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Bicarbonate binding to the water-oxidizing complex in the photosystem II. A Fourier transform infrared spectroscopy study

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Abstract The light-induced Fourier transform infrared difference (FT-IR) spectrum originating from the donor side of O_2-evolving photosystem (PS) II was obtained in non-depleted and CO_2-depleted PSII membrane preparations. The observed spectrum free of contributions from the acceptor side signals was achieved by employing 2 mM/18 mM ferri-/ferrocyanide as a redox couple. This spectrum showed main positive bands at 1589 and 1365 cm^{-1} and negative bands at 1560, 1541, 1522 and 1507 cm^{-1}. CO-depleted PSII preparations showed a quite different spectrum. The main positive and negative bands disappeared after depletion of bicarbonate. The addition of bicarbonate partially restored those bands again. Comparison between difference FT-IR spectra of untreated and bicarbonate-depleted PSII membranes indicated that the positive bands at 1589 and 1365 cm^{-1} can be assigned to COO^- stretching modes from bicarbonate. The higher frequency corresponds to u_{as} (COO^-) and the lower frequency to u_s (COO^-). ^{13}C-Labeling FT-IR measurements confirmed these findings and also suggested that the negative band at 1560 cm^{-1} can be ascribed to u_{as} (COO^-). The data are discussed in the framework of the suggestion that bicarbonate can be a ligand to the Mn-containing water-oxidizing complex of PSII.

Key words: Photosystem II; Bicarbonate; Donor side; Fourier transform; Infrared spectroscopy

1. Introduction

Bicarbonate is known to be required for the maximal activity of photosystem (PS) II [1,2]. However, the interpretation of the stimulating effect of bicarbonate on PSII activity and its specific binding site still remain unclear. In the early 1970s the water-oxidizing side of PSII was considered to be the acting site of bicarbonate [3,4]. Later the proposal of bicarbonate binding at the acceptor side of PSII between Q_A and Q_B, the primary and secondary plastoquinone electron acceptors, was supported by numerous experimental data [1,2]. Recently, bicarbonate requirement for the donor side of PSII was shown [5–9]. It was suggested that bicarbonate takes part in the formation of the Mn cluster capable of water oxidation as an obligatory ligand or through modification of the binding site(s) of Mn [5–9]. Recently, we have provided evidence for bicarbonate requirement during re-assembly of the Mn-containing center capable of water oxidation and showed that bicarbonate is an essential constituent of the water-oxidizing complex (WOC) [10].

The structure of the Mn cluster has been studied mainly by means of X-ray absorption and electron paramagnetic resonance (EPR) spectroscopies, both of which detect signals directly from Mn ions. At present, the most probable structure model of the Mn cluster is a tetranuclear cluster in which the Mn ions are connected by oxo and carboxylate bridges [11]. Fourier transform infrared (FT-IR) difference spectroscopy is a powerful method to investigate the structures of proteins and cofactors in the active site of a large protein complex [12]. In the field of photosynthesis, light-induced FT-IR difference spectra of photochemical intermediates were obtained for bacterial reaction centers (RCs) [13–16] and higher plant photosystems [17–20].

Noguchi et al. [21] investigated the structure of the Mn cluster in O_2-evolving PSII membranes using this technique. They observed the difference spectrum only due to the S_1 to S_2 transition which reflected the changes in vibrational modes of ligands of the redox-active Mn ions and/or the conformational changes of proteins. Based on these findings they suggested that FT-IR difference spectroscopy is a valid method to investigate the structure of the Mn cluster and O_2-evolving mechanisms. Thus, we have used FT-IR difference spectroscopy in order to investigate the role of bicarbonate in the WOC of PSII.

2. Materials and methods

2.1. Preparation of oxygenic and non-oxygenic PSII membranes

Oxygenic PSII membranes were isolated from spinach by the method of Berthold et al. [22] with the modifications of Yruela et al. [23]. Samples were resuspended in 0.4 M sucrose, 15 mM NaCl, 5 mM $CaCl_2$ and 50 mM MES-NaOH, pH 6.0, frozen and stored at −80°C until use. This sample exhibited oxygen evolution rates of 520 μmol O_2/mg Chl/h in the presence of 0.5 mM 2,6-dichloro-*p*-benzoquinone (DCBQ) as artificial electron acceptor. Removal of bicarbonate from PSII membranes was achieved by a 250-fold dilution of concentrated PSII preparations with a medium previously depleted of endogenous bicarbonate by means of 60-min flushing with CO_2-depleted air and N_2. The CO_2-depleted air was prepared by passing through a solution of 50% NaOH. The final concentration of the medium was 0.4 M sucrose, 20 mM NaCl, 5 mM $CaCl_2$, 50 mM MES-NaOH (pH 6.0) [10]. The sample was subsequently incubated in this medium at a Chl concentration of 50 μg/ml for 2 h at 4°C in the dark and tightly

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Abbreviations: Chl, chlorophyll; D1, polypeptide of PSII reaction center; DCBQ, 2,6-dichlorobenzoquinone; FT-IR, Fourier transform infrared spectroscopy; MES, 2-(*N*-morpholino)ethanesulfonic acid; OEC, oxygen-evolving complex; Pheo, pheophytin, the primary electron acceptor; P680, the primary electron donor; PSII, photosystem II; Q_A and Q_B, primary and secondary plastoquinone electron acceptors of PSII; RC, reaction center; WOC, water-oxidizing complex

The authors would like to dedicate this paper to the memory of José V. Ibarra.

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closed. After that the PSII preparation was washed twice with the same buffer in the absence or presence of 1 mM $NaHCO_3$. The centrifugations were done at 38 000×*g* for 25 min. The pellets were resuspended in the same buffer with or without $NaHCO_3$. For exchange with isotopic [^{13}C]bicarbonate, the samples resuspended in buffer at pH 6.0 were incubated in the presence of 0.1 M [^{13}C]bicarbonate for 1 h at 4°C followed by two washing steps in the assay medium at pH 5.5 containing 20 mM [^{13}C]bicarbonate.

2.2. Oxygen evolution activity

Oxygen evolution activity was measured in a closed 3-ml cell using a Clark-type electrode under continuous illumination with white light (2500 μE/m^2/s) in the presence of 0.5 mM DCBQ dissolved in ethanol. Samples were resuspended in non-depleted and CO_2-depleted medium containing 0.4 M sucrose, 15 mM NaCl, 5 mM $CaCl_2$ and 50 mM MES-NaOH, pH 5.5 in the absence or presence of $NaHCO_3$ (for more details see figure legends). Oxygen evolution upon the first 1-min illumination by continuous actinic light was measured.

2.3. Chlorophyll fluorescence measurements

Chl fluorescence yields were measured by using a modulated fluorescence technique (PAM fluorometer, model KS1101, H. Walz, Effeltrich, Germany). The intensity of the modulated measuring light was 12 μE/m^2/s and the red actinic light approximately 700 μE/m^2/s. For measurements samples were resuspended in 0.4 M sucrose, 15 mM NaCl, 5 mM $CaCl_2$ and 50 mM MES-NaOH, pH 5.5 at a Chl concentration of 20 μg/ml.

2.4. FT-IR measurements

FT-IR spectra were measured on a Nicolet Magna 550 spectrophotometer equipped with an DGTS detector. For measurements the PSII samples, resuspended in 0.4 M sucrose, 15 mM NaCl, 5 mM $CaCl_2$ and 50 mM MES-NaOH, pH 5.5, with and without $NaHCO_3$ (for details see figure legends), were supplemented with 2 mM/18 mM potassium ferri-/ferrocyanide in order to allow every oxygen-evolving complex to relax to the thermally stable S_1 state [24,25]. The E_h value of the MES buffer (pH 5.5) including 2 mM/18 mM potassium ferri-/ferrocyanide was 364 mV at which the non-heme iron should stay reduced at pH 5.5 [26]. After that samples were centrifuged for 3–4 min in a microfuge and the resulting pellet pressed between a pair of BaF_2 plates. The absorbance at 1656 cm^{-1} which is due to amide I and some contribution by H_2O absorption was maintained between 0.5 and 1.0 for all the samples. Light-induced difference spectra were obtained by subtracting the two spectra taken before and after illumination. Each spectrum was an average of 200 scans and the spectral resolution was 4 cm^{-1}. Light illumination was performed at room temperature with red actinic light from a 150-W tungsten lamp powered with a stabilized power supply through several heat-cut filters (KG1 Schott infrared filters) plus a 620 nm cut-off filter. For the final data the characteristic FT-IR spectrum of water vapor was subtracted from the all difference spectra to cancel the water band contributions. For this substraction spectra were normalized at about 2200 cm^{-1}. The water vapor was measured from the empty cavity of the spectrometer.

3. Results

Fig. 1A shows the light-induced FT-IR spectra in the 1600–1300 cm^{-1} region of PSII membranes at pH 5.5 in the presence of 2 mM/18 mM ferri-/ferrocyanide. This spectrum solely exhibits photoinduced transitions in the donor side of PSII [21,24,27]. In this case ferricyanide acts as an exogenous electron acceptor, as shown in the inset (Fig. 1A). The negative band at 2117 cm^{-1} and the positive band at 2036 cm^{-1} (Fig. 1A, inset) are assignable to the CN stretching modes of ferricyanide and ferrocyanide, respectively [21], indicating that ferricyanide accepts an electron to become ferrocyanide. The absence of a band at 1478 cm^{-1} associated with Q_A^- [21] confirms that this spectrum involves no contribution from acceptor side signals. Thus, acceptor side quinone signals were eliminated and redox reactions of the non-heme iron were also suppressed by controlling the redox potential in the sample by the ferri-/ferrocyanide couple (1:9) at pH 5.5 [27]. The magnitude of spectral changes in our experiments is about 10^{-3}–10^{-4}, i.e. much higher than those published by Noguchi et al. [21,27], since we use saturating continuous light instead of a single flash. In the 1600–1400 cm^{-1} spectral region negative bands at 1560, 1541, 1522, 1507, 1421 and 1402 cm^{-1} and positive bands at 1589, 1550, 1531, 1502, 1438 and 1365 cm^{-1} were observed in control PSII membranes (Fig. 1A, solid line). The shape of this spectrum was drastically

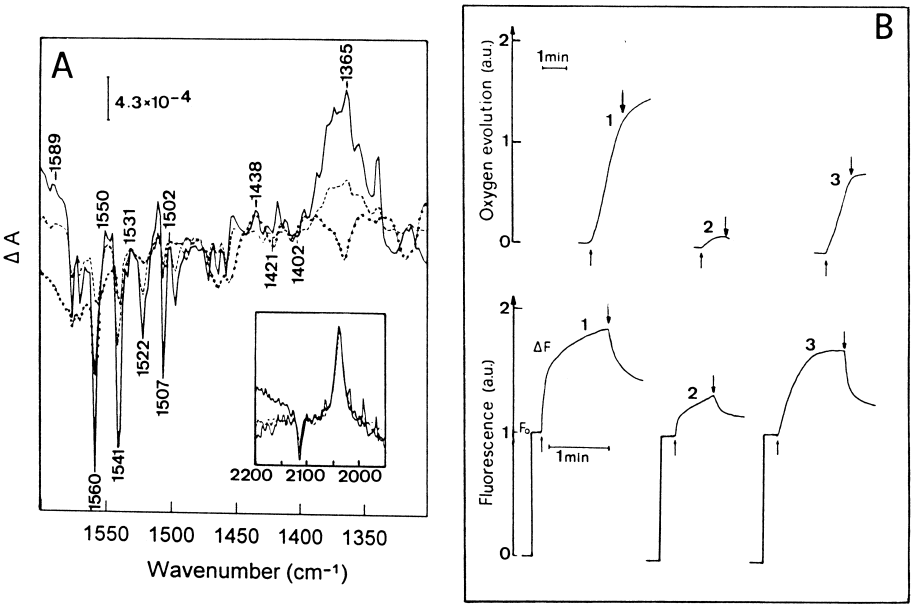

Fig. 1. A: Light-induced FT-IR difference spectra of PSII membranes at pH 5.5. Control experiment (solid line); bicarbonate-depleted medium (dotted line); after addition of 1 mM $NaHCO_3$ to the bicarbonate-depleted medium (dashed line). Samples were illuminated with continuous light at room temperature in the presence of 2 mM/18 mM ferri-/ferrocyanide. Spectra were normalized at the CN stretching region of ferri- and ferrocyanide as shown in the inset. B: Kinetics of oxygen evolution activity and photoinduced changes of chlorophyll fluorescence yield in PSII membranes in control medium (1) and in bicarbonate-depleted medium with no addition (2) and after addition of 1 mM $NaHCO_3$ (3).

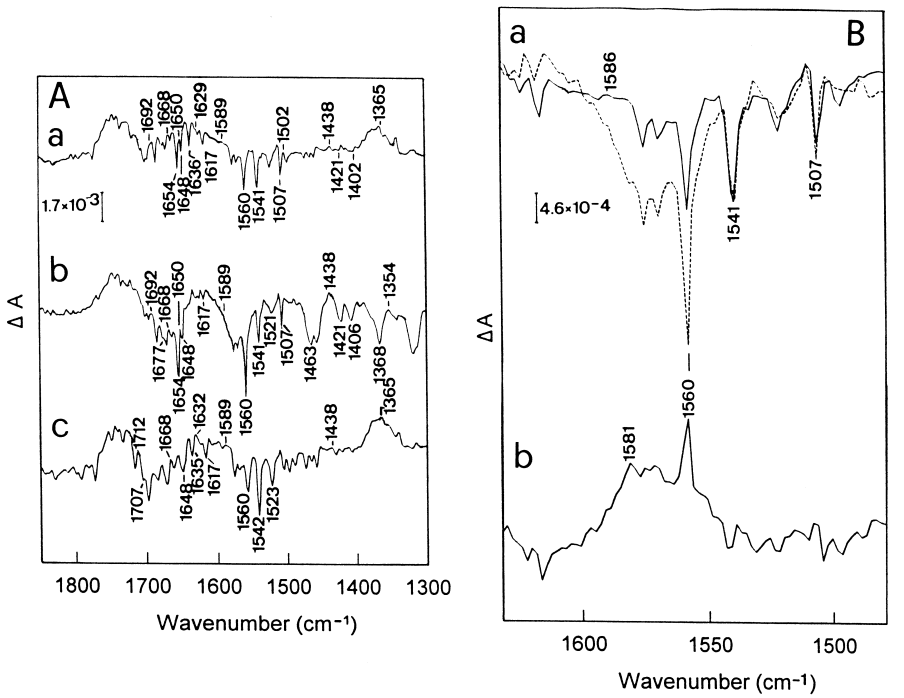

Fig. 2. A: Light-induced FT-IR difference spectra of PSII membranes in control medium (a) and in bicarbonate-depleted medium with no addition (b) and after addition of 1 mM $NaHCO_3$ (c) at pH 5.5. Spectra were normalized in the unaffected 1750–1700 cm^{-1} spectral region. B: Expanded view (1640–1480 cm^{-1}) of the light-induced FT-IR difference spectra of PSII membranes in non-depleted bicarbonate medium (solid line) and after depletion of bicarbonate (dashed line) (a); double difference spectrum (b) by subtracting of the FT-IR difference spectrum in bicarbonate-depleted buffer (a, dashed line) from that in non-depleted bicarbonate buffer (a, solid line). The experimental set-up was as described in Fig. 1A.

modified when bicarbonate was removed from the medium (Fig. 1A, dotted line). It is clear that the main positive bands at 1589 and 1365 cm^{-1} are not present and the intensity of the negative bands at 1560, 1541 and 1522 cm^{-1} is greatly reduced. On the other hand, the addition of bicarbonate to the CO_2-depleted PSII samples partially restored the spectral features of the FT-IR spectrum (Fig. 1A, dashed line). The observed differences in the spectra cannot be attributed to some local pH shifts since the bicarbonate concentration was by two orders lower than that of buffer. Spectra in Fig. 1A were normalized in the ferrocyanide band (2036 cm^{-1}) as shown in the inset. In these conditions the restoration of the main bands was not complete. For example, a 37% restoration of the broad band at 1365 cm^{-1} with bicarbonate addition was achieved. The fact that the characteristic bands of the PSII donor side disappeared and reappeared after depletion and addition of bicarbonate, respectively, suggests that these bands could be assigned to COO^- stretching modes of the bicarbonate. The broad shape of some of these bands may be due to the strong band overlapping in this spectral region. Measurements in this spectral region are difficult due to water vapor contribution because its spectrum has a number of sharp bands in the 1500–1800 cm^{-1} region; however, this contribution was eliminated by subtraction (see Section 2). On the other hand, the main band at 1364 cm^{-1} is far from the water bands.

In order to examine the bicarbonate effect on the photosynthetic activity of PSII oxygen evolution and chlorophyll-modulated fluorescence (Fig. 1B) were measured in the same experimental conditions as in Fig. 1A. Oxygen evolution was measured during the first 1-min illumination by continuous actinic light. PSII membranes under the control conditions exhibited an oxygen evolution rate of 520 μmol O_2/mg Chl// h using DCBQ as artificial electron acceptor. The oxygen evolution activity decreased drastically (up to 81% decrease) when PSII membranes were washed and resuspended in CO-depleted buffer (Fig. 1B, line 2) compared with the control (Fig. 1B, line 1). However, the addition of bicarbonate stimulated the water oxidation activity again (Fig. 1B, line 3). The oxygen evolution activity increased up to 60% compared to the control, this means a 41% restoration which is consistent with that of Fig. 1A, dashed line. These results indicate that bicarbonate restores the capacity to evolve oxygen. Similar results were obtained using chlorophyll-modulated fluorescence measurements (Fig. 1B). Chlorophyll fluorescence can be used as an intrinsic sensor of photosynthetic activity [28]. The absorption of a quantum of light by the PSII RC results in a fast charge separation between the primary electron donor, P680, and the primary electron acceptor, Pheo. This light-induced charge separation process initiates the transport of reducing equivalents from the PSII RC to the plastoquinone pool via a specially organized complex of two bound plastoquinones, Q_A and Q_B. Chlorophyll fluorescence depends upon the redox state of Q_A being minimal (F_o) when this quinone is fully oxidized. However, when Q_A is fully reduced a maximum fluorescence yield (F_m) is obtained. Fig. 1B shows that the bicarbonate addition is also required for maximum reactivation of ΔF ($\Delta F = F_m - F_o$) related to photoreduction of Q_A in the bicarbonate-depleted medium. Thus, the data showed that the reactivation of ΔF upon addition of bicarbonate is accompanied by restoration of oxygen evolution. This suggests that bicarbonate is required to activate the WOC in agreement with our previous results [5–10].

In Fig. 2 the light-induced FT-IR spectra shown in Fig. 1

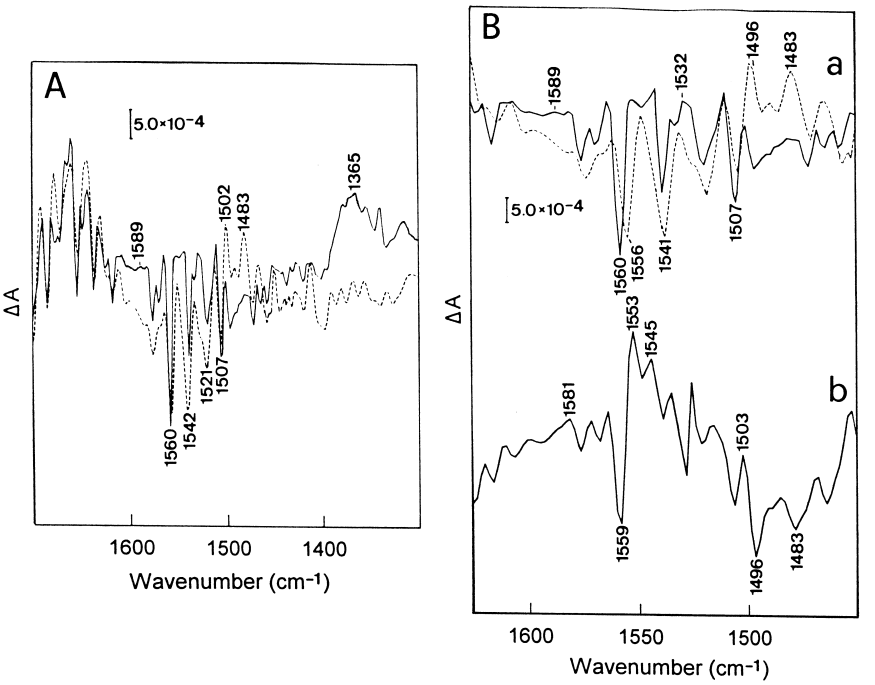

Fig. 3. A: Light-induced FT-IR difference spectra in the 1650–1350 cm^{-1} region of PSII membranes in control medium (solid line) and in the presence of 1 mM [^{13}C]$NaHCO_3$ (dashed line) in the medium at pH 5.5. Spectra were normalized in the 1750–1700 cm^{-1} region. B: (a) Expanded view (1640–1480 cm^{-1} region) of the light-induced FT-IR difference spectra of PSII membranes in control medium (solid line) and in the presence of 1 mM [^{13}C]$NaHCO_3$ (dashed line) in the medium at pH 5.5; (b) double difference spectrum by subtracting the FT-IR difference spectrum in the presence of [^{13}C]$NaHCO_3$ buffer (a, dashed line) from that in the presence of unlabeled bicarbonate buffer (a, solid line). Experimental conditions were as described in Fig. 1A.

were normalized in the unaffected 1760–1720 cm^{-1} spectral region. The normalized spectra also showed that the main bands affected by the depletion of bicarbonate were those at 1589 and 1365 cm^{-1} (Fig. 2A, a and b). For a better visualization an expanded view of the 1640–1480 cm^{-1} region of FT-IR spectra normalized in the 1760–1720 cm^{-1} region in the presence and absence of bicarbonate is shown in Fig. 2B,a. The bands at 1541 and 1507 cm^{-1} were unaffected after bicarbonate depletion. However, it is clear in this superimposed view that the broad band at around 1589 cm^{-1} disappeared in the CO_2-depleted preparations. Since many bands overlap in this region, the spectral changes are more easily seen in the double difference FT-IR spectrum (Fig. 2B,b) obtained by subtracting the spectrum in the bicarbonate-depleted medium (Fig. 2B,a, dashed line) from that in non-depleted medium (Fig. 2B,a, solid line). As expected a broad positive band between 1590–1540 cm^{-1} was observed (Fig. 2B,b). The contributions of two components with maxima at 1581 and 1560 cm^{-1} are apparent. These two maxima should correspond to the disappearance of the positive band at 1589 cm^{-1} and an intensity change of the 1560 cm^{-1} band after bicarbonate depletion.

To determine the specific contributions of bicarbonate we studied the effect of labeling with isotopic [^{13}C]bicarbonate on the light-induced FT-IR spectra. Fig. 3 compares the donor side FT-IR difference spectra in untreated PSII preparations at pH 5.5 in the presence of [^{12}C]bicarbonate (solid line) and [^{13}C]bicarbonate (dashed line). The spectra were quite similar above 1650 cm^{-1}; however, they were influenced by isotope labeling below this frequency. In particular the main broad positive bands at around 1589 and 1365 cm^{-1} disappeared and some changes at 1600–1400 cm^{-1} were observed. These results are better visualized in the expanded view of the 1650-1400 cm^{-1} region of FT-IR spectra normalized in the 1760–1720 cm^{-1} region in the presence and absence of bicarbonate (Fig. 3B,a). The strong overlapping band described in the 1650–1400 cm^{-1} region [24,25,29] and observed in Fig. 3A masks bicarbonate contributions. Fig. 3B,b shows the result of subtracting the FT-IR spectrum of PSII membranes in the presence of [^{13}C]bicarbonate (Fig. 3B,a, dashed line) from that in the presence of non-isotopic bicarbonate (Fig. 3B,a, solid line). This difference spectrum should exhibit only the modes sensitive to isotopic labeling. Two sharp bands, one negative at 1559 cm^{-1} and another positive at 1553 cm^{-1}, were observed. The band at 1559 cm^{-1} corresponds to the negative band observed at 1560 cm^{-1} in the unlabeled donor side difference FT-IR spectrum (Fig. 3B,a, solid line). This band was clearly shifted down 5 cm^{-1} upon [^{13}C]bicarbonate substitution, resulting in a new position at 1556 cm^{-1} (Fig. 3B,a, dashed line). The positive band at 1553 cm^{-1} confirmed this assignment. Thus the 1560 and 1556 cm^{-1} bands may be assigned to modes of [^{12}C]- and [^{13}C]bicarbonate, respectively. The [^{12}C]bicarbonate minus [^{13}C]bicarbonate spectrum (Fig. 3B,b) also shows broad positive and negative bands at 1600–1540 cm^{-1} and 1532–1450 cm^{-1}, respectively. In those regions the assignment of bicarbonate modes is complicated due to the overlap with strong signals from proteins in each individual FT-IR spectrum [24,25,29]. Since the ^{13}C labeling results in downshifts of bicarbonate bands [29] the negative band at around 1532–1450 cm^{-1} may be interpreted as the downshift upon [^{13}C]bicarbonate substitution of the positive broad band between 1600–1540 cm^{-1} (Fib. 3B,b). Furthermore, the positive band at 1589 cm^{-1} in the [^{12}C]bicarbonate spectrum could be tentatively assigned to a

mode of [^{12}C]bicarbonate. The corresponding mode of [^{13}C]bicarbonate could be the band at around 1496 cm^{-1}. It is known that only frequency downshifts less than 60 cm^{-1} are expected for modes of bicarbonate upon ^{13}C labeling in the 1800–1000 cm^{-1} spectral region [29]. Our data indicate a 93 cm^{-1} shift, however, it should be considered that the indicated maxima may not correspond to the exact frequency position of the [^{12}C]bicarbonate modes due to band overlapping.

4. Discussion

Recently, we have shown that restoration of photoinduced electron flow and oxygen evolution with Mn^{2+} in Mn-depleted PSII membrane preparations is considerably increased when bicarbonate is added to a bicarbonate-depleted medium. We concluded, therefore, that bicarbonate is an essential constituent of the WOC of PSII which is important for assembling and maintaining it in the functionally active state. For that, some frequencies in the donor side difference FT-IR spectra can be assigned to bicarbonate modes. The FT-IR difference spectra in the presence and absence of bicarbonate showed clear differences that could not be explained simply by degradation of a sample since removal of bicarbonate was reversible. The main frequencies at 1589 and 1365 cm^{-1} in the light-induced difference FT-IR spectrum of untreated PSII membranes were modified after bicarbonate depletion indicating that bicarbonate modes make a contribution to these bands. Comparison between donor side FT-IR difference spectra in the presence and absence of bicarbonate showed that the positive broad bands at 1589 and 1365 cm^{-1} can be tentatively assigned to asymmetric and symmetric COO^- stretching modes of bicarbonate, respectively. Furthermore, the ^{13}C-labeled FT-IR measurements showed downshifts of the 1589 and 1560 cm^{-1} bands. These data confirmed the above results and also indicated that the negative band at 1560 cm^{-1} can be assigned to the asymmetric stretching mode of bicarbonate. Previously Noguchi et al. [24] assigned similar bands at 1587, 1560, 1365 and 1403 cm^{-1} to the asymmetric (higher frequency bands) and symmetric (lower frequency bands) COO^- stretching modes of a certain carboxylate group in Asp, Glu or the C-termini of the surrounding protein, which bridge between Mn^{2+} and Ca^{2+}. These assignments were made based on the comparison between the two S_2/S_1 FT-IR difference spectra using untreated and Ca^{2+}-depleted PSII membranes. It is known that Ca^{2+} is an indispensable cofactor for photosynthetic oxygen evolution [30]. The binding site of Ca^{2+} in PSII has not been identified yet although Ca^{2+} is thought to be located in the close vicinity of the Mn cluster [24,30]. On the other hand, it has been suggested that bicarbonate takes part in the formation of the Mn center capable of water oxidation as an obligatory ligand [5,6,8,10]. Considering that Ca^{2+} depletion can modify the bicarbonate binding site in the WOC, the above assignment of the bands at 1587, 1560 and 1364 cm^{-1} can be reconsidered. Since these frequencies were modified after bicarbonate depletion and [^{13}C]bicarbonate labeling, our results further indicate that they can be ascribed to stretching modes of the COO^- group of bicarbonate. The fact that no change is observed at 1403 cm^{-1} may be due to the low intensity of this band. Thus, it could be possible that bicarbonate acts as a bridging ligand between the redox-active Mn and Ca^{2+}. These findings are also consistent with our previous proposal of bicarbonate as a ligand of Mn [5,6,8,10].

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