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Network Characteristics of Individual Pigments in Cyanobacterial Photosystem II Core Complex

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Part of the excitation energy transfer (EET) characteristics of the photosystem II (PSII) comes from the interconnection between pigments. To understand the correlation between the EET and pigments' interaction structure, we construct a network from the EET rates which are related to both the distance of the pigments (chlorophylls and pheophytins) and their spatial orientation. Especially, we investigate how well of the PS II core complex's EET functionality that can be explained by just the network topology in *Thermosynechococcus vulcanus* 1.9Å. Starting from the Förster theory we construct a network of EET pathways. For an analysis of the network structure, we calculate common network-structural measures like betweenness centrality, eigenvector centrality and weighted clustering. These measurements can reflect the role of individual pigments in the EET network. In our work, we found that some well-known properties are reproduced by the network analysis of the simplified network. It means that the topology of the network encodes functionally relevant information. For example, from the network structural analysis, we can infer that most of chlorophylls in pigment-protein complex CP47 have heightened probability to transfer the energy compared with other chlorophylls. We also see that the active branch chlorophylls in the reaction center are characterized by a high eigenvector

centrality, a high betweenness centrality and a low weighted clustering coefficient. This is indicative of functionally important vertices.

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I. BACKGROUND

Photosynthetic organisms are able to generate the chemical energy from sun. The efficiency of harvesting of solar energy is almost unity. This impressive mechanism begins from the EET in PSII that is located on thylakoid membrane of chloroplast in photosynthetic cells [1]. Especially, there are many experiments focusing on relating the structure and EET properties [2,3,4]. Because the chlorophylls in these pigment-protein complexes are arranged in a peculiar pattern, many researchers have studied the overall EET of system with the orientation and distances of pigment in protein environment [5,6]. In the case of PSII core complex, these kinds of researches are possible since the crystal structure has been mapped out at resolutions from 1.9Å to 3.8Å in two cyanobacteria, *Thermosynechococcus elongatus* [7,8,9] and *Thermosynechococcus vulcanus* [10,11]. In the PSII core complex crystal structure, there are 70 chlorophylls containing the so-called D1, D2 protein complex and CP47, CP43 complex. For understanding the mechanism of PSII EET exactly, we can have two options. One is adding the additional variables estimated by spectroscopy studies. The other is simplifying the EET system information to understand big picture. There are some researches assume the EET dynamics as interactive network to improve the general understanding in photosystem I(PSI) EET [12,13]. The studies are applied to PSI and they focus on the theoretical calculation. In our research, we try to see the big picture of EET in PSII with minimizing the photosynthetic EET system as a network with nodes and links; pigment (chlorophylls and pheophytins) becomes a single node and link connects two nodes with high enough EET rate. In this work we will focus on investigating the hypothesis is that the each pigment (chlorophylls and pheophytins) in the PSII core complex can be seen as a node in a network, and the network topology explains some of the functionality of the EET.

II. METHODS

In large interconnected systems the way pigments are connected—the network topology—can explain (several features of) the functionality of the system and its constituents. One of the most important

ways of characterizing the role of a node in the network is by measuring its centrality [14, 15]. In fact, there are a number of centrality measures, each corresponding to one aspect of the umbrella concept centrality. In this section, we will present the calculation and algorithm for constructing the simplified network, centrality measures, and also several parameters related to other structures of the network, that we use.

A. Calculation of the Excitation-Energy Transfer (EET) Rate

As mentioned above, we use the dimeric PSII core complex. The direction of the dipole-moment vector of the lowest excited (Q_y) state of chlorophyll and pheophytin is approximately following a line connecting the NB and ND atom in the porphyrin ring of the chlorophyll and pheophytin [16,29]. We obtain the orientation of dipole vector from the crystal structure. The rate of EET can represent the probability of energy transfer between pairs of nodes. We will use the EET rate as the transfer probability, which could indirectly represent the amount of energy in the identical time range with formula (6).

$$P_{DA_x} = \frac{r_{DA_x}}{\sum_{n=1}^N r_{DA_n}} \quad (6)$$

To calculate the EET rate, we should calculate the coupling strength first. W_{ij} denotes the coupling strength between the i th and the j th chlorophylls. The electric coupling W_{ij} can be divided into two terms

$$W_{ij} = W_{ij}^c + W_{ij}^{ex} \quad (7)$$

where W_{ij}^c corresponds to a direct coulomb term and W_{ij}^{ex} corresponds to an electron exchange term. In PSII core complex, all of the pigment distance between Mg–Mg is mostly greater than 7Å so, we assume the Coulomb interaction dominates the electric coupling strength [12]. From this assumption, it follows that exciton states are fairly well localized to individual pigments, which is a basic assumption

of Förster theory [17]. Therefore, we keep only the direct Coulomb term W_{ij}^c . For calculation of the Coulomb term, we assume the dipole-dipole interaction between transition dipole moments of the chlorophyll Q_y states. With this approximation, the couplings are given by

$$W_{ij} = \alpha \left(\frac{\mathbf{d}_i \cdot \mathbf{d}_j}{r_{ij}^3} - \frac{3(\mathbf{r}_{ij} \cdot \mathbf{d}_i)(\mathbf{r}_{ij} \cdot \mathbf{d}_j)}{r_{ij}^5} \right) \quad (8)$$

where $\mathbf{d}_i$ are unit vectors along transition dipole moments from the ground state to the Q_y state of the i 'th chlorophyll and $\mathbf{r}_{ij}$ is the vector connecting the Mg atoms of chlorophyll i and j . Here, we use the value of parameter C as $116,000 \text{ \AA}^3 \text{ cm}^{-1}$ [12].

In addition to the coupling strength between nodes, the energy of nodes can play an important role in determining the direction of excitation energy flow. Because the nodes correspond to the chlorophylls, we can measure the energy of nodes from the absorption spectrum of chlorophylls. We used the site energy of special pair chlorophylls as $14,630 \text{ cm}^{-1}$ and the others are $14,814 \text{ cm}^{-1}$ [18].

After the setting of site energy and coupling strength, we calculate the EET rate between chlorophylls based on Förster theory [13] with Eq. 9. The EET rate from pigment i to pigment j is calculated by

$$T_{ij} = \frac{4\pi^2}{h} |W_{ij}|^2 J_{ij} \quad (9)$$

Here, J represents the spectral overlap of the donor emission and acceptor absorption. We can calculate this quantity as follow

$$J_{ij} = \int S_i^D(E) S_j^A(E) dE \quad (10)$$

In this formula, $S_i^D(E)$ is the donor's emission spectrum and $S_j^A(E)$ is the acceptor's absorption spectrum. We approximate these spectra by Gaussians as follows

$$S_i^D(E) = \frac{1}{\sqrt{2\pi\nu}} \exp \left[-\frac{(E_i - S - E)^2}{2\nu} \right] \quad (11)$$

$$S_j^A(E) = \frac{1}{\sqrt{2\pi\nu}} \exp\left[-\frac{(E_j - E)^2}{2\nu}\right] \quad (12)$$

where E_i and E_j are the absorption peaks for the pigments and S represents the Stokes shift. We take the Stokes shift to be equal to 180cm^{-1} at room temperature and assume the widths for the emission and absorption spectra to be the same value [18,19]. Combining the coupling strength and spectral overlap, we are able to get EET rate between pigments of PSII dimeric core complex.

B. Constructing the chlorophyll network: Overview

To construct the EET network, we start from the crystal structure of the PSII core complex of *T. vulcanus* obtained with $1.9\text{\AA}$ resolution from Protein Data Bank [11]. This database contains information about the coordinates of the Mg atoms of the chlorophylls and their orientation. From this information, one can assign an EET rate (explained above) to pairs of chlorophylls. Using the ‘Minimization algorithm’ to make a simplified network which keeps the whole connection, we assign a link between the nodes. It such that we have a minimum number of links and the network keeps the connection. The below part is for the specific description of the simplified network.

C. Details of the network construction and dynamic simulation

Based on the calculated EET rate (Eq. 9), we construct the networks of the PSII core complex as described above. We sort the descending order list of links according to weight to minimize the network with the strong EET rate until keeping the connection between all pigments. The cut-off value for simplified network is $4.2 \times 10^{10} \text{ s}^{-1}$ after the network minimization process. Then we will use the simplified network to distribute EET by an algorithm described below. In real spectroscopy experiments, it is almost impossible to exclusively excite a pigment. This is just what we do in our simulations to find out the functionality of pigments in the excitation transmission. We excite every one node (chlorophyll and pheophytin) and monitor the ingoing and outgoing flow of excitation energy through the each node until there is no excitation left. Our simulation algorithm is illustrated in Fig. 1. First, we give one unit of excitation to one node. Second, we transfer the excitation to neighbors of the

excited node with probability proportional to the EET rate. Third, in this process, we choose one of two ways for the excitation to disappear in the network. One is a self-dissipation pathway for the every chlorophyll, in which one unit of excitation leaves the network in one nanosecond [20]. The other one, for nodes in the reaction center, is charge separation, which happens in the picoseconds [21]. To solve the technical problem, we add auxiliary, dummy nodes to express the effects of charge separation and self-dissipation. For these two cases, we set the weight of additional nodes with self-dissipation rate (10^9) and charge separation rate (10^{12}). The active branch chlorophyll in reaction center (labeled as 1604, 2604) and accessory chlorophyll (labeled 1606, 2606) in each reaction center's active branch are controversial regarding the charge separation [22,23]. In this work, we assume the charge separation will occur on the special pair active chlorophyll. Calculating the excitation population by master equation could be similar with this algorithm. We construct this, however, with reason that we want to measure not the final population but also total sum of in and out flow in each node.

D. Degree centrality

The simplest measure of network centrality we measure is called *degree centrality* [14,15,24]. The degree centrality is simply the number of other nodes a node is connected to. As opposed to betweenness and eigenvector centrality (discussed below), degree centrality is local in the sense that the degree centrality of i is independent of the network outside of i 's neighborhood. If a network property is determined entirely by a local quantity, it means that processes at a distance (involving many nodes connected indirectly by paths of links) are not important for the dynamics of the system.

E. Betweenness centrality

Another centrality concept comes from thinking about the flow of a dynamic system through a node. If we assume flow originate between pairs of nodes with equal rate, and travel through the network along shortest paths, then the amount of traffic through a node would be proportional to its *betweenness centrality* (proposed in Ref. [25], see also Refs. [14,15]). More specifically, let $\sigma(i,j)$ be the number of shortest paths between i and j (a shortest path does not have to be unique) and let $\sigma_i(i,j)$ be the number

of shortest paths between i and j that pass l , then l 's betweenness centrality is

$$C_B(l) = \sum_j \sum_{i \neq j} \frac{\sigma_l(i, j)}{\sigma(i, j)} \quad (13)$$

This definition holds for both weighted and unweighted networks (although for weighted networks the shortest path is more often unique and so the denominator is usually strictly one).

F. Eigenvector centrality

A third concept of centrality comes from the observation that if the neighbors of a node are central, then this node is probably central too. We denote this centrality $C_E(i)$ and assume it can be transferred between connected nodes. If we let the superscript denote the time of the spreading, then one can summarize the above concept as

$$C_E^{t+1}(i) = \lambda^{-1} \sum_{j \in \Gamma_i} C_E^t(j) \quad (14)$$

Where Γ_i is the neighborhood of i (i.e. all vertices that have a link to i), and λ is a constant to ensure the iterations to converge. We are interested in the long time limit when $t \rightarrow \infty$, so we can set $t = t + 1$ in Eq. 2. This means that the C_E can be phrased as an eigenvector problem

$$\mathbf{C}_E = \lambda^{-1} \mathbf{A} \mathbf{C}_E \quad (15)$$

where $\mathbf{A}$ is the adjacency matrix (where the ij element is 1 if there is a link between i and j , and 0 otherwise) and $\mathbf{C}_E$ is the vector of centrality values for all vertices.

G. Clustering coefficient

There are other types of network structure than centrality. The *clustering coefficient* [14,15] is a measure how well-connected the neighborhood of a node is. A node with high clustering coefficient is the member of relatively many triangles (relative to the maximal number given the number of neighbors). Triangles introduce redundancy in the sense that paths including a certain link only become one step longer if the link vanishes. We define the clustering coefficient of node i as

$$c(i) = \frac{t_i}{\binom{k_i}{2}} \quad (16)$$

Where t_i is the number of triangles that i is a part of. The binomial factor $\binom{k_i}{2} = \frac{1}{2}k_i(k_i - 1)$ gives the maximal number of triangles given the degree of i .

III. RESULTS

A. Basic properties of the network and dynamics

First, we discuss the basic structure of the excitation networks derived from the relative location and orientation of pigments. In Fig. 2, we display the crystal structure of chlorophylls and pheophytins. The EET network is shown in Fig. 3. The layout of EET network in Fig. 3 is not same as pigments location in crystal structure (Fig. 2). A short distance in this plot represents short graph distance, which is correlated by, but not identical to the physical distance. The EET network has 70 chlorophylls and 4 pheophytins as nodes and 278 links between chlorophylls based on the EET rate. The size of network is rather small compared with other typical empirical datasets studied in the research field of complex networks [14]. For simplification, we assumed the links as bidirectional. This is possible assumption because we need the averaged EET rate between the nodes. To quantify the importance of a node in the excitation transfer dynamics, we propose to measure the *total passed excitation* (TPE). We calculated the TPE by summing the ingoing and outgoing excitation energy through each node. This shows how much amount of excitation flow goes in and out through the node.

B. Degree centrality

In the case of degree centrality [14,15], most of nodes shows a positive correlation with the TPE value (Fig. 4). The special pairs display a different characteristic, where the TPE is exceptionally large but the degree centrality is only intermediate. This means that even though these nodes (special pair chlorophylls) are only connected to a limited amount of others, there is a large amount of energy passing through them. Focusing on the main cloud of points, 1613, 1614, 2613 and 2614 (all in the

CP47 complex) are somewhat outliers having both very large degrees and TPE. Furthermore, we note that the within the special pairs the ones belonging to the chlorophylls active branch of the reaction center have higher degree centralities than the ones in the inactive branch.

C. Eigenvector centrality

Results for eigenvector centrality can be seen in (Fig. 5). Compared to degree and betweenness centrality the correlation to TPE is weaker (albeit positive). Many of the active branch's chlorophylls are ranked higher than the inactive branch, which could indicate that the active branch has a more important role in the EET. On the other hand, since TPE is our major quantity of functional importance the main conclusion is that eigenvector centrality cannot capture that. Eigenvector centrality is, in a sense, an extension of degree centrality to become a global quantity. Since degree centrality is more strongly correlated with TPE, charge transfer is a rather local process in this model with shorter cascades of excitation.

D. Betweenness centrality

Looking at the betweenness centrality [14,15] in (Fig. 6), we see the difference between the active and inactive branch of the reaction center even more clearly than for the degree centrality. The special pair of the active branch has an almost 14 times higher betweenness centrality than the special pair of the inactive branch. The nodes that are close in the network can still have different betweenness values (which is typical for this measure). The reason is that some nodes, although central in other respects, can lie a bit off the main avenues of shortest paths and thus get much fewer shortest paths passing than their neighbors. We note that the motivation of betweenness centrality assumes objects travelling on the network that actively tries to take shortest paths. This is of course not the case in the system we study; nevertheless, betweenness manages to highlight the difference between the active and inactive branch of the reaction center. Moreover, the network structure can be optimized so that the excitation with a heightened probability travels short paths to the reaction center.

E. Clustering coefficient

The weighted clustering coefficient measures how much connected the neighborhood of a node is [26]. A large value of this quantity also means that charge is likely to pass through the neighborhood of a node rather than through the node itself. There is nothing *a priori* that dictates a positive correlation between the weighted clustering coefficient and TPE—indeed many networks show a negative correlation between clustering coefficient and degree, see Ref. [27] (Fig. 7). In this case, there are no clear outliers, rather a positively correlated point cloud. The special pairs are the nodes with highest weighted clustering and highest TPE.

III. DISCUSSION

In our investigation of the relation between the network topology and EET dynamics of PSII, we found that network structural measures that are designed to capture some aspect of a pigment importance are positively correlated with a measure of the functional importance. This means that the much of the dynamics of the PSII EET can be explained by the network topology qualitatively. One such example is the active branch chlorophyll that is an outlier in many of our correlation plots, in other words it seems to be more important in EET by its position in the network. They show higher betweenness and weighted clustering coefficient than the chlorophylls in the inactive branch. This is especially true for the betweenness centralities of the special pair that has almost 14 times higher values in the active than in the inactive one. From these results, we can infer that chlorophyll in active branch is located to absorb the excitation more than inactive one in the view of EET network.

Even though we estimate the EET before the charge separation process, the chlorophyll in active branch shows high functionality. In the literature, there is quite a consensus that the chlorophyll in active branch of special pair is important for charge separation [23,28]. Combining with those results and ours, we can infer the network characteristics which is represented as the probability of getting the EET could be correlated to charge separation.

Chlorophyll 1613, 1614, 2613 and 2614 are another groups with conspicuous structural features. These chlorophylls are included in the CP47 complex and are peculiarly central in the network given their TPE values. Furthermore, second monomer has higher eigenvector centrality than the first. From the construction of the eigenvector centrality, this suggests that second monomer could have a somewhat more important role in relaxation process after photon absorption. It is difficult to make a direct experimental verification of this conclusion, but it is our hypothesis for future studies. One more future topic would be that even though the dimer structure makes the system resilient to failure by introducing redundancy, evolution has favored one branch. On the other hand, the eigenvector centrality is rather weakly correlated with the dynamic measure of importance, TPE. Our hypothesis is that TPE contains more functionally relevant information. However, once again, how to weight this different information together will ultimately need experimental evaluation. The latest theoretical calculation for PSII EET might be able to compare with simplified result.

To epitomize, we see that network theory confirms well-known structural properties of bacterial PS II core complex and verify their functions in EET with broad picture. This can be useful in future studies to make a sketchy overview of systemic organization and to map out the optimized structure of photosynthesis. In future work, we also hope to extend assumptions behind the network construction, such as the Förster theory, and study the efficiency of the network as a whole, not just the individual nodes. We anticipate future investigations of photosynthesis and similar spatially constrained complex biochemical processes by network theory.

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REREFENCES

- [1] R. E. Blankenship, *Molecular mechanisms of photosynthesis* (Hoboken NJ, Blackwell Science, 1999).
- [2] N. P. Pawlowicz, M. L. Groot, I. H. M. van Stokkum, J. Breton and R. van Grondelle R, *Biophysical Journal* **93**, 2732 (2007).
- [3] G. Raszewski and T. Renger, *J. Am. Chem. Soc.* **130**, 4431 (2008).
- [4] V. I. Novoderezhkin, E. Romero, J. P. Dekker and R. van Grondelle, *Chem. Phys. Chem.* **12**, 691 (2011).
- [5] J. Adolphs, F. Müh, M.-A. Madjet, M. S. am Busch and T. Renger, *J. Am. Chem. Soc.* **132**, 3331 (2010).
- [6] M. Byrdin, P. Jordan, N. Krauss, P. Fromme, D. Stehlik and E. Schlodder E, *Biophys. J.* **83**, 433.
- [7] A. Zouni *et al.*, *Nature* **409**, 739 (2001).
- [8] K. N. Ferreira, T. M. Iverson, K. Maghlaoui, J. Barber and S. Iwata, *Science* **303**, 1831 (2004).
- [9] A. Guskov *et al.*, *Nature Struct. Mol. Biol.* **16**, 334 (2009).
- [10] N. Kamiya and J. R. Shen, *Proc. Natl. Acad. Sci. USA* **100**, 98 (2003).
- [11] Y. Umena *et al.*, *Nature* **473**, 55 (2011).
- [12] M. K. Sener *et al.*, *J. Phys. Chem. B* **106**, 7948 (2002).
- [13] M. K. Sener, C. Jolley, A. Ben-Shem, P. Fromme, N. Nelson, R. Croce and K. Schulten, *Biophys. J.* **89**, 1630 (2005).
- [14] M. E. J. Newman, *Networks: An Introduction* (Oxford, Oxford University Press, 2010).

- [15] E. Estrada, *The structure of complex networks: Theory and applications* (Oxford, Oxford University Press, 2011).
- [16] H. Van Amerongen, L. Valkunas and R. van Grondelle, *Photosynthetic excitons* (Singapore, World Scientific, 2000), p. 77.
- [17] Y. Mino and G. R. Fleming, *Chem. Phys.* **275**, 355 (2002).
- [18] G. Raszewski, W. Saenger and T. Renger, *Biophys. J.* **88**, 9868 (2005).
- [19] G. Raszewski and T. Renger, *J. Am. Chem. Soc.* **130**, 4431 (2008).
- [20] Y. Miloslavina, M. Szczepaniak, G. Müller, J. Sander, M. Nowaczyk, M. Rögner and A. R. Holzwarth, *Biochem.* **45**, 2436 (2006).
- [21] N. P. Pawlowicz, M. L. Groot, I. H. M. van Stokkum, J. Breton and R. van Grondelle, *Biophys. J.* **93**, 2732 (2007).
- [22] T. Cardona, A. Sedoud, C. Nicholas and A. W. Rutherford, *Biochimica et Biophysica Acta.* **1817**, 26 (2012).
- [23] I. V. Shelaev, *et al. Journal of Photochemistry and Photobiology B* **104**, 44 (2011).
- [24] G. Sabidussi, *Psychometrika* **31**, 581 (1966).
- [25] L. C. Freeman, *Sociometry* **40**, 35 (1977).
- [26] J. Saramäki, M. Kivelä, J. P. Onnela, K. Kaski and J. Kertész, *Phys. Rev. E* **75**, 027105 (2007).
- [27] E. Ravasz, A. L. Somera, D. A. Mongru, Z. N. Oltvai and A.-L. Barabási, *Science* **297**, 1551 (2002).
- [28] L. Huang, N. Ponomarenko, G. P. Wiederrecht and D. M. Tiede, *Proc. Natl. Acad. Sci. USA* **109**, 4851 (2012).
- [29] T. Renger, R.A. Marcus. *J Phys Chem B.* **106**, 1809 (2002)

Figures

Fig. 1. Flow chart for EET distribution algorithm on an EET network.

Fig. 2. PSII of the *Thermosynechococcus vulcanus*. The figure shows the crystal structure in 1.9Å resolution (3ARC in Protein Data Bank) of pigments (chlorophylls and pheophytins). For convenience, we separated the dimeric structure as two monomeric structures adding the prefix as '1' and '2'. Deep blue color shows reaction center components and linker chlorophylls which are 1610, 1611, 2610 and 2611. (Figure produced with Discovery Studio Visualizer.)

Fig. 3. The EET network of PS II. We used and modified the chlorophyll numbering of PDB entry 3ARC [11]. Node number 1604, 1605, 2604, 2605 represents the special pairs of reaction centers. This graph seeks to display the network topology in a clear way. Two nodes are close if they are have a short network distance between one another (the position is only indirectly related to the spatial configuration of the chlorophylls).

Fig. 5. Scatter plot of the total passed energy versus the eigenvector centrality. Symbols are the same as in Fig. 4.

Fig. 6. Scatter plot of the total passed energy versus the betweenness centrality. The nodes of the reaction center are plotted with a darker shade. Errorbars correspond to one standard error.

Fig. 7. Scatter plot of the total passed energy versus the weighted clustering coefficient.

Symbols are the same as in Fig. 4.