

1 **Title**

2 Structure and energy transfer pathways of the plant photosystem I-LHCI supercomplex

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14 Short Title: Structure of plant PSI-LHCI supercomplex

15

16 **Abstract**

17 Photosystem I (PSI) is one of the two photosystems in oxygenic photosynthesis, and  
18 absorbs light energy to generate reducing power for the reduction of NADP<sup>+</sup> to NADPH  
19 with a quantum efficiency close to 100%. The plant PSI core forms a supercomplex  
20 with light-harvesting complex I (LHCI) with a total molecular weight of over 600 kDa.  
21 Recent X-ray structure analysis of the PSI-LHCI membrane-protein supercomplex has  
22 revealed detailed arrangement of the light-harvesting pigments and other cofactors  
23 especially within LHCI. Here we introduce the overall structure of the PSI-LHCI  
24 supercomplex, and then focus on the excited energy transfer (EET) pathways from  
25 LHCI to the PSI core and photoprotection mechanisms based on the structure obtained.

26

27 **Introduction**

28 Oxygenic photosynthesis is catalyzed by two photosystems, photosystem II (PSII) and  
29 photosystem I (PSI). Both photosystems capture light energy from the sun; PSII  
30 oxidizes water molecules to generate electrons, protons and molecular oxygen, whereas  
31 PSI accepts electrons from PSII and transfers them to ferredoxin, thereby generating the  
32 reducing power for reduction of NADP<sup>+</sup> into NADPH. The core complex of PSI is

33 largely conserved from prokaryotic cyanobacteria to eukaryotic higher plants.  
34 Cyanobacterial PSI core contains 12 subunits and forms a trimer with a total molecular  
35 weight of 1,068 kDa. On the other hand, higher plant PSI exists in a monomeric form,  
36 and is surrounded by four transmembrane light-harvesting complex I (LHCI) subunits  
37 Lhca1-Lhca4 to form a PSI-LHCI supercomplex, which has a total molecular weight  
38 over 600 kDa. The function of LHCI is to harvest light energy and transfer them to the  
39 PSI core to initiate the charge separation and electron transfer reactions. One of the  
40 most significant features of the plant PSI-LHCI supercomplex is its extremely high  
41 efficiency of energy transfer, and it is estimated that the energy absorbed by LHCI may  
42 induce charge separation with an efficiency close to 100% [1].

43

44 The structure of cyanobacterial PSI core trimer has been solved at a resolution of 2.5 Å,  
45 revealing the detailed organization and arrangements of subunits and various pigments  
46 [2]. The structure of plant PSI-LHCI was solved first at 4.4 Å resolution by the Nelson  
47 group, and the resolution limits were gradually improved to 3.3 Å [3,4,5]. These  
48 structures showed that the architecture of the PSI core is largely unchanged from  
49 cyanobacterial PSI core [2] over 3 billion years of evolution, and that each of the  
50 Lhca1-Lhca4 subunits shares a general folding and some common binding sites for  
51 chlorophylls (Chls) as seen in the LHC protein family [6-9]. However, due to the  
52 limited resolution the exact position and number of cofactors associated with each of the  
53 LHCI subunits were not resolved, which have hampered the understanding of the  
54 mechanisms of light capturing, excitation energy transfer and dissipation within the  
55 PSI-LHCI supercomplex. Recently, we succeeded in solving the structure of PSI-LHCI  
56 from pea at 2.8 Å resolution [10••], which was followed by another report by Nelson's  
57 group at the same resolution [11••]. Although there are some slight differences between  
58 the two structures in relation to the species, position and numbers of cofactors  
59 associated with LHCI, these structures revealed the detailed organization of protein  
60 subunits and various cofactors. In this review, we summarize the overall structure  
61 briefly, and then focus on the excitation energy transfer pathways and photoprotection  
62 mechanisms based on the structure obtained. Other mechanisms related to the  
63 PSI-LHCI structure can be found in [12-16].

64

65 **Overall structure**

66 The PSI-LHCI supercomplex is composed of two functional moieties: the PSI core and  
67 the peripheral LHCI. The PSI core contains nine membrane-embedded PsaA, PsaB,  
68 PsaF, PsaG, PsaH, PsaI, PsaJ, PsaK, PsaL, and three hydrophilic, peripheral subunits  
69 PsaC, PsaD and PsaE. Among these subunits, the PsaG and PsaH membrane-spanning  
70 subunits are unique to plant and not found in cyanobacterial PSI [2]. LHCI contains four  
71 trans-membrane Lhca proteins arranged as a dimer of hetero dimers between  
72 Lhca1/Lhca4 and Lhca2/Lhca3, and forms a belt associated with the PsaF side of the  
73 PSI core (Figure 1a-b). Intensive interactions are formed between Lhca1 and the PSI  
74 core subunits PsaB, PsaG, and between Lhca3 and PsaA, PsaK, at both stromal and  
75 luminal sides, while interactions between Lhca2 and the PSI core subunit PsaJ and  
76 between Lhca4 and PsaF are rather weak and limited to the stromal side. This results in  
77 a hollow between the PSI core and LHCI at the luminal side, which may allow  
78 regulatory co-factors and proteins to come in to interact with LHCI and the PSI core  
79 during light-energy dissipation. In addition to the protein subunits, a total of 205  
80 cofactors were identified in the PSI-LHCI supercomplex [10••]. These include 155 Chls  
81 (143 Chls *a* and 12 Chls *b*), 35 carotenoids [26  $\beta$ -carotenes (BCRs), five luteins (Luts),  
82 and four violaxanthins (Vios)], three Fe<sub>4</sub>S<sub>4</sub> clusters, two phylloquinones (Figure 1).  
83 Among them, the PSI core contains 98 Chls *a*, 22 BCRs, three Fe<sub>4</sub>S<sub>4</sub> clusters and two  
84 phylloquinones, whereas LHCI contains 45 Chls *a*, 12 Chls *b*, four BCRs, five Luts and  
85 four Vios.

86

87 Comparison of the pigments between the plant and cyanobacterial PSI core reveals how  
88 their positions and orientations are maintained, adjusted or newly achieved during the  
89 evolutionary process. Out of the 96 Chls and 22 BCRs reported in the cyanobacterial  
90 PSI structure [2], two Chls and two BCRs are missing in the higher plant PSI core.  
91 Among the remaining 94 Chls and 20 BCRs, eleven Chls and eight BCRs slightly  
92 changed their positions and orientations, while 83 Chls and 12 BCRs remained  
93 unchanged. Furthermore, four Chls and two BCRs bound to new sites in the plant PSI  
94 core (Figure 1c-e). All these changes are found to be located at the “peripheral” rather  
95 than the “core” region of the PSI core, and can be categorized into two groups: (i) on the  
96 PsaH side (cyanobacterial PSI monomer-monomer interface side), and (ii) on the LHCI

97 side. In the former case, the changes are likely due to the loss of PsaM and/or the  
98 addition of PsaH in the higher plant PSI, and some of the changes are located close to  
99 the putative binding site for the main light-harvesting-complex II (LHCII) based on  
100 single particle analysis [17]. These changes may facilitate energy transfer from LHCII  
101 to the PSI core upon formation of a PSI-LHCI-LHCII super-supercomplex under the  
102 "state II" condition [18]. In fact, time-resolved fluorescence measurements of  
103 PSI-LHCI-LHCII super-supercomplex of *Chlamydomonas reinhardtii* showed that Chl  
104 *a*1401 in PsaK, a Chl whose position was shifted significantly in plant PSI, could be  
105 involved in energy transfer pathways from Chl *a*605 of LHCII to the PSI core [19]. On  
106 the LHCI side, the changes may be caused by the loss of PsaX and/or addition of PsaG  
107 and LHCI in plant PSI, which may maximize the efficiency of energy transfer from  
108 LHCI to the PSI core as described below.

109

110 In spite of the slight changes described above, most of the Chls and BCRs remained  
111 largely unchanged from cyanobacterial to the plant PSI core, suggesting that the  
112 excitation energy transfer kinetics and pathways may be largely similar between them.  
113 However, cyanobacterial PSI core contains "red Chls", whereas most of the red Chls are  
114 located in LHCI in the higher plant PSI-LHCI supercomplex (see below). Thus, some  
115 differences are expected in the energy migration mechanism between the cyanobacterial  
116 and plant PSI core.

117

### 118 **Energy transfer pathways from LHCI to PSI core**

119 The excitation energy transfer (EET) efficiency is close to 100% in the plant PSI-LHCI  
120 supercomplex, which means that almost all of the photons absorbed by LHCI may be  
121 utilized to initiate the charge separation at the PSI reaction center [1,16]. A number of  
122 studies have been carried out to elucidate the pathways and mechanism for this highly  
123 efficient EET process in the PSI-LHCI complex [20-28]. These studies showed that the  
124 light-induced charge separation at P700, the reaction center of PSI, occurs very fast with  
125 a lifetime of ~6 ps, whereas the energy-trapping at the reaction center is rather slow  
126 with a trapping lifetime of 50 ps, indicating that the whole EET process is trap-limited.  
127 Furthermore, several pair of red Chls that absorbs lower energy than the PSI reaction  
128 center due to a strong coupling between two Chl molecules, were found to be present in

129 Lhca subunits and play important roles in the EET.

130

131 Structural analysis of the PSI-LHCI supercomplex yielded important information  
132 regarding the EET pathways and mechanism within the supercomplex. It was revealed  
133 that each of the four Lhca subunits has a pair of red Chls (Chl 603-609) located in the  
134 stromal side interface between Lhca and the PSI core, connecting LHCI with the PSI  
135 core. This well explains why a large part of the EET goes through the red Chls [14]. The  
136 phytol tails of these red Chls protrude into “the gap region” between LHCI and the PSI  
137 core, which may not only anchor the Lhca subunits to the PSI core, but is also suited to  
138 collecting the excited energy from neighboring pigments and transferring it to the PSI  
139 core.

140

141 In spite of the common general features of the protein and pigment arrangement of the  
142 Lhcas, there are apparent differences in interactions between each of the Lhca subunits  
143 and the PSI core, leading to possible differences in the EET efficiency from the  
144 individual Lhca subunit to the PSI core. Lhca1 and Lhca3 in the two sides of the LHCI  
145 belt were found to have stronger interactions with the PSI core, whereas Lhca2 in the  
146 middle of the belt interacts with the PSI core rather weakly, and Lhca4 has almost no  
147 direct interaction with the core. Based on the strengths of interactions between Lhcas  
148 and the PSI core, the following EET pathways were identified: 1Bl/1Bs, 1Fl, 2Jl, and  
149 3Al/3As (which are named in the order of the number of Lhca subunit-PSI core  
150 subunit-stromal or luminal side interaction) (Table 1, Figure2) [10••]. The 1Bl pathway  
151 has a connection between *b607* of Lhca1 with three Chls (*a1231*, *a1232* and *a1233*) of  
152 the PsaB subunit at the luminal side, with a shortest edge-to-edge distance of 5.5 Å.  
153 Importantly, the three Chls (*a1231*, *a1232*, and *a1233*) are proposed as the putative red  
154 Chls in the cyanobacterial PSI core [2], and Chl *a1233* in the plant PSI core changed its  
155 ring position significantly compared to the cyanobacterial one, resulting in an ideal  
156 short distance from Chl *b607* of Lhca1. However, since energy transfer from Chl *a* to  
157 Chl *b* is inefficient in general, Chl *b607* may partially limit the energy transfer, or the  
158 binding site may be able to bind both Chl *a* and Chl *b* as seen in LHCII and a minor  
159 LHCII component CP29 [8,29-33]. The 1Bs pathway transfers the energy from the red  
160 Chl pair *a603-a609* of Lhca1 to three Chls (*a1218*, *a1219*, and *a1802*) of PsaB at the

161 stromal side (Figure 2b-c), with a shortest edge-to-edge distance of 7.5 Å (Table 1),  
162 suggesting that this pathway is highly efficient. The Chl *a*1802 is one of the newly  
163 achieved Chls in the plant PSI core during the evolution from cyanobacteria to plants,  
164 which is accompanied by significant structural changes in a loop region connecting  
165 transmembrane helices *d* and *e* of PsaB. The middle part of the loop region  
166 (Ala<sup>307</sup>-Gly<sup>318</sup>) of PsaB flipped by about 10 Å toward the PSI core with a flipping angle  
167 of about 60 degree. A Chl *a*40 in the similar position to Chl *a*1802 of the plant PSI core  
168 was found in the structure of a monomeric *Synechocystis* PSI core, and Mazor et al.  
169 suggested that the Chl trimer (*a*1218, *a*1219, and *a*40) may be the red Chls [34].

170

171 The 1Fl pathway transfers energy from Chl *a*616 of Lhca1 to Chl *a*1701 of the PsaF  
172 subunit in the luminal side, with a shortest edge-to-edge distance of 8.2 Å (Table 1).  
173 The chlorine ring of Chl *a*1701 has a significant positional shift of 9 Å in comparison  
174 with the cyanobacterial PSI, which may facilitate the EET through this pathway. The  
175 Chls in Lhca4 have no direct interactions with those of the core, and its Chls are rather  
176 closer to Lhca1. In particular, an edge-to-edge distance of 5.9 Å was found between  
177 *a*616 of Lhca1 and *a*617 of Lhca4. Thus, the energy absorbed by Lhca4 may be  
178 transferred to the PSI core through the 1Fl pathway (Figure 2d). In the stromal side, the  
179 1Bs pathway may also accept energy from Lhca4 and transfer them to the core.

180

181 In the 2Jl pathway, the shortest edge-to-edge distance is 12.8 Å between Chl *b*607 of  
182 Lhca2 and *a*1302 of PsaJ in the luminal side. Due to the presence of a Chl *b* and the  
183 rather long distance, it seems that the energy transfer from Lhca2 to the PSI core is not  
184 very efficient. This is different from the fast EET kinetics estimated from picosecond  
185 fluorescence spectroscopic studies [28]. However, weak electron densities were  
186 observed in “the gap region” between Lhca2 and the PSI core in our structure analysis  
187 which were not assigned in the model; these densities may represent an additional Chl  
188 [10••]. Alternatively, the gap region may undergo dynamic structural changes under  
189 physiological conditions to facilitate the energy transfer.

190

191 The shortest edge-to-edge distances between pigments of Lhca3 and PsaA are 5.8 Å and  
192 10.2 Å in the luminal and stromal side, respectively, forming the 3Al and 3As pathways

193 (Figure 2f-g, Table 1). The 3A1 pathway may transfer energy through both the red Chl  
194 pair *a603-a609* and other Chls, whereas the 3As pathway collects energy mostly  
195 through the red Chl pair. There are also Chls of Lhca2 that are close to these pathways,  
196 suggesting that the energy absorbed by Lhca2 may also be transferred to the core  
197 through these pathways in Lhca3.

198

199 It should be mentioned that both structures from the two groups [10••,11••] contained  
200 much less Chls in the gap region than the previous structures determined at lower  
201 resolutions [3,4,5]. Because many previous studies have been performed on the basis of  
202 the structure containing those gap Chls, re-examinations of those results may be  
203 necessary based on the new structures. To summarize, the red forms play important  
204 roles in EET from LHCI to the core, whereas other pathways are also present that do not  
205 involve the red Chls. However, there may be some ambiguities in the position and  
206 orientation of some of the pigments in the current structure due to the limited resolution,  
207 and further refined structures are required to reveal the full picture of EET in this  
208 enormously large pigment-protein complex.

209

### 210 **Photoprotection and nonphotochemical quenching mechanisms**

211 Our structural analysis identified a total of 13 carotenoids in the four Lhca subunits,  
212 with each Lhca binding three carotenoids (one Lut, one Vio, and one BCR) at three sites  
213 (L1, L2, and N1, respectively) and an additional lutein (Lut624) bound in the interface  
214 between Lhca1 and Lhca4 (Figure 3). This is in comparison with 10 carotenoids (9 Luts  
215 and 1 BCR) reported by Mazor et al. [11••]. Importantly, we found that each Lhca  
216 subunit binds one Vio at its "L2" site. Vio is known to be converted to zeaxanthin (Zea)  
217 by de-epoxidation via Vio deepoxidase (VDE) upon acidification in the lumen induced  
218 by excess light illumination, thereby triggering the xanthophyll cycle. This is a cycle of  
219 interconversion between Vio and Zea. Upon conversion of Vio into Zea, the light energy  
220 is dissipated through the Zea-binding site; thus, the xanthophyll cycle is important for  
221 energy dissipation under excess light illumination, a process known as Zea-dependent  
222 non-photochemical quenching (NPQ) [35,36]. This process is important for  
223 photoprotection under strong light illumination.

224

225 The xanthophyll cycle has been found and studied in LHCII extensively [37,38].  
226 Recently, the Zea-dependent NPQ in LHCI has also been reported [39•], and our  
227 structure provided evidence for the possible operation of this mechanism in LHCI. In  
228 the crystal structure, the Vio is located in a groove formed by two transmembrane  
229 helices A and B of Lhca subunits that face the PSI core. When VDE binds to the  
230 luminal side to catalyze de-epoxidation, the two Lhca subunits (Lhca2 and Lhca4) in  
231 the middle of the LHCI belt would be more accessible than the side ones (Lhca1 and  
232 Lhca3) because of the deep “hollow” in the middle between LHCI and the PSI core. In  
233 addition, the luminal end of the Vio in each Lhca is surrounded by three Chls (*a*604,  
234 *a/b*606, *a/b*607) and capped by the loop between transmembrane helices A and C (AC  
235 loop), and differences are also found in the organization of the AC loops between  
236 Lhca2/4 and Lhca1/3. The AC loops of Lhca2 and Lhca4 consist of 21 residues and bind  
237 Chl *b*607 indirectly via water molecules, whereas the AC loops of Lhca3 and Lhca1 are  
238 ten residues longer in order to make interactions with the PSI core, and coordinate Chl  
239 *a/b*607 directly. These structural differences imply that the AC loops of Lhca2 and  
240 Lhca4 are more flexible and may allow larger dynamic structural changes to occur than  
241 that of Lhca1 and Lhca3, making the Vio in Lhca2/4 more likely to be involved in the  
242 xanthophyll cycle. Furthermore, differences are also found in the hydrogen-bonding  
243 pattern between the Vio bound to Lhca1/3 and that bound to Lhca2/4. In Lhca2 and  
244 Lhca4, only one hydrogen-bond is found between the hydroxyl group of Vio (pointing  
245 to the luminal side) and a carbonyl oxygen atom from the main chain of Trp 127<sup>Lhca2</sup>  
246 and Trp 126<sup>Lhca4</sup>, whereas the Vio bound to Lhca1 and Lhca3 makes one additional  
247 hydrogen-bond (to Gln 105<sup>Lhca1</sup> and Thr 133<sup>Lhca3</sup> respectively). This suggests that the  
248 affinity for Vio is lower in the middle Lhcas than that in the two side Lhca subunits  
249 (Lhca1/3). Based on these structural features, we propose that Zea-dependent NPQ may  
250 function more efficiently in the middle Lhcas than that in the side Lhcas.

251

## 252 **Conclusions**

253 The structural analysis of the plant PSI-LHCI supercomplex at a resolution of 2.8 Å  
254 reveals many new features of the arrangement of protein subunits and cofactors of this  
255 extremely large membrane-protein complex, such as the first identification of Chl *b*  
256 from Chl *a*, clarification of many Chls assigned in the "gap region" between LHCI and



257 the PSI core in the previous low-resolution structures, and identification of the  
258 Vio-binding sites in each of the Lhca subunits. These results provide a basis for  
259 elucidating the mechanism of highly efficient energy transfer from LHCI to the PSI core,  
260 and possible photoprotection mechanism under excess light illumination. On the other  
261 hand, there is still a need for higher-resolution structures in order to fully reveal the  
262 mechanisms of energy transfer, electron transfer, and photoprotection occurring within  
263 this supercomplex. Given the recent developments in high-resolution structural analysis  
264 of large membrane-protein complexes such as photosystem II [40, 41], advancement on  
265 the structural analysis of the PSI-LHCI complex may be expected in the near future.

266

267

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290 **Reference and recommended reading**

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412 **Figure legends**

413

414 **Figure 1 Structure of the plant PSI-LHCI supercomplex and its comparison with**  
415 **cyanobacterial PSI.** Stereo views of the overall structure of the supercomplex with a  
416 view from the LHCI side (**a**) and a view along the membrane normal from the stromal  
417 side (**b**). **c**, The arrangement of cofactors with the view direction same as in panel **b**.  
418 Color code: red, Chls involved in the electron transfer chain (ETC) and red Chls;  
419 magenta, Chls and BCRs that are newly found or having significant positional shift in  
420 the plant PSI core; green, other Chls in the PSI core; gray, Chls and carotenoids in LHCI.  
421 Numbers indicate Chls of the PSI core involved in the EET pathways. **d**, The  
422 arrangement of cofactors of cyanobacterial PSI with the view direction same as in panel  
423 **b**. Color code: cyan, Chls and BCRs that were not found in the plant PSI core; brown,  
424 Chls and BCRs that have slight positional movements between plant and cyanobacterial  
425 PSI; black, Chls involved in ETC, and the other Chls and BCRs which are found to be  
426 in equivalent positions and orientations between the plant and cyanobacterial PSI core.  
427 Overlay of panels **c** and **d**.  
428

429 **Figure 2 Possible EET pathways from LHCI to the PSI core.** **a**, Overall location of  
430 pigments involved in EET pathways from LHCI to the PSI core. Locations of the Red  
431 Chls in each Lhca subunits and the putative binding site of LHCII are represented by  
432 red ovals and a blue circle, respectively. Spheres indicate magnesium ions of Chls.  
433 Arrows in panels (**a-g**) indicate the possible EET pathways from LHCI to the PSI core.  
434 Red color and blue color of the arrows indicate the pathways either in the liminal side or  
435 the stromal side, respectively. **b**, Stromal side EET pathway 1Bs from Lhca1 to PsaB in  
436 the PSI core. **c**, Stromal and luminal EET pathways 1Bs and 1Bl from Lhca1 to PsaB in  
437 the PSI core. In panels (**b**, **c**), plant and cyanobacterial loop regions connecting the  
438 transmembrane helices *d* and *e* in PsaB are colored in red and magenta, respectively. **d**,  
439 Luminal side EET pathway 1Fl from Lhca1 to PsaF in the PSI core. **e**, Luminal side  
440 EET pathway 2Jl from Lhca2 to PsaJ in the PSI core. **f** and **g**, Stromal and luminal EET  
441 pathways 3As and 3Al from Lhca3 to PsaA in the PSI core. Color code for cofactors for  
442 panels **b-g**: red, red Chls; magenta, Chls newly found in plant PSI or having significant  
443 positional change from cyanobacterial PSI; orange, Chls and BCRs having slight  
444 positional change from cyanobacterial PSI; green, Chls remain unchanged between  
445 cyanobacterial and plant PSI; blue, BCRs remain unchanged between cyanobacterial

446 and plant PSI; gray, Chls and carotenoids in LHCI; black, Chls and BCRs in  
447 cyanobacterial PSI. The phytol chains of Chls except red Chls were omitted for clarity.  
448 View directions are from the stromal side for panels **a**, **b**, **d**, **e** and **f**, and perpendicular  
449 to the membrane normal for panels **c** and **g**.

450

451 **Figure 3 Arrangement of carotenoids in LHCI.** **a**, Top view along the membrane  
452 normal from the stromal side. **b**, Side view of LHCI. The three carotenoid binding sites  
453 L1 (Lut 620), L2 (Vio 621) and N1 (BCR 623) in each Lhca subunit were shown in  
454 green, yellow and magenta, respectively. Lut 624 in the L3 site of Lhca4 was shown in  
455 light blue. Chls *a* and *b* were shown in gray and orange, respectively.

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463 **Table 1. Major energy transfer pathways from Lhcas to PSI core.**

Pathways	Luminal or Stromal		Lhca	Chl (Lhca)	PSI core	Chl (PSI core)	Distance (Å) <sup>1</sup>	Red Chls <sup>2</sup>	Remarks <sup>3</sup>	
				PDB #	LHCII #	PDB #	LHCII #			
1Bl	L	a1	307	<i>b607</i>	B	<b>101(G)</b>	<b><i>a1233</i></b>	5.5	N	–
1Bs	S	a1	304, 309	<i>a603, a609</i>	B	821, <b>822, 841</b>	<i>a1218,</i> <b><i>a1219, a1802</i></b>	7.5	Y	Lhca4
1Fl	L	a1	315	<i>a616</i>	F	<b>304</b>	<b><i>a1701</i></b>	8.2	N	Lhca4 (Red Chl)
2Jl	L	a2	606	<i>b607</i>	J	<b>3002</b>	<b><i>a1302</i></b>	12.8	Y/N	–
3Al	L	a3	306	<i>a607</i>	A	<b>817</b>	<b><i>a1114</i></b>	5.8	N	Lhca2
3As	S	a3	303, 308, 315	<i>a603,</i> <i>a609, a619</i>	A	<b>811, 813</b>	<b><i>a1108, a1110</i></b>	10.2	Y	Lhca2

464 Bold characters indicate structures significantly changed compared with those in  
465 cyanobacterial PSI core.

466 <sup>1</sup>Shortest edge-to-edge distances.

467 <sup>2</sup>Involving the red Chls or not.

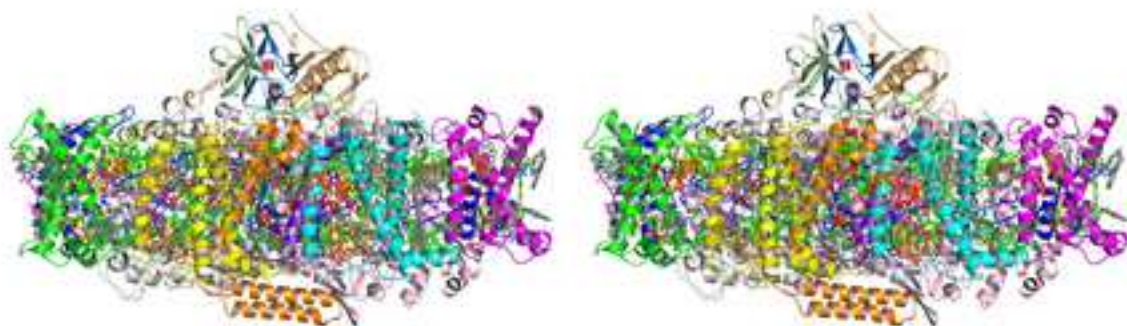
468 <sup>3</sup>Energy from other Lhcas (red Chls indicating involvement of the red Chls) may also be  
469 transferred through this pathway.

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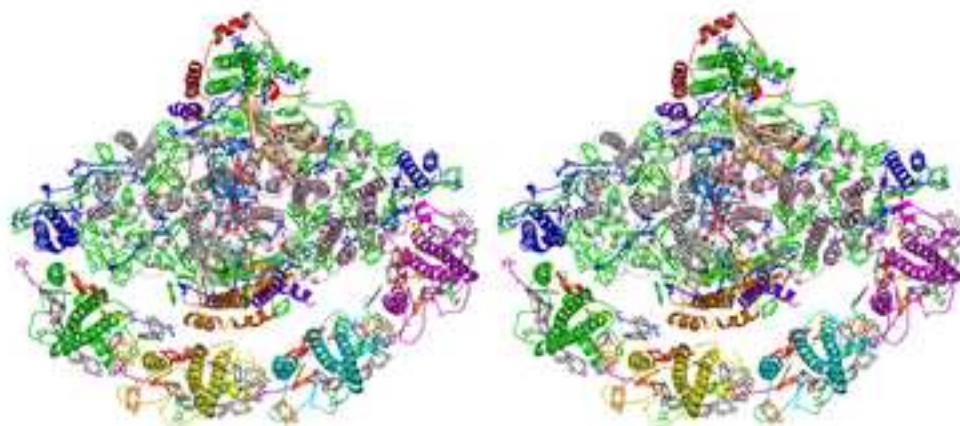
Figure

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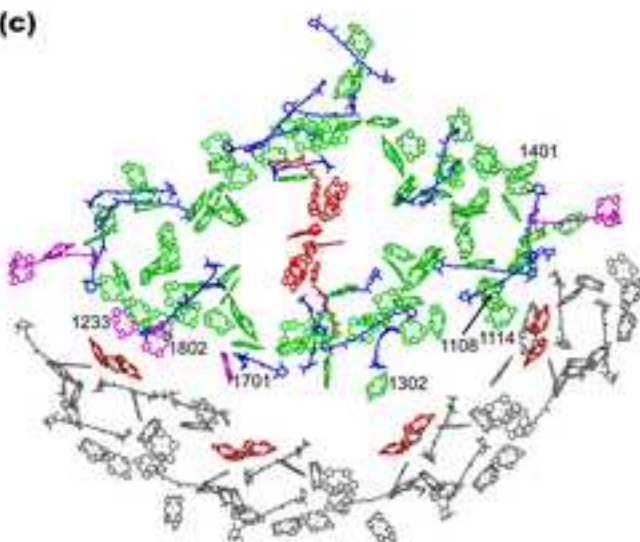
(a)



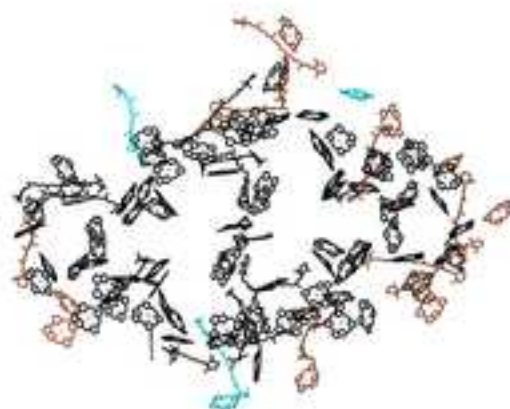
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(c)



(d)



(e)

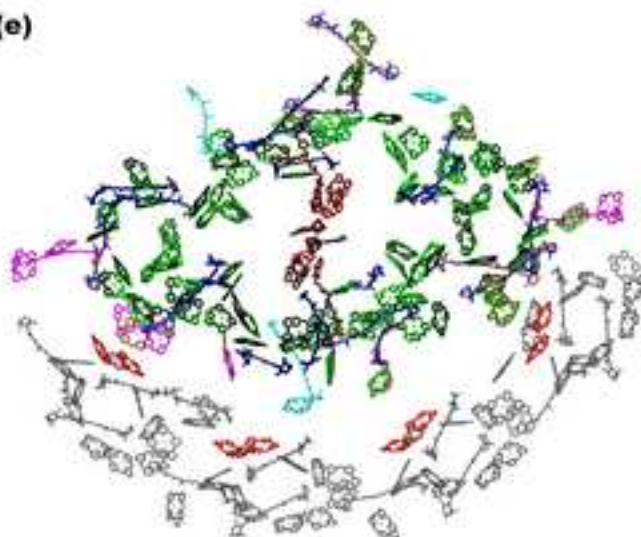




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