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The effect of amphiphilic peptide surfactants on the light-harvesting complex II

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Abstract

The peptide surfactants are amphiphilic peptides which have a hydrophobic tail and a hydrophilic head, and have been reported to stabilize and protect some membrane proteins more effectively than conventional surfactants. The effects of a class of peptide surfactants on the structure and thermal stability of the photosynthetic membrane protein light-harvesting complex II (LHCII) in aqueous media have been investigated. After treatment with the cationic peptide surfactants A_6K, V_6K_2, I_5K_2 and I_5R_2, the absorption at 436 nm and 470 nm decreased and the absorption at 500–510 nm and 684–690 nm increased. Moreover, the circular dichroism (CD) signal intensity in the Soret region also decreased significantly, indicating the conformation of some chlorophyll (Chl) *a*, Chl *b*, and the xanthophyll molecules distorted upon cationic peptide surfactants treatment. The anionic peptide surfactants A_6D and V_6D_2 had no obvious effect on the absorption and CD spectra. Except for A_6D, these peptides all decreased the thermal stability of LHCII, indicating that these peptides may reconstitute protein into a less stable conformation. In addition, the cationic peptide surfactants resulted in LHCII aggregation, as shown by sucrose gradient ultracentrifugation and fluorescence spectra.

Additional key words: circular dichroism; light-harvesting complex II; peptide surfactants; thermal stability.

Introduction

The light-harvesting complex II (LHCII) is the most plentiful photosynthetic pigment-protein complex in green plants. As the main protein constituent of the thylakoid membranes, LHCII plays an important role in harvesting solar energy, formation and stabilization of the grana structure, lateral separation of PSI and PSII, dissipation of excess excitation energy and adjusting the excitation energy distribution between the two photosystems (Green and Durnford 1996, van Amerongen and Dekker 2003). The three-dimensional structure of LHCII was determined at atomic resolution recently (Liu *et al*. 2004, Standfuss *et al*. 2005). The complex is present in trimeric form in the grana membranes. Each monomer in this trimer comprises 8 Chl *a*, 6 Chl *b*, and 4 xanthophylls. Because LHCII can harvest and deliver solar energy efficiently, this pigment-protein complex potentially becomes useful for technical applications such as photovoltaics, biosensors, or molecular-optical devices (Wolf-Klein *et al*. 2002). It is important to select the right surfactants to stabilize this complex for biochemical and structural analysis.

Amphiphilic peptides possess surfactant properties and some of the properties of lipid surfactant molecules, and can be called peptide surfactants or peptergents (Zhang 2003). Peptide surfactants typically consist of consecutive hydrophobic amino acids as the tail and one or two hydrophilic amino acids as the head. The head can be either positively charged or negatively charged so that peptide surfactants are consequently categorized as cationic or anionic surfactants, respectively. Negatively charged heads consist of one or two aspartate or glutamate residues, and positively charged heads consist of one or two lysine, arginine, or histidine residues. When dissolved in water or ionic solutions, these peptide surfactants, like lipids, undergo self-assembly to form micelles, nanovesicles, or nanotubes (von Maltzahn *et al*. 2003, Vauthey *et al*. 2002, Santoso *et al*. 2002). The hydrophobic and hydrophilic ratios of peptide surfactants would affect homogeneity and stability of self-assembling structure (Zhao 2009).

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Abbreviations: A – alanine; CD – circular dichroism; D – aspartic acid; DM – dodecyl β-D-maltoside; I – isoleucine; K – lysine; LHCII – light-harvesting complex II; OG – n-octyl-β-D-glucopyranoside; R – arginine; V – valine.
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Some peptide surfactants resemble bilayer formation by native lipids. The effects of some peptide surfactants on the structure and function of membrane protein have been investigated. Schafmeister *et al*. (1993) designed the first α-helix peptide surfactant, which could solubilize 85% bacteriorhodopsin and approximately 60% rhodopsin for over 2 days. McGregor *et al*. (2003) designed a monomeric α-helix coupled with two alkyl chains at both N- and C-termini. This type of hybrid peptide–alkyl surfactant solubilized and stabilized several membrane proteins. Recently Kiley *et al*. (2005) designed a class of shorter peptide surfactants and found that acetyl-AAAAAAK (A_6K) and acetyl-VVVVVVD (V_6D) could stabilize photosystem I (PSI) complex on a dry surface. In addition, A_6D and V_6D also stabilized bovine rhodopsin for an extended time at elevated temperatures (Zhao *et al*. 2006). V_6D, V_6K (VVVVVVK), A_6D (AAAAAAD), A_6K, and mixtures of A_6D:A_6K and A_6D:V_6K are capable of efficiently extract and stabilize two kinds of enzyme, the integral membrane flavoenzyme, glycerol-3-phosphate dehydrogenase (GlpD), and the soluble redox flavoenzyme, NADH peroxidase (Npx) (Yeh *et al*. 2005).

In this study, the effects of several peptide surfactants including acetyl-AAAAAAK-NH2 (ac-A_6K-NH_2, A_6K), acetyl-AAAAAAD-OH (ac-A_6D-OH, A_6D), acetyl-VVVVVVKK-NH2 (ac-V_6K_2-NH_2, V_6K_2), acetyl-VVVVVVDD-OH (ac-V_6D_2-OH, V_6D_2), acetyl-IIIIIRR-NH2 (ac-I_5R_2-NH_2, I_5R_2), acetyl-IIIIIKK-NH2 (ac-I_5K_2-NH_2, I_5K_2), on structural feature and thermal stability of LHCII were studied by circular dichroism (CD) and fluorescence spectra, to investigate how the peptides affect the conformation of LHCII, and whether the peptide surfactants are capable of stabilizing the LHCII protein.

Materials and methods

Preparation of LHCII complex: LHCII was isolated from spinach leaves according to (Xu *et al*. 1994) with some modifications. The BBY preparation (photosystem II enriched membranes isolated according to Berthold *et al.* (1981) was washed with Buffer A containing 15 mM NaCl, 5 mM $MgCl_2$, and 20 mM MES-NaOH (pH 6.0), and centrifuged at 37,000 × *g* for 10 min. The pellet was resuspended in Buffer A to Chl concentration of 0.8 mg ml^{-1} and Triton X-100 was added to give a final concentration of 0.8% (w/v), continuous stirring for 15 min at 4°C, and centrifuged at 10,000 × *g* for 5 min. The supernatant was centrifuged at 40,000 × *g* for 10 min. The pellet was resuspended in Buffer B containing 0.4 M sucrose, 10 mM $CaCl_2$, 1M NaCl and 50 mM MES-NaOH (pH 6.0) to Chl concentration of 1.5 mg ml^{-1}, after treated with 35 mM n-octyl-β-D-glucopyranoside (OG) and stirring for 15 min at 4°C, 2 volume Buffer B was added and centrifuged at 40,000 × *g* for 40 min. The pellet was suspended in the Buffer C containing 0.4 M sucrose, 15 mM NaCl and 20 mM MES-NaOH (pH 6.0), frozen in liquid nitrogen and stored at –80°C. The Chl concentration was determined according to Arnon (1949).

The peptide surfactants synthesis and preparation: The peptide surfactants were custom-synthesized and characterized by the Biopolymers Laboratory at the Massachusetts Institute of Technology and *Synpep* (Dublin, Canada).

The peptide surfactants stock solutions were made by dissolving these peptides at a concentration of 1% (w/v) in Buffer C containing 0.1% dodecyl β-D-maltoside (DM), and then sonicating in a water bath sonicator for 20 min.

LHCII treatment with detergents and peptide surfactants: For all experiments, the LHCII complex solubilized with 0.1% DM was used as a control, labeled as CK. LHCII was treated with peptide surfactants at final Chl concentration of 20 μg ml^{-1}, and the final concentration of peptide was 0.05% (m/v).

Measurement of absorption spectra and fluorescence spectra: Absorption spectra were recorded using a *Shimadzu* (Kyoto, Japan) *UV/VIS 2450* spectrophotometer at room temperature. The samples were scanned at 100 nm min^{-1} with 0.5 nm resolution.

Fluorescence emission spectra were measured with a *FluoroMax-4* fluorescence spectrophotometer (*Horiba Jobin Yvon*) between 600 and 780 nm at room temperature and 77 K, with 436 nm as the excitation wavelength, and slit width set to 2 nm. The Chl concentration of the samples was adjusted to 20 μg ml^{-1} and the path length of cell was 0.5 cm.

CD measurements and temperature treatment: CD spectra were recorded on a *MOS 450* spectropolarimeter (*Bio-Logic*, France) equipped with a temperature control set. The spectral range was from 400 to 750 nm, data pitch 1 nm, response time 2 s, band width 2 nm and scanning speed 500 nm min^{-1}. Temperature scans were from 25°C to 80°C at a rate of 1°C min^{-1}. The scans were stopped at every 5°C for 1 min, in order to record CD spectra. The CD signal at 475 nm was recorded continuously during a temperature scan at time intervals of 10 s. The data were fitted with a sigmoid curve {Y = a/(1+exp[−(X−b) /c])} based on a Levenberg-Marquardt algorithm procedure. The inflection point (b) was taken as the dissociation temperature (Tm) of the pigment-protein complexes. All data were averaged from 3 independent measurements.

Sucrose density gradient ultracentrifugation: To prepare sucrose density gradients, centrifuge tubes were filled with 10 ml sucrose solution containing 0.4 M

sucrose, 0.1% (w/v) DM and 20 mM MES-NaOH (pH 6.0), frozen at –20°C for 8 h and then thawing at 4°C, according to the method of Hankamer *et al.* (1997). The sample was loaded on a freshly prepared sucrose gradient and centrifuged at 190,000 × *g* for 15 h at 4°C.

Results

The effect of peptide surfactants on the absorption spectra of LHCII: In Fig. 1, the room temperature absorption spectra of LHCII dissolved in 0.1% DM (CK) treated respectively with 0.05% A_6K (Mr: 615, 0.81 mM), A_6D (Mr: 602, 0.83 mM), V_6K_2 (Mr: 911, 0.55 mM), V_6D_2 (Mr: 885, 0.56 mM), I_5K_2 (Mr: 882, 0.57 mM) and I_5R_2 (Mr: 938, 0.53 mM) were presented. The amplitude of the Soret band at around 436 nm and 470 nm decreased considerably and the absorption at 500–510 nm and 684–690 nm increased upon A_6K, V_6K_2, I_5K_2, and I_5R_2 treatment. As for A_6K, I_5K_2, and I_5R_2 treated, there was decreased absorption at around 648 nm and 671 nm. The two kinds of anionic peptide surfactants A_6D and V_6D_2 had slight effect on the absorption spectra of LHCII.

The effect of peptide surfactants on the CD spectra of LHCII: CD in the visible spectral region is used to monitor the protein and pigment structure of LHCII. The CD spectrum of LHCII in solution containing 0.1% DM (CK) exhibited positive bands at 447, 484, and 672 nm, and negative bands at 440, 475, 493, 655, and 684 nm.

The CD spectra of LHCII after peptides treatment corresponding to the absorption spectra were measured as shown in Fig. 2*A* for Soret band and Fig. 2*B* for red region. The cationic peptide surfactants including A_6K, V_6K_2, I_5K_2, and I_5R_2 decreased CD signal intensity significantly in the Soret region. In addition, I_5K_2 and I_5R_2 treatment led to a red shift of the band maximums about 2 nm. A_6D and V_6D_2 treatment had little impact on CD spectra and there were no obvious changes in the band position and intensity compared with CK.

The cationic peptide surfactants induced formation of LHCII aggregate: Fig. 3 shows the room temperature fluorescence emission spectra of the LHCII in the presence of peptide surfactants. When excited at 436 nm

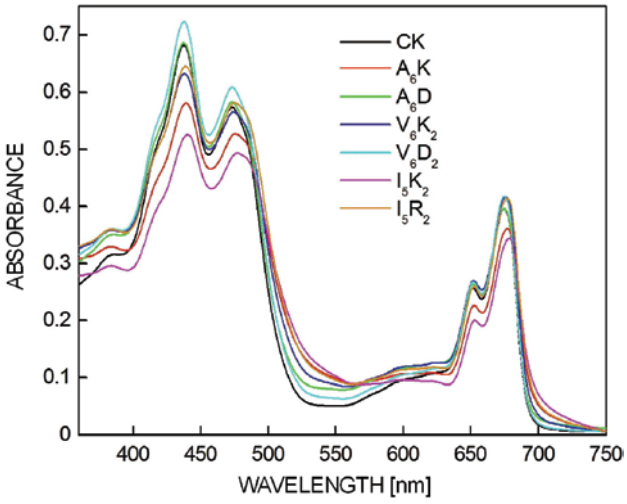

Fig. 1. Absorption spectra of LHCII containing different peptide detergents (A_6K, A_6D, V_6K_2, V_6D_2, I_5K_2, and I_5R_2), respectively, at room temperature. LHCII was dissolved in 0.1% DM and the final concentration of peptides is 0.05% (m/v). CK – control.

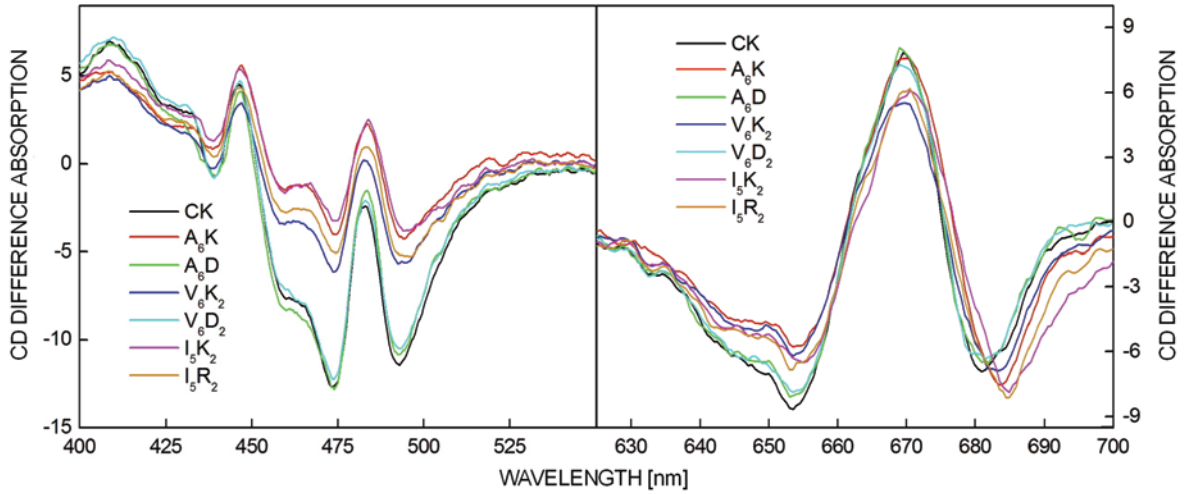

Fig. 2. Comparison of circular dichroism (CD) spectra of detergent-dissolved LHCII in the presence of 0.05% peptide detergents (A_6K, A_6D, V_6K_2, V_6D_2, I_5K_2, and I_5R_2), respectively, in the (*A*) blue region (420–550 nm) and (*B*) red region (625–700 nm). The spectra are normalized according to the absorbance at 680 nm. CK – control.

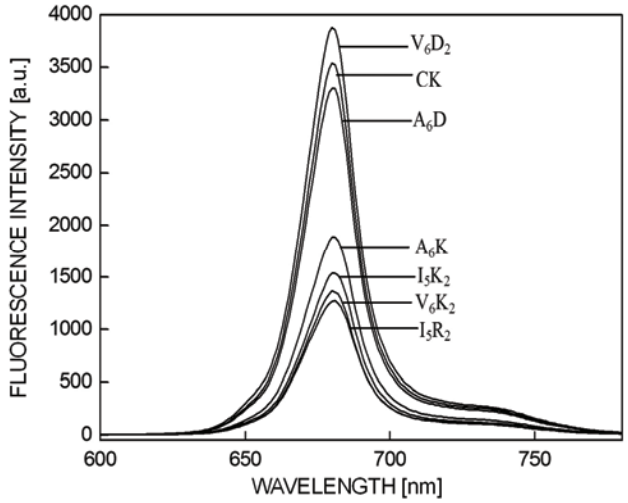

Fig. 3. Comparison of room temperature fluorescence emission spectra of LHCII treated with different peptides at equal Chl concentrations, excited at 436 nm. CK – control.

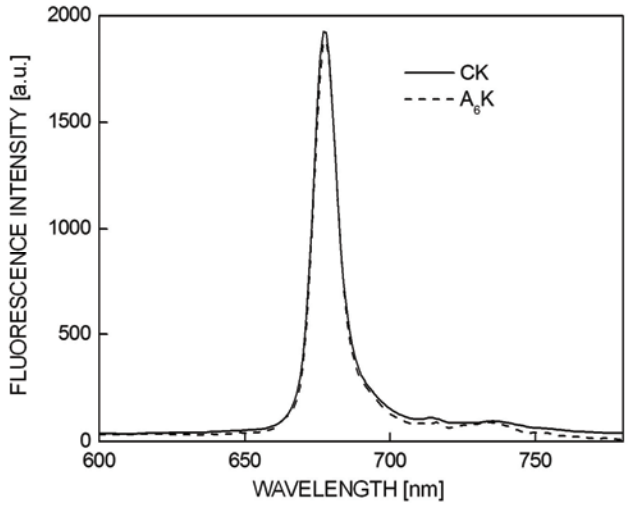

Fig. 4. The 77-K fluorescence emission spectra of LHCII treated with A_6K with excitation at 436 nm. Spectra were normalized at the wavelength of the maximum signal. CK – control.

at equal Chl concentrations, the addition of 0.05% of the anionic peptide surfactant V_6D_2 resulted in an increase in the fluorescence emission intensity of LHCII. However, the cationic peptide surfactants A_6K, V_6K_2, I_5K_2, and I_5R_2 all decreased the fluorescence emission intensity dramatically, indicating that they induced fluorescence quenching. None of the peptide surfactants affected the peak position and shape of the fluorescence spectra. This is illustrated for A_6K treatment and CK by the 77-K fluorescence spectra in Fig. 4. They had the 77-K fluorescence maximum at around 678 nm; similar to the other peptides (A_6D, V_6D_2, V_6K_2, I_5K_2, and I_5R_2)-treated LHCII (data not shown).

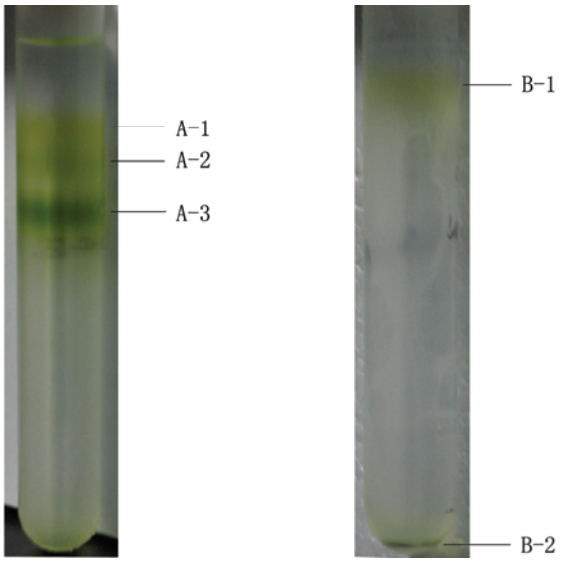

Fig. 5. Separation of LHCII samples by sucrose gradient density centrifugation respectively in the presence of different peptides or not (CK). (A) CK, similar to A_6D or V_6D_2; (B) A_6K, similar to V_6K_2, I_5K_2 or I_5R_2. From the top of the gradient, A-1 represents the free pigment, A-2 represents the monomeric forms of LHCII, and A-3 represents the trimeric forms of LHCII. B-1 represents the free pigment and B-2 represents the aggregated LHCII.

In order to identify if the change of fluorescence yield was due to aggregation of LHCII, the LHCII samples in the presence of various peptide surfactants were separated by sucrose gradient ultracentrifugation. In the anionic peptide, A_6D- or V_6D_2-treated LHCII, three main fractions including free pigment, monomeric and trimeric LHCII were harvested, similar to CK (Fig. 5*A*). After treatment with the cationic peptide surfactants A_6K, V_6K_2, I_5K_2, and I_5R_2, almost all LHCII was precipitated (Fig. 5*B*). The difference between anionic and cationic peptides is shown in Fig. 5. In addition, when A_6K, V_6K_2, I_5K_2, or I_5R_2 was added, the LHCII sample could not pass through 0.22 μm filters, while CK and LHCII in the presence of A_6D or V_6D_2 could pass through the filters. Thus cationic peptide surfactants resulted in aggregation of LHCII, but anionic peptide surfactants did not.

The effect of peptide surfactants on the thermal stability of LHCII: The conformation of LHCII was sensitive to the changing temperature. As shown in Fig. 6, when the CD spectra were measured at 60°C, the negative band at 438 nm associated with aggregated state of LHCII has disappeared, and the CD signal at 446 nm, 475 nm, 493 nm, and 670 nm decreased apparently. Thermal denaturation of LHCII with I_5K_2 and I_5R_2 led to a more dramatic decrease in the whole CD spectra and elimination of excitonic features in the blue region. A_6D-treated LHCII changed to a lesser extent than CK and other peptides.

In order to assess the effect of various peptide surfactants on the thermal stability of LHCII precisely, the CD signal at 475 nm of LHCII-DM sample with and without peptide surfactants during the temperature gradient was continuously monitored. The negative band at 475 nm in the CD spectrum is indicative of trimeric state of LHCII and is sensitive to temperature (Yang *et al*. 2006, Hobe *et al*. 1994). The basic functional unit of LHCII is the trimer and the dissociation of trimeric LHCII may be of significance for the degradation of the complex (Wentworth *et al*. 2003). Therefore, monitoring the CD 475 nm signal can be used to study the structural stability of the LHCII complex. The thermal denaturation curves of different LHCII samples were shown in Fig. 7, and the apparent Tm were summarized in Table 1. The table shows that these peptides did not improve the thermal stability of LHCII except that A_6D increased it slightly.

Discussion

We have tested the effect of various peptides which have a hydrophobic tail and a hydrophilic head on LHCII in aqueous media.

Significant changes were observed in the Chl Soret and xanthophyll absorption region of LHCII treated with the cationic peptide surfactants including A_6K, V_6K_2, I_5K_2, and I_5R_2, which might be due to the increased scattering of the sample or distortion of pigment brought by LHCII aggregation. Similar changes in the blue region were also found in the aggregated LHCII shown previously (Ruban *et al*. 1997). CD measurements showed that the signal intensity decreased significantly in the Soret region after treated with the cationic peptide surfactants (Fig. 2*A*). Together with the absorption data, this suggested that the conformation of some Chl *a*, Chl *b* and the xanthophyll molecules distorted upon cationic peptide surfactants treatment. Analysis of CD spectra revealed red shift of peaks in I_5R_2-and I_5K_2-treated samples, suggesting alteration in the organization of pigments.

It has been found that quenching of Chl fluorescence is associated with a decrease in the CD signal of LHCII (Wentworth *et al*. 2003). In agreement with this result, it was found by sucrose gradient ultracentrifugation and fluorescence spectra that the cationic peptide surfactants induced the LHCII aggregate formation and fluorescence quenching, while the anionic peptide surfactants did not. The reason for the result is that surface charge of LHCII is essentially negative, as shown by the structure of pea LHCII determined by X-ray crystallography (Standfuss *et al*. 2005). The positive charge on the hydrophilic head of the cationic peptide surfactants neutralized the surface charge of LHCII, and thus led to its aggregate. However, the aggregated LHCII induced by peptides seemed different from that without surfactant or that induced by $MgCl_2$, because there were distinct differences in the CD- and fluorescence spectra properties. Upon aggregation induced by $MgCl_2$ or removing surfactant, the low-temperature fluorescence spectrum of LHCII is characterized by a maximum at 680 nm and a shoulder at 700 nm (Kirchhoff *et al*. 2003, Ruban *et al*. 1997, Vasil'ev *et al*. 1997), while the fluorescence emission of LHCII in the presence of cationic peptide surfactants was at around 678 nm. The CD spectra of LHCII aggregate induced by peptides did not show psi-type CD bands (Barzda *et al*. 1994) or characters of aggregate as

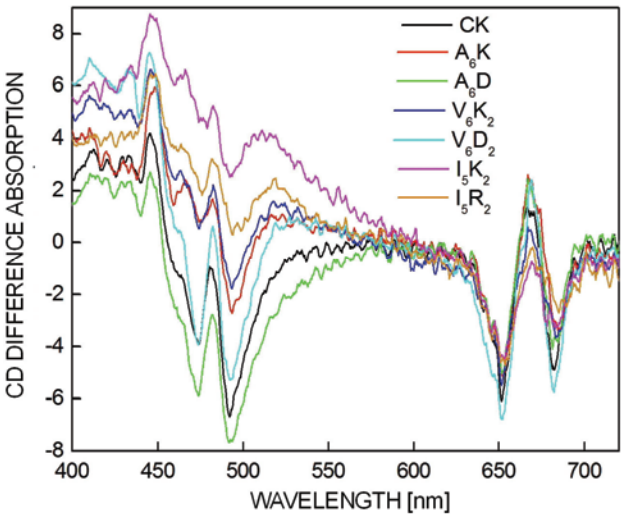

Fig. 6. Circular dichroism (CD) spectra of detergent-dissolved LHCII containing different peptide detergents (0.05% A_6K, A_6D, V_6K_2, V_6D_2, I_5R_2, and I5K2), respectively, measured at 60°C (temperature inside the cuvette). CK – control.

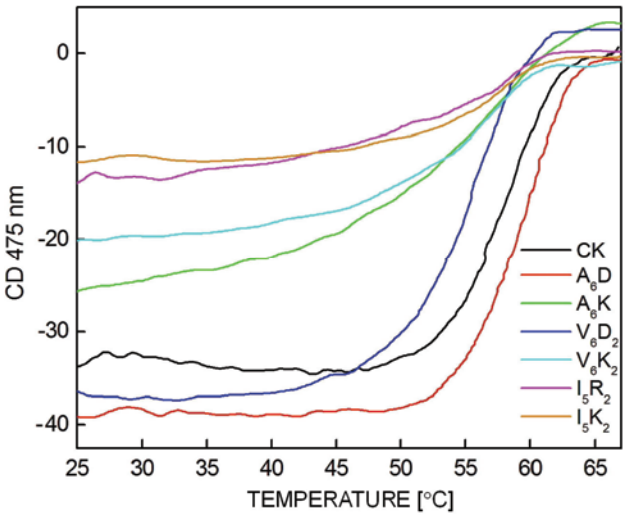

Fig. 7. Temperature dependence of CD signal at 475 nm (CD 475 nm) of LHCII treated with different peptides during the temperature gradient (the shown temperatures are those inside the cuvette), at equal Chl concentrations. CK – control.

Table 1. Thermal stability of LHCII samples treated with different peptides. CK – control.

LHCII sample	Tm [°C] ± SD
CK	57.0 ± 0.3
A_6D	58.4 ± 0.8
A_6K	54.0 ± 0.2
V_6D_2	55.0 ± 0.5
V_6K_2	54.0 ± 1.0
I_5R_2	54.0 ± 0.5
I_5K_2	54.0 ± 0.6

previously reported, such as significantly decreased negative band around 677 nm and intense negative CD at 686 nm (Ruban *et al*. 1997, Lambrev *et al*. 2007). The cationic peptide surfactants and protein perhaps form aggregates different from LHCII aggregation. It was proposed that the peptide surfactant, detergent micelles, and LHCII formed large vesicles, similar to PSI/I_5K_2/Triton X-100 (Ge *et al*. 2010).

Designed peptide surfactants have been shown to be more effective than conventional surfactants for protecting some membrane proteins. However, it was proposed that chemical and structural compatibility between peptide surfactant and membrane protein are crucial for the stabilization effect on protein. The peptide surfactant's amphiphilic properties alone are not sufficient to stabilize the membrane protein complex in a functional state and that the conformational characteristics of the peptides are important (Matsumoto *et al*. 2009). At present the selection of proper peptides to stabilize a specific membrane protein is still entirely empirical. Our results showed that A_6D might improved the thermal stability of LHCII slightly, but the peptides that stabilize PSI complex such as A_6K (Kiley *et al*. 2005, Yeh *et al*. 2005), V_6K_2 (Matsumoto *et al*. 2009), I_5R_2, and I_5K_2 (Ge *et al*. 2010) showed no positive effect on the thermal stability of LHCII. Moreover, the peptides with a negative stabilization effect also changed the conformation of LHCII complex, suggesting the peptides reconstitute protein into a less stable conformation.

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