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Characterization of the Gene for the Light-Harvesting Peridinin-Chlorophyll-Protein of *Alexandrium tamarense*

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Abstract Photosynthetic dinoflagellates contain a water-soluble, light-harvesting antenna called the peridinin-chlorophyll-protein (PCP) complex, which has an apoprotein with no sequence similarity to other known proteins. There are two forms of PCP apoproteins; the 15-kDa short form and the 32- to 35-kDa long form. The present study describes the PCP protein and its cDNA from *Alexandrium tamarense*. A cDNA library was constructed from mRNA isolated from *A. tamarense*. The complete PCP cDNA was generated by reverse-transcription coupled to polymerase chain reaction (RT-PCR), together with rapid-amplification of cDNA ends (RACE). The *A. tamarense* PCP cDNA encoded a 55-amino acid signal peptide and a 313-amino acid mature protein with a calculated mass of 32 kDa, which corresponded to that of the long form of PCP. Phylogenetic analysis indicated that the sequence of *A. tamarense* PCP did not cluster with the short-form PCPs, to which it was only about 55% identical, but which were 79–83% identical to other long-form PCPs. The deduced amino acid sequence of *A. tamarense* PCP contains an internal duplication, which suggests the possibility that long-form PCPs arose by gene duplication or by the fusion of genes encoding the short form. The abundance of PCP mRNA changed substantially in response to different light conditions, indicating the possible existence of a photo-acclimation response in *A. tamarense*.

Key words: PCP, *Alexandrium tamarense*, dinoflagellates, peridinin, transit peptide

Photosynthetic dinoflagellates, a class of phytoplankton that causes toxic red tides and kills fish [1, 4, 15], contain a membrane-bound, light-harvesting complex similar to that of higher plants. In addition, they have developed a unique photosynthetic, water-soluble antenna, the peridinin-chlorophyll-protein (PCP) complex, which extensively uses both carotenoids and chlorophylls (Chls), as opposed to primarily Chls, as the main light absorbers. The predominant carotenoid of dinoflagellates is peridinin, which enables the organism to collect light in the 470–550 nm range in which chlorophyll does not absorb. Peridinin has an unusual C_{37} carbon skeleton, instead of the usual C_{40} skeleton found in most carotenoids, and contains epoxy, hydroxy, and acetyl groups on β-rings, as well as an allene moiety and a lactone group conjugated to the π-electron system [2].

The peridinins in PCP and in model light-harvesting systems effectively transfer electronic excitation to chlorophyll a (88 to 95%), which is able to pass this excitation energy to the membrane-bound, light-harvesting complexes of photosystem II (PSII) [3, 6, 16, 22]. Recently, Pinto *et al.* [1, 4, 14] demonstrated that peridinin is the major singlet molecular oxygen quencher in *Lingulodinium polyedra*, despite being less efficient than β-carotene. However, it has not yet been clearly established whether dinoflagellates contain peridinin molecules in the light-harvesting complexes of the photosystems within the thylakoid membranes [29].

To date, the genes or cDNAs encoding five PCP apoproteins have been sequenced [21, 27, 30, 31], and none has shown significant identity to any other light-harvesting proteins from higher plants or other photosynthetic autotrophs [31]. PCP apoproteins occur in two forms: as a homodimer of two 15-kDa "short form" subunits and as a 35-kDa "long form" monomer. It is hypothesized that the long form arose from a gene duplication and fusion event of an ancestral short form of the *pcp* gene [11, 17, 21]. Some species of dinoflagellates appear to have only one form of the PCP apoprotein; however, several species possess both the long and short forms [7, 28]. In the

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present study, we report the isolation, characterization, and nucleotide sequence of a cDNA clone that encodes the PCP of *Alexandrium tamarense*. Our results support the notion that the long form of PCP originated from gene duplication and fusion events of a gene encoding a short form of PCP. In addition, we examined the regulation of *pcp* mRNA expression by exposure to varied light conditions.

MATERIALS AND METHODS

Source and Maintenance of Cultures

A unialgal culture of *Alexandrium tamarense* (Jinhae Bay, Korea) was obtained from the KORDI (Korea Ocean Research Development Institute, Korea). Cells were grown axenically in seawater filtered through a 0.4-mm filter (Millipore, Billerica, MA, U.S.A.) and supplemented with Provasoli's (Sigma, St. Louis, MO, U.S.A.). Generally, 100 ml of cultures were grown at 18°C in 250-ml culture bottles without agitation until the density reached 0.5 to 3.0×10^6 cells/ml. Irradiance of approximately 50 µmol of photons m^{-2} s^{-1} was provided by cool white fluorescent bulbs on a cycle of 14 h of light and 10 h of darkness, referred to here as medium-light conditions. For various treatments, cells were grown under medium-light conditions for 1 week before being transferred to conditions with either 100 (high-light cultures) or 20 µmol of photons m^{-2} s^{-1} (low-light cultures) for 14 d. Cultures were harvested in mid-exponential phase.

RNA Purification

Cells were harvested by centrifugation at 4,000 ×*g* for 5 min at 4°C, and the pellets were frozen in liquid nitrogen. For RNA extraction, the pellets were resuspended in 1 ml of TRI reagent (Molecular Research Center, Inc., Cincinnati, OH, U.S.A.), and the homogenates were processed according to the manufacturer's protocol. The RNA was quantified and stored at −70°C.

Cloning of PCP by RT-PCR and RACE

Reverse-transcription polymerase chain reaction (RT-PCR) was carried out to obtain a partial clone of *A. tamarense* PCP cDNA. The first-strand cDNA was synthesized with AMV reverse transcriptase (Promega, Madison, WI, U.S.A.) from approximately 1–2 µg of total RNA and was amplified with degenerate primers designed from conserved amino acid sequences of the PCPs of *Amphidium* and *Gonylaux*. The forward and backward primers were 5'-GCNCAY-CAYAARGCNATHGG-3' (based on the peptide AHHKAI) and the modified oligo (dT) primer 5'-TTCTAGAATT-CAGCGGCCGCT$_{18}$-3', respectively. PCR was performed with TaKaRa LA Taq polymerase (TaKaRa Korea, Sungnam, Gyeonggi, Korea) in a thermal cycler (Perkin-Elmer, Boston, MA, U.S.A.). The size of the PCR product was verified by 1% agarose gel electrophoresis. The 570 bp product was subcloned in the pGEM-T vector (Promega, Madison, WI, U.S.A.) and sequenced using the BigDye Terminator Cycle Sequencing reaction mix (PE Applied Biosystems, Foster City, CA, U.S.A.) and an ABI 3100 Genetic Analyzer (PE Applied Biosystems).

The 5' end of the PCP cDNA was amplified using the Marathon 5'-RACE kit (Clontech, Palo Alto, CA, U.S.A.) according to the manufacturer's instructions. The sequence of the primer used for the 5'-RACE was 5'-CTGGGAGC-GGCTTAAGGTAG-3', and that of the primer used for the nested PCR was 5'-GTTGACAAGGGACTTCATGTAC-3'. The PCR fragment was purified, subcloned into the pGEM-T vector, and sequenced to identify the 5'-end of the PCP cDNA. The combined sequences of the RT-PCR and 5'-RACE products yielded a 1,350-bp cDNA containing the entire PCP coding region. The sequences reported in this study were submitted to GenBank under accession number AY847685. The translation of the predicted amino acid sequences, multiple sequence alignment, calculation of molecular masses, and estimation of the isoelectric points were performed using DNASTARS software (LASERGENE software, DNASTARS, Inc., Madison, WI, U.S.A.). The phylogenetic tree was generated using Poisson-corrected amino acid distances by the MEGA2.1 software (www. megasoftware.net).

RNA Blot Analysis

For Northern blot analysis, total RNA (10 µg) was denatured with 50% formamide and 6.3% formaldehyde and was separated on a denaturing agarose gel. The RNA was transferred onto a nylon membrane (Hybond™-H^+; Amersham Pharmacia Biotechnology, Piscataway, NJ, U.S.A.) and fixed by UV cross-linking. The cDNA fragments were labeled with biotin using a commercially available system (KPL, Inc., Baltimore, MD, U.S.A.) and were used as the hybridization probe. The membranes were hybridized at 60°C for 16 h and washed twice with 0.1× SSC/1% SDS at 60°C for 15 min. The hybridized bands were detected using the CDP-Star™ system (Tropix, Bedford, MA, U.S.A.).

RESULTS AND DISCUSSION

Characteristics of the *pcp* Transcript and Predicted Amino Acid Sequence

The nucleotide and deduced amino acid sequences of the *pcp* gene of *A. tamarense* are shown in Fig. 1. The nucleotide sequence of the *pcp* cDNA consists of 1,380 bp with a 1,107 bp open reading frame. The deduced amino acid sequence is 368 residues in length. Based on similarity to other known PCPs [17, 21, 30, 31] for which the N-terminal sequence of the mature protein is known,

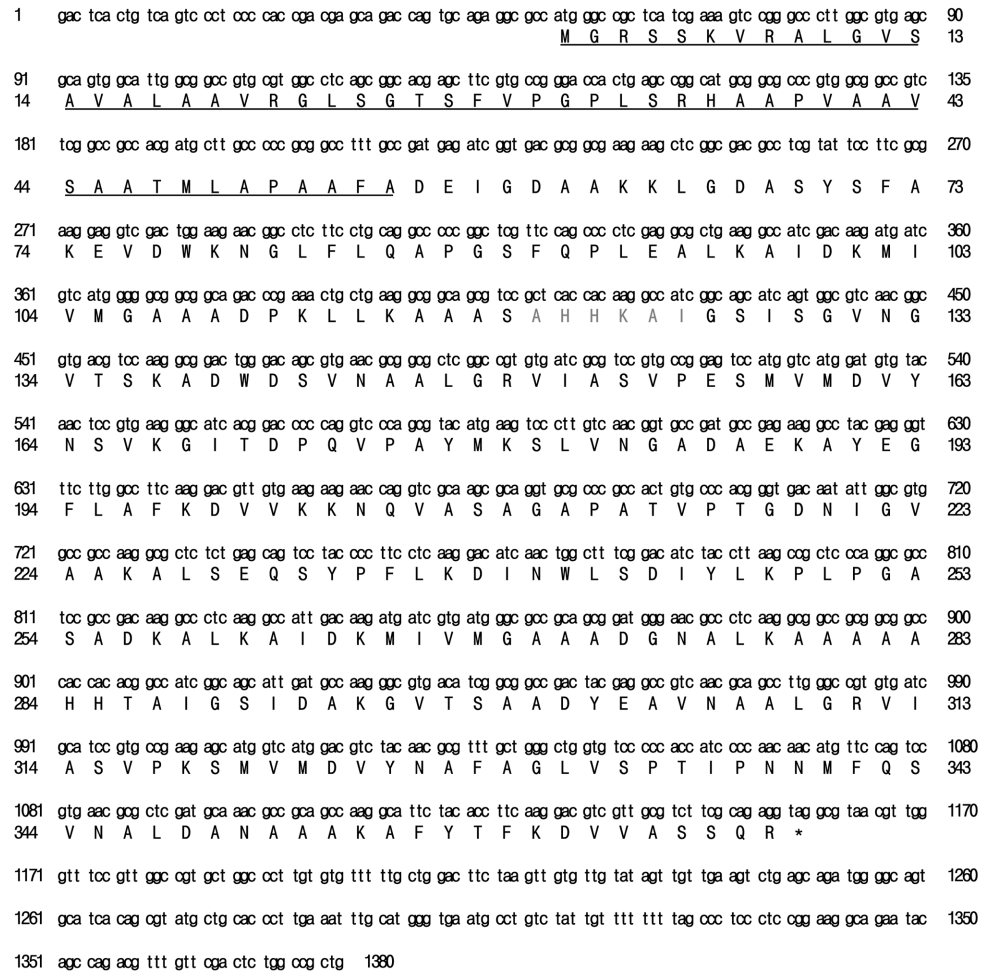

Fig. 1. The nucleotide and deduced amino acid sequences of the full-length cDNA encoding the PCP of *A. tamarense*.
The sequence data are available from GenBank (AY847685). Nucleotides and amino acids are numbered in the margins. The cDNA sequence is shown in lower case. The translated regions of the sequence are indicated using the single-letter amino acid code. The proposed 55-amino acid signal peptide sequence is underlined.

we identified the first 55 amino acids of the *A. tamarense* PCP sequence as a presumptive leader sequence required for targeting to the chloroplast [9, 20], including an A-X-A signal peptide cleavage site immediately upstream of the N-terminus of the mature protein sequence (Fig. 1). The first part of the leader sequence contains five positively charged and nine polar amino acids distributed throughout the sequence and no sizable hydrophobic core. This sequence is more consistent with targeting of PCP to the chloroplast stroma rather than to the endoplasmic reticulum (ER), as conventional ER signal peptides contain a positively charged N-terminal region, a 10- to 15-residue hydrophobic core, and a polar C-terminal region. The predicted size of the 313-amino acid final protein product, calculated using the deduced amino acid content and specific masses of each amino acid (DNASATRS software), was 32 kDa, and the predicted pI of the mature polypeptide was 6.8.

PCP Alignment and Phylogenetic Analysis

The *A. tamarense* PCP amino acid sequence was aligned with the sequences of PCPs from other dinoflagellates (Fig. 2), such as *Gonyaulax polyedra* (GenBank accession number AAC23723), *Amphidinium carterae* (2392502), *Symbiodinium* sp. (S43780 or AAA19814), *Heterocapsa pygmae* (CAC19482), and *Symbiodinium muscatinei* (AF425735). The mature form of *A. tamarense* PCP showed a high degree of sequence identity (79 to 85%) with the PCPs from *G. polyedra*, *A. carterae*, and *Symbiodinium* sp, all of which are long-form PCPs (Fig. 2). In contrast, the sequence of the second half of the *A. tamarense* PCP (beginning at Asp219) showed only 50% and 59.6% identity to the short-form PCPs of *H. pygmae* and *S. muscatinei*, respectively (Fig. 2). A phylogenetic analysis (Fig. 4) indicated that the *A. tamarense* PCP does not cluster with short-form PCPs, with which it has limited similarity, but which are themselves 79–85% identical to other long-

Fig. 2. Multiple sequence alignment of the predicted *A. tamarense* PCP amino acid sequences and the PCP sequences from other dinoflagellates.

The alignment was performed using the Clustal W algorithm. Identical amino acids are highlighted in black. Introduced gaps are shown as dashes.

form PCPs. The alignments and phylogenetic analyses (Figs. 2 and 4) of the predicted amino acid sequences of the six known *pcp* genes (four long and two short forms) present a complex picture of PCP genetics and phylogeny.

Symbiodinium sp. (also called zooxanthellae) are symbiotic dinoflagellates that reside in members of several invertebrate

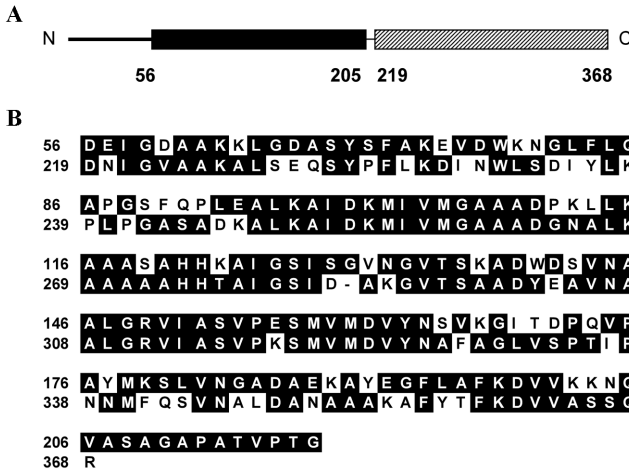

Fig. 3. A. Schematic diagram of *A. tamarense* PCP which is assumed to have been duplicated from two short forms (black and hatched rectangular regions) of PCP proteins. B. Alignment of the N-terminal region (Asp 56-Gly 205) and the C-terminal region (Asp219-Arg368) of the amino acid sequence of the mature *A. tamarense* PCP.

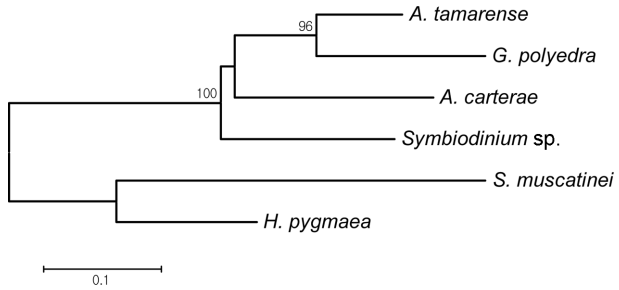

Fig. 4. The neighbor-joining tree showing the relationship of the deduced *A. tamarense* PCP amino acid sequence to the sequences of other known PCPs.

The tree was generated using Poisson-corrected amino acid distances by the MEGA2.1 software (www. megasoftware.net). Numbers along branches denote bootstrap support of over 50%. The number of the scale bar is the number of amino acid substitutions per residue.

and protozoan phyla, for which two complete PCP cDNAs corresponding to the long form from a *Symbiodinium* sp., and the short form, from *S. muscatinei*, have been reported [31]. It is noteworthy that the short-form PCP from *S. muscatinei* clustered more closely with another short-form sequence from *H. pygmaea* than with the long-form PCP protein from *Symbiodinium* sp. (Fig. 4). However, it has been reported that both short and long forms of PCP can be found in material harvested from the *Symbiodinium* host anemone, *Anthopleura elegantissima* [7].

There are several possible explanations for the appearance of multiple forms of PCPs in dinoflagellates. First, the short and long forms could be differentially synthesized, depending on varying environmental conditions. Such differential production has been dramatically illustrated in studies of *S. bermudense*, a symbiont of the tropical anemone *Aiptasia pallida*, which synthesizes the short form when in the host, but the long form when cultured separately from the host [28]. Other studies have provided ample evidence of multiple copies of PCP genes and the complex regulation of their expression [17, 18, 30, 31]. A second possibility that could explain the existence of multiple forms of PCP in *A. elegantissima* material is that this anemone may, when collected at different times from different sites, harbor taxonomically distinct zooxanthellae populations that have different types of PCP.

The comparison of the deduced amino acid sequence of *A. tamarense* PCP with the known PCP sequences revealed that the mature protein begins at Asp56 (Figs. 1 and 2), and that the N-terminal 55 amino acid residues are identical to those of the known PCP apoproteins (underlined in Fig. 1). The N-terminal region of the deduced amino acid sequence for the mature protein (Asp56 to Gly218) shares approximately 60% identity with the C-terminal region (Asp219 to Arg55; Fig. 3). This fairly high degree of similarity is interesting because, whereas PCP from *A. tamarense* is a monomeric protein of approximately

35 kDa, the corresponding proteins in several other species of dinoflagellates are short-form homodimers composed of 14- to 16-kDa subunits [7, 10, 24, 25]. This implies that, among dinoflagellates, the long form of PCP, such as that of *A. tamarense* in this study, may have arisen by gene duplication and fusion events of an ancestral short form of the *pcp* gene [11, 17, 21].

Light-Regulated Transcription of PCP Genes

PCPs are the crucial light-harvesting pigment proteins and may account for up to 95% of the total soluble proteins in the dinoflagellate cell [25]. However, only a few studies have been carried out on the light-regulated synthesis of PCP in dinoflagellates [18, 26]. Here, we examined the modulation of PCP expression by light exposure in *A. tamarense* (Fig. 5). Northern analysis (Fig. 5A) clearly demonstrated that the abundance of the PCP mRNA changed substantially in response to the light conditions: Quantitative analyses indicated that the abundance of the PCP transcript was decreased by approximately 54% and 17% in cells grown in medium- and high-light conditions, respectively, as compared with cells grown under low-light conditions (Fig. 5B).

Light harvesting in dinoflagellates is mediated by two classes of proteins; those of the light-harvesting protein complexes (LHCs) and the PCPs [10, 18, 27]. The LHC apoproteins are related to the chlorophyll a/b binding (cab) proteins of higher plants [10] and their algal homologs. Both PCPs and LHCs are present in multiple forms in dinoflagellates. Previous studies have shown that the light stress downregulates LHCs at the transcriptional level in green algae and higher plant [5, 8, 12, 13, 19]. The downregulation of the Chl antenna size in the photosystems of green algae and higher plants during light stress is a well-known photoacclimation mechanism [13, 14]; however, almost nothing is known about the molecular basis of photoacclimation in dinoflagellates at this time. Our results, therefore, may help advance the understanding of the molecular basis of photoacclimation in dinoflagellates.

In summary, this study provides the first description of a complete *pcp* cDNA from *A. tamarense.* The deduced amino acid sequence of the *A. tamarense pcp* cDNA contains a peptide sequence, located upstream of the N-terminus of the mature protein, that fits the profile of a signal peptide for nuclear-encoded genes targeted to the chloroplast. The phylogenetic analysis provides strong molecular support for previous biochemical evidence, placing the short and long PCP forms into two distinct clades. *A. tamarense* PCP clustered with other long-form PCPs. The abundance of PCP mRNAs changed substantially in response to light conditions, indicating a possible photoacclimation response. However, future studies of the evolution, regulation, and expression of *pcp* genes are needed to expand our preliminary knowledge of this unique dinoflagellate gene family.

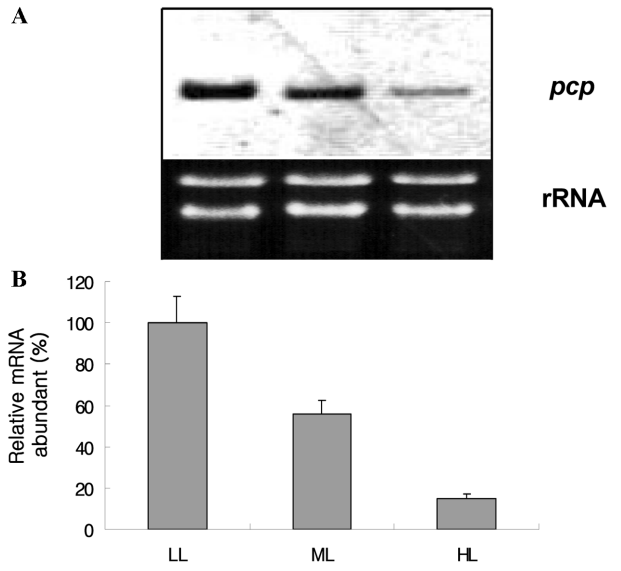

Fig. 5. Regulation of the expression of PCP mRNA by varied light exposure.

A. Northern blot of total RNA (10 μg/lane) from *A. tamarense* grown under various light conditions (see axis label of panel B). The loading of an equal amount of total RNA in each lane was verified by ethidium bromide staining. B. Quantification of the PCP mRNA levels. The intensity of each band on the blot in (A) was quantified by scanning and was compared with the control value under low-light (LL) conditions, which was set as 100%. ML, medium-light conditions; HL, high-light conditions. All values are means of triplicate determinations±SD.

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