A CONSIDERATION OF THE ORGANIZATION OF CHLOROPLAST PHOTOSYSTEM I*

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ABSTRACT
Procedures that allow the fractionation of a native Photosystem I complex (PSI-200) into several chlorophyll-containing complexes are now available. Two complexes, each containing ~50% of the total chlorophyll of the photosystem, can be isolated. One complex contains both chlorophyll a and b and serves as antenna complex for the reaction center while the reaction center complex contains 100 Chl a molecules per P700 and has 7 different polypeptides. Only two of the latter (62 and 58 kDa) contain chlorophyll a and these can be isolated as the photochemically active CPI complex. Based on these fractionation methods, a model that describes the overall organization of the chlorophyll in Photosystem I is presented.

1. INTRODUCTION
The recent isolation of three highly resolved thylakoid membrane complexes (PSI, PSII, and the cytochrome bc-f complex) (2,7,13) in functionally active form has allowed for detailed studies of structure-function relations in vitro (8). In the case of the case of PSI, Mullet et al (13), described the purification of a "native" PSI complex that retains the spectral properties of PSI in vivo. In studies of this complex, it has been found that there is chlorophyll b associated with PSI as well as with PSII and that this pigment is present in a specific PSI antenna complex, known as LHCPI (5,10). The native PSI complex has also been used to examine the structural organization of the polypeptide subunits in the complex as well as in thylakoid membranes (15). In the present review, the chlorophyll proteins of PSI are considered in greater detail. Based on the fractionation of the native complex into several resolved chlorophyll protein complexes, the overall organization of Photosystem I is considered and a model describing the photosystem is presented.

2. REVIEW OF RESULTS AND DESCRIPTION OF A MODEL OF PSI
A flow-diagram for the fractionation of the chlorophyll-protein complexes of PSI from spinach thylakoids is shown in Fig. 1.

*Dedicated to the memory of Warren Butler, who was both a friend and a colleague.
The starting complex, PSI-200, has ~200 Chl molecules per P700, contains Chl a and Chl b (Chl a/b ~5-6) and has approximately 10 polypeptide subunits [10,13]. Subsequent fractionation separates this complex into two chlorophyll-containing complexes, one which contains the photochemical reaction center (PSI-100) and the second which contains a Chl a/b light-harvesting antenna complex (16). The reaction center complex contains ~100 Chl/P700 and has seven major polypeptides. This fraction still contains the entire PSI primary electron acceptor complex, based on EPR measurements at cryogenic temperature (3), and is able to utilize either reduced plastocyanin or DCPIP as electron donors in the photoreduction of NADP. The antenna complex contains three polypeptides of molecular weights 23, 22 and 20 kDa and has been fractionated into two chlorophyll-protein complexes: LHCPIa and LHCPIb (9). These have similar Chl a/b ratios, but differ in polypeptide composition. It should be stressed that the separation of PSI-200 into these two chlorophyll-containing complexes is essentially quantitative in that little free chlorophyll is dissociated by the procedure, and the recovery of chlorophyll in each fraction is approximately 50%.

While PSI-100 is a relatively simple preparation in terms of polypeptide composition, it is possible to fractionate it further to separate the reaction center polypeptides from the low-molecular weight polypeptides in the preparation and obtain a photochemically active fraction known as CPI. This is accomplished by SDS treatment (17). In this case, P700 photoreduction activity has been observed under steady-state illumination even though the bound iron-sulfur centers associated with the stable primary electron acceptor complex are absent. Presumably the early electron acceptors, A₀ and/or A₁, are present in CPI although documentation of this is not complete. CPI has the simplest polypeptide composition of any photochemically active PSI fraction: only the 62 and 58 kDa subunits are present (17). However, the Chl/P700 ratio of 100/1 is the same as in the PSI-100 fraction. This demonstrates that all the chlorophyll a in CPI as well as in PSI-100 is localized in the high-molecular weight subunits, with no chlorophyll in the lower molecular weight subunits, since these are totally absent in CPI. This characterization of CPI also localizes P700 in the high-molecular weight subunits.

The separation of the LHCPI antenna complex into two chlorophyll-con-