-39 **NIES39_03080**
Arthrospira platensis NIES-39 **NIES39_R00140**	*Thermosynechococcus elongatus* BP-1 **Tlr1477**	*Thermosynechococcus elongatus* BP-1 **Tlr1844**
Synechococcus sp. JA-2-3B'a(2-13) **CYB_0371**	*Synechococcus sp.* JA-2-3B'a(2-13) **CYB_0433**	*Synechococcus sp.* JA-3-3Ab **CYA_1811**
Synechococcus sp. JA-3-3Ab **CYA_1849**	*Synechococcus sp.* PCC 7002 **SynPCC7002_A2164**	*Arthrospira platensis* NIES-39 **NIES39_O04720**
Gloeobacter violaceus PCC 7421 **Glr0779**	*Gloeobacter violaceus* PCC 7421 **Glr2322**	*Gloeobacter violaceus* PCC 7421 **Glr2656**
Gloeobacter violaceus PCC 7421 **Glr1706**	*Gloeobacter violaceus* PCC 7421 **Gll3144**	*Cyanothece sp.* ATCC 51142 **Cce_3411**

Another specific isoform of the D1 protein (D1') is induced in microaerobic conditions (Sicora et. al., 2009). Based on the alignment, we searched the sequenced with the three changes in the aminoacid structure characteristic cu D1' isoform (Table 3). This table, shows that out of thirty cyanobacterial strains studied, ten have the D1' isoform of the D1 protein, the isoform that is induced in microaerobic conditions and probably helps the cells adapt to low oxygen conditions.

Table 3.

List of proteins from studied cyanobacterial strains that exhibit aminoacid changes characteristic for the D1' isoform.

D1'		
80 Gly to Ala	**158 Phe to Leu**	**286 Thr to Ala**
Thermosynechococcus elongatus BP-1 **Tlr1844**	*Thermosynechococcus elongatus* BP-1 **Tlr1844**	*Thermosynechococcus elongatus* BP-1 **Tlr1844**
Synechococcus sp. PCC 7002 **SynPCC7002_A2164**	*Synechococcus sp.* PCC 7002 **SynPCC7002_A2164**	*Synechococcus sp.* PCC 7002 **SynPCC7002_A2164**
Arthrospira platensis NIES-39	*Arthrospira platensis* NIES-39	*Arthrospira platensis* NIES-39

NIES39_O04720	**NIES39_O04720**	**NIES39_O04720**
Synechocystis sp. PCC 6803 **Slr1181**	*Anabaena sp.* PCC 7120 **Alr3742**	*Synechocystis sp.* PCC 6803 **Slr1181**
Anabaena sp. PCC 7120 **Alr3742**	*Anabaena variabilis* ATCC 29413 **Ava_1583**	*Anabaena sp.* PCC 7120 **Alr3742**
Anabaena variabilis ATCC 29413 **Ava_1583**	*Cyanothece sp.* ATCC 51142 **Cce_3411**	*Anabaena variabilis* ATCC 29413 **Ava_1583**
Cyanothece sp. ATCC 51142 **Cce_3411**	*Synechococcus sp.* JA-3-3Ab **CYA_1748**	*Cyanothece sp.* ATCC 51142 **Cce_3411**
Synechococcus sp. JA-3-3Ab **CYA_1748**	*Synechococcus sp.* JA-2-3B'a(2-13) **CYB_0216**	*Synechococcus sp.* JA-3-3Ab **CYA_1748**
Synechococcus sp. JA-2-3B'a(2-13) **CYB_0216**	*Anabaena variabilis* ATCC 29413 **Ava_4121**	*Synechococcus sp.* JA-2-3B'a(2-13) **CYB_0216**
Cyanothece sp. ATCC 51142 **Cce_3477**	*Acaryochloris marina* MBIC11017 **AM1_0448**	*Cyanothece sp.* ATCC 51142 **Cce_3477**
Anabaena variabilis ATCC 29413 **Ava_4121**		*Anabaena variabilis* ATCC 29413 **Ava_4121**
Acaryochloris marina MBIC11017 **AM1_0448**		*Acaryochloris marina* MBIC11017 **AM1_0448**

By bioinformatic analysis of D1 aminoacid compositionMurray (2012) concluded that a possible new isoform of the D1 protein that putatively blocks the Photosystem II during night and allows for nitrogen fixation. This isoform of the D1 protein ('D1 rogue') has 6 major changes in the aminoacids structure. The presence at the position 61 of glutamic acid (Glu) instead of aspartic acid (Asp), at position 130 of a glutamic acid (Glu) or serine (Ser) instead of an aspartic acid (Asp), at position 189 of an aspartic acid (Asp) or alanine (Ala) or arginine (Arg) instead of a glutamic acid aminoacid, are only 3 changes that suggest the presence of the D1 rogue isoform. From what we can see below (Table 4), five out of thirty cyanobacterial strains analyzed have three, four or five changes in the peptide structure characteristic to the D1 rogue protein.

Table 4.

List of proteins from studied cyanobacterial strains that exhibit aminoacid changes characteristic to the D1rogue isoform.

D1r		
61 Asp to Glu	**170 Asp to Asp/Glu/Ser**	**189 Glu-Asp/Ala/Arg**

Cyanothece sp. ATCC 51142 **Cce_3477**	*Synechococcus sp.* JA-3-3Ab **CYA_1748**	*Cyanothece sp.* ATCC 51142 **Cce_3477**
Acaryochloris marina MBIC11017 **AM1_0448**	*Synechococcus sp.* JA-2-3B'a(2-13) **CYB_0216**	*Anabaena variabilis* ATCC 29413 **Ava_4121**
	Cyanothece sp. ATCC 51142 **Cce_3477**	
	Acaryochloris marina MBIC11017 **AM1_0448**	

Table 4. (continued)
List of proteins from studied cyanobacterial strains that exhibit aminoacid changes characteristic to the D1rogue isoform

D1r		
333 Glu to Ala/Ser	**342 Asp to Thr/Leu/Val**	**344 Ala to Ser**
Synechococcus sp. JA-3-3Ab **CYA_1748**	*Synechococcus sp.* JA-3-3Ab **CYA_1748**	*Anabaena variabilis* ATCC 29413 **Ava_4121**
Synechococcus sp. JA-2-3B'a(2-13) **CYB_0216**	*Synechococcus sp.* JA-2-3B'a(2-13) **CYB_0216**	
Cyanothece sp. ATCC 51142 **Cce_3477**	*Cyanothece sp.* ATCC 51142 **Cce_3477**	
Anabaena variabilis ATCC 29413 **Ava_4121**	*Anabaena variabilis* ATCC 29413 **Ava_4121**	
Acaryochloris marina MBIC11017 **AM1_0448**	*Acaryochloris marina* MBIC11017 **AM1_0448**	

Based on the analysis of the tables 2, 3 and 4, we observed the possible presence of several types of D1 protein at the same cyanobacteria strain, without a very obvious relation between them. To better highlight the number of cyanobacterial strains which contain several different isoforms of the D1 protein, we built a Venn diagram (Fig. 1). We observed that from the total of thirty cyanobacterial strains analyzed, four strains have all the three isoforms of D1 protein (D1:2, D1' and D1r).

Seventeen cyanobacterial strains contain the D1:2 isoform of D1 protein. From these seventeen genomes, nine have just the D1:2 isoform, four have both the D1:2 and D1' isoform and four of them have all the 3 isoforms discussed.

As concerns the D1' isoform, ten cyanobacteria contain this isoform of D1 protein; one strain has only the D1' isoform out of the three studied isoforms. Four strains contain the D1:2 and D1' isoform, four strains contain all the three isoforms and only one strain contains the D1' together with the D1r isoform.

The D1 rogue isoform is present in five cyanobacterial genomes, from which four genomes have all the three isoforms and one have the D1r and D1' isoforms.

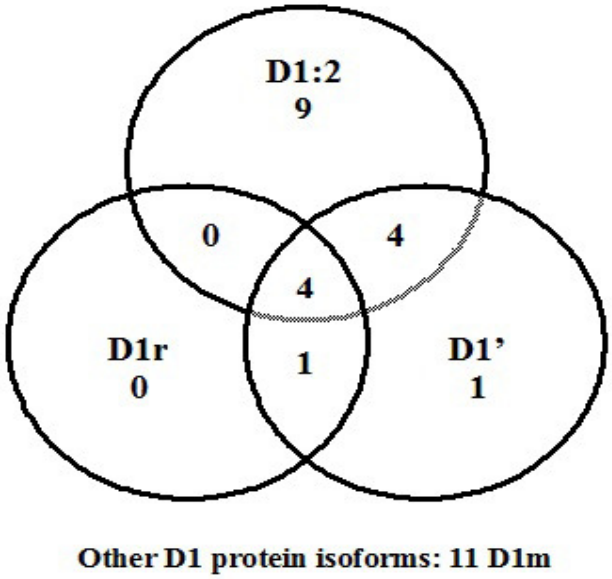

Figure 1: Venn diagram summarizing the distribution of D1 protein isoforms among the cyanobacterial strains analyzed.

Based on the alignment done with the sequences imported in the CLC sequence Viewer 6.9.1 software, a phylogenetic tree including all 91 sequences was constructed by using Neighbour Joining method, (Fig. 2). Analyzing the tree it becomes evident that specific isoforms are grouped together independent of the cyanobacterial strain they belong to. D1' protein from *Arthrospira platensis* NIES-39 (NIES39_O04720) is grouped with the one from *Synechococcus sp*. PCC 7002 (SYNPCC7002_A2164), *Synechocystis sp*. PCC 6803 (Slr1181), *Anabaena variabilis* ATCC 29413 (Ava_1583), *Anabaena sp*. PCC 7120 (Alr3742) and *Cyanothece sp*. ATCC 51142 (Cce_3411). There are, however, several D1 protein families grouped after the strain they belong. Examples for this case are the D1 protein family from *Gloeobacter violaceus* PCC 7421 (glr0779, gll3144, glr2322,

glr2656, glr1706) or *Thermosynechococcus elongatus* BP-1 (tlr1843, tlr1477, tlr1844).

Based on our results, we can conclude that there are two possible ways in which the *psbA* genes and the D1 protein encoded by them developed.

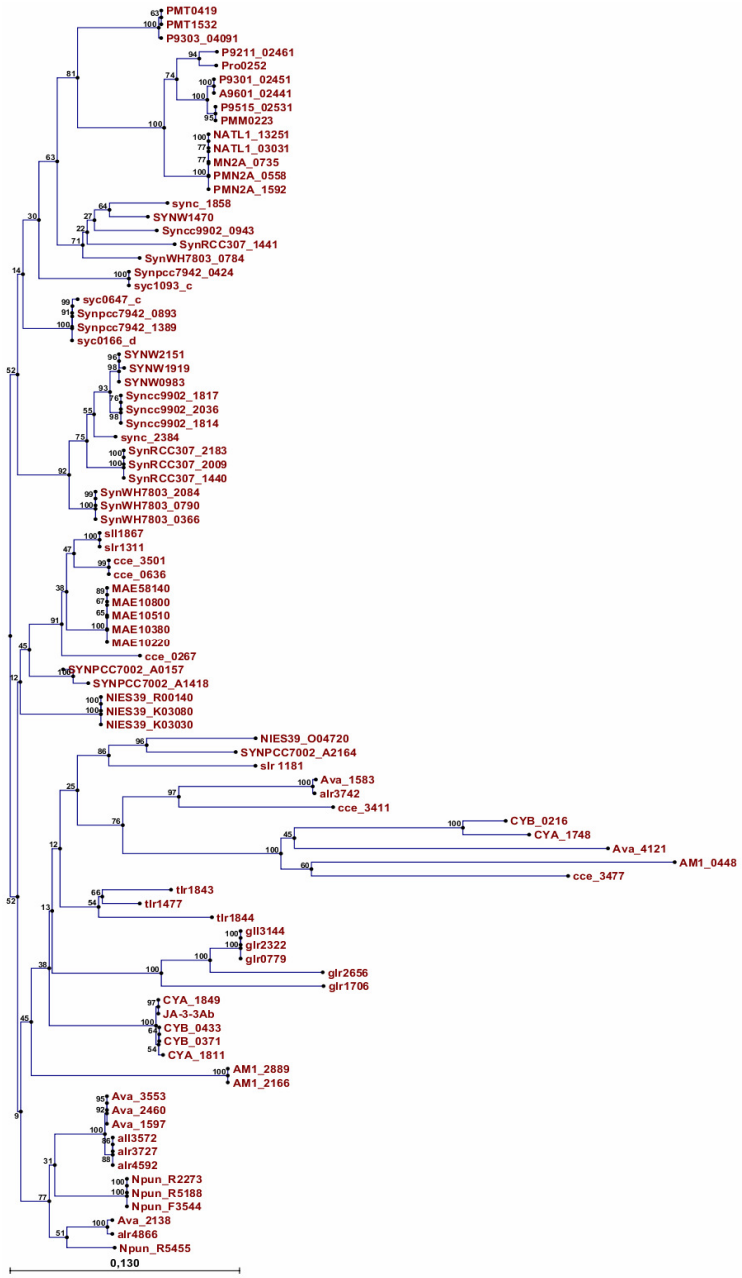

Figure 2. Phylogenetic tree of the 91 protein sequences from Cyanobase, made with Neighbour Joining method, 1000 bootstrap replicates. The scale bar represents number of insertions, deletions/time.

One strategy is by horizontal transfer, when the proteins are more closely related to each other than to the other members of the gene family from the same strain, it can be observed that the D1' protein from different species that group together (Fig. 2). An explanation can be the fact that the strains sharing the same environment conditions managed to adapt by the importing a gene that will give them an evolutionary edge. The transfer can be intermediated by common phages infecting a specific community.

The second strategy is by intraspecific duplication of the genes. In this way the strains create new forms of D1 protein by duplication from the existing ones as a response to the need to adapt to changes in the environment (Sajjaphan *et al*., 2002).

Conclusions

Herewith, we reviewed the available new information regarding the D1 protein isoforms from newly sequenced cyanobacteria genomes and we presented a possible functional distribution of these forms based upon the available knowledge. This information can trigger further functional studies leading to characterization of new D1 protein families. We also processed these data into an evolutionary tree that gives indications regarding the evolutionary strategies of the *psbA* gene family from cyanobacteria. The presented data bring, original interpretation of updated information regarding the *psbA* gene families and the encoded D1 protein isoforms available from the newly sequenced cyanobacterial genomes.

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