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INACTIVATION OF CHLOROPLAST PHOTOSYNTHETIC ELECTRON-TRANSPORT ACTIVITY BY Ni^{2+}

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Ni^{2+} inhibits electron-transport activity of isolated barley chloroplasts and this inhibition of electron transport by Ni^{2+} is distinctly different from other heavy metal ion (e.g., Pb^{2+}, Cd^{2+}, Zn^{2+})-induced inhibition of chloroplast function. Ni^{2+} inactivates Photosystem II (PS II) activity at a lower concentration than that required for the same extent of inhibition of Photosystem I (PS I)-mediated electron flow. Ni^{2+} induces changes in chlorophyll *a* (Chl *a*) emission characteristics and brings about a lowering of the Chl *a* fluorescence yield, and this lowering of Chl *a* fluorescence intensity is not relieved by the exogenously supplied electron donor NH_2OH which donates electrons very close to the PS II reaction centres. Immobilization of the chloroplast membrane structure with glutaraldehyde fails to arrest the Ni^{2+}-induced loss of PS II activity. Also, Ni^{2+}-treated chloroplasts do not regain the ability to photoreduce 2,6-dichlorophenolindophenol even after washing of chloroplasts with buffer. These results indicate that unlike Zn^{2+} or Pb^{2+}, Ni^{2+} induces alterations in the chloroplast photosynthetic apparatus resulting in an irreversible loss of electron-transport activity.

Introduction

Heavy metal ions such as Pb^{2+}, Cd^{2+}, Hg^{2+}, Zn^{2+}, Ni^{2+} and Co^{2+}, when present at an elevated level in the environment, are taken up by root systems and are accumulated in different parts of plants, thereby leading to reduced growth and impaired metabolism [1].

Many investigators have studied the effect of heavy metal ions such as Pb^{2+}, Cd^{2+} and Hg^{2+} on the electron transport of isolated chloroplasts to ascertain the mode of action of these ions on the primary photosynthetic electron-transport processes of photosynthesis [2–6]. These results suggest that many carriers in the electron-transport chain are specifically affected by the presence of heavy metal ions [6]. It is also of interest to note that the oxidizing side of the electron-transport chain of PS II is extremely susceptible to heavy metal ion inhibition [2–4]. Besides Mn^{2+}, which is known to be intimately connected with the O_2-evolving system [7], Cu^{2+} seems to be associated with the electron-transport carriers located in the oxidizing side of PS II [8]. Thus, it is possible that many of the heavy metal ions affect electron flow from H_2O to PS II reaction centres by altering the interaction of metal ions with the carriers [9].

Some of the heavy metal ions, such as Ni^{2+}, Co^{2+} and Zn^{2+} which are required as trace elements for plant mineral nutrition, occur in some places at high concentrations, and when taken up by plants impair plant growth and development. Only a few studies have been made on the effect of some of these essential heavy metal ions on the photosynthetic electron-transport processes in isolated chloroplasts [10].

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Abbreviations: PS, photosystem; Chl, chlorophyll; DCIP, 2,6-dichlorophenolindophenol; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; Hepes, *N*-2-hydroxyethylpiperazine-*N'*-2-ethanesulphonic acid.

Recently, it has been shown that Zn^{2+} inhibits the electron transport of isolated chloroplasts at the oxidizing side of PS II and this inhibition site is localized close to the site where NH_2OH, an artificial electron donor, feeds electrons to PS II [10]. Furthermore, the Zn^{2+} inhibition could not be arrested by fixation of chloroplasts with glutaraldehyde [11] although it could be relieved by washing [10].

The present work aims at investigating the effect of another trace metal ion. Ni^{2+}, on the photosynthetic electron-transport processes of isolated barley and spinach chloroplasts. The results indicate that Ni^{2+} at millimolar concentrations inactivates PS II- and PS I-dependent electron transport of isolated chloroplasts and this inactivation, unlike that of Zn^{2+} or Pb^{2+} [4], is due to irreversible structural changes in the membrane matrix of the photosynthetic apparatus.

Materials and Methods

Plant material. Barley (*Hordeum vulgare* L. CV 1B 65) was grown on petri plates, fitted with water-soaked filter sheets at 25°C under continuous illumination as described previously [7]. Fully expanded primary leaves of 11–13-day-old healthy seedlings were selected for isolation of chloroplasts. For some experiments spinach leaves were also used.

Chloroplast isolation. Chloroplasts were isolated as described previously [7]. The grinding medium consisted of 0.5 M sucrose, 10 mM NaCl and 20 mM Hepes-NaOH buffer (pH 7.6). The same grinding medium was also used for suspending chloroplasts. Chlorophyll was determined according to the method of Arnon [12].

Chloroplast assays. The electron-transport activities of chloroplasts were determined by three basic assays. Firstly, electron transport through PS II was determined by photoreduction of DCIP, measured spectrophotometrically [10], and DCIP-supported O_2 evolution, monitored polarographically [11]. For spectrophotometric assay, 3 ml of assay medium consisted of 50 mM Hepes-NaOH buffer (pH 7.0), 10 mM NaCl, 2 mM $MgCl_2$, 30 μM DCIP. Chloroplasts were added to the above reaction mixture at a concentration of 15 μg Chl/ml. The detailed assay procedure has been described elsewhere [10]. DCIP-supported O_2 evolution was measured polarographically by a YSI model 53 Clark-type O_2 electrode connected to a recorder. The reaction mixture for O_2 evolution (3 ml) consisted of 3 mM $MgCl_2$, 10 mM $NaCl_2$, 400 μM DCIP and 50 mM Hepes-NaOH buffer (pH 7.0). Chloroplasts were added to the above reaction mixture to a final concentration of 15 μg Chl. The assay mixture was irradiated with saturating white light (1.0 cal/cm^2 per min) that had been filtered through 10 cm of water.

In the second type of assay, the electron transport through the whole chain of photosynthesis, i.e., from water to methyl viologen, was measured polarographically as O_2 uptake [10]. The assay medium contained 50 mM Hepes, 10 mM NaCl, 2 mM NH_4Cl, 3 mM $MgCl_2$, 1.0 mM NaN_3 and 0.5 mM methyl viologen, adjusted to pH 7.5. Chloroplasts were added to the above reaction mixture to give a final concentration of 100 μg Chl. The light intensity used for irradiation was the same as that above.

In the third type of assay, the electron transport through PS I was also measured polarographically as above except that reduced DCIP was used as the electron donor. Assay conditions were identical to those of the whole-chain assay except that 10 μM DCMU, 1 mM sodium ascrobate and 100 μM DCIP were added to the above reaction mixture.

Chl a luminescence measurement. Chl *a* fluorescence intensity and emission spectra were measured both at room and at liquid nitrogen temperatures. The excitation light (436 nm) was obtained through a monochromator with a mercury lamp as the exciting source. The fluorescence intensity and spectra were measured at 90°C to the direction of exciting light through another monochromator as described previously [10,13]. The Chl *a* fluorescence intensity measured at 686 nm was found to be linear up to a concentration of 40 μg Chl/ml. The chloroplasts were suspended in 30 mM Hepes-NaOH buffer (pH 7.0). The fluorescence data are presented as the relative fluorescence intensity in arbitrary units. Chl *a* fluorescence emission spectra have not been corrected for the efficiency of the spectrofluorometer. However, all the spectra were measured under identical conditions and thus they can be compared [13]. The delayed light emission in the millisecond (1–2 ms) region was measured using a Bacqurel type phosphoroscope. Chloroplasts at a concentration of 4 μg

Chl/ml were suspended in Hepes-NaOH buffer (pH 7.0). Delayed light emission was measured after 5 min of incubation of chloroplasts with $NiCl_2$.

Glutaraldehyde fixation of chloroplasts. Chloroplasts were fixed with glutaraldehyde essentially as described by Zilinskas and Govindjee [14]. The degree of fixation was checked by subjecting chloroplasts to osmotic shock and observation under a microscope as described earlier [11].

Treatment with heavy metal ions. Chloroplast suspensions were incubated with $NiCl_2$ in the dark for the described periods as described in the legends to the figures. Control samples were incubated in the dark at 0°C without Ni^{2+} for comparable lengths of time and the time-dependent loss in activity of control sample was less than 2–3%. All chemicals were of analytical grade and were used without any further purification.

Results

Whole-chain electron transport (H_2O to methyl viologen)

Fig. 1 shows the effect of treatment of chloroplasts with $NiCl_2$ on the whole-chain electron transport of photosynthesis as measured by photoreduction of methyl viologen with H_2O as electron donor. It can be seen that methyl viologen photoreduction and its auto-oxidation-linked O_2 uptake were inhibited to the extent of 70% within 5 min of incubation with 4 mM $NiCl_2$. The extent of inhibition of methyl viologen reduction by Ni^{2+} became maximal after 15 min of incubation of chloroplasts with the metal ions.

PS II-supported DCIP Hill reactions

The assay of the partial chloroplast reaction of PS II was carried out with DCIP as an electron acceptor. Fig. 2 shows the time course of inhibition of DCIP-supported O_2 evolution in chloroplasts incubated with two different concentrations of $NiCl_2$. There was a rapid initial loss of O_2 evolution within 5 min of incubation. The extent of inhibition increased with the increase in concentration of $NiCl_2$. $NiCl_2$ (4 mM) inhibited O_2 evolution by as much as 80% of the initial activity (not shown).

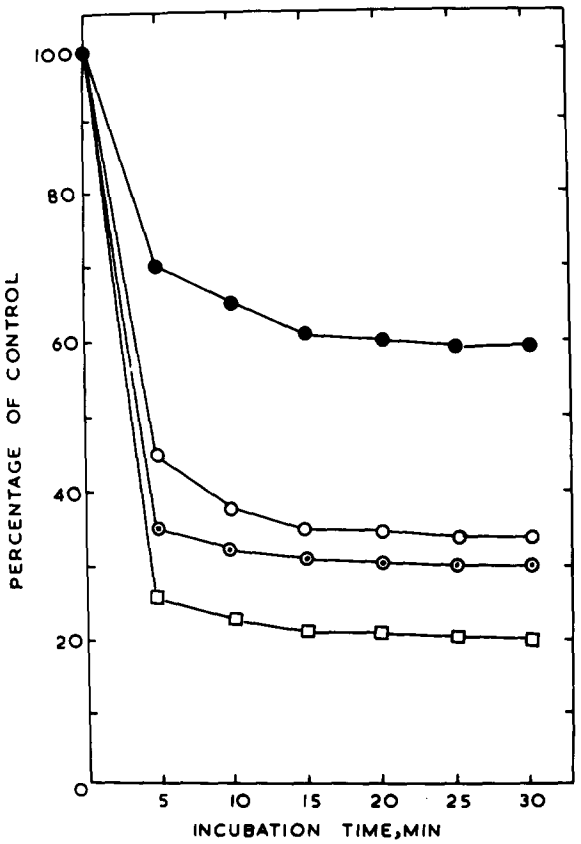


Fig. 1. Time-dependent loss of whole-chain ($H_2O \rightarrow$ methyl viologen) electron-transport activity of barley chloroplasts treated with different concentrations of $NiCl_2$. Chloroplasts were incubated with Ni^{2+} at 0–4°C and aliquots were taken for O_2 uptake measurements; the control rate, without Ni^{2+} (48–50 μmol O_2/mg Chl per h), was set at 100%. Control samples without Ni^{2+} treatment were also incubated in the dark for equivalent times for comparison. The time-dependent loss in controls (incubated without Ni^{2+}) was approx. 2–3%. $NiCl_2$ present at: (●——●) 1, (○——○) 2, (⊙——⊙) 3, (□——□) 4 mM.

PS I-supported electron transport ($DCIPH_2$ to methyl viologen)

Fig. 3 shows the time-dependent loss of PS I-mediated electron transport $DCIPH_2$ to methyl viologen, monitored polarographically as O_2 uptake by Ni^{2+} treatment. Unlike PS II, where 4 mM $NiCl_2$ could cause 80% inactivation, the PS I supported reaction was inhibited, to a similar extent only at a much higher concentration (8 mM) of $NiCl_2$. A low concentration (1 mM) of $NiCl_2$ inhibited the PS I reaction by 30%.

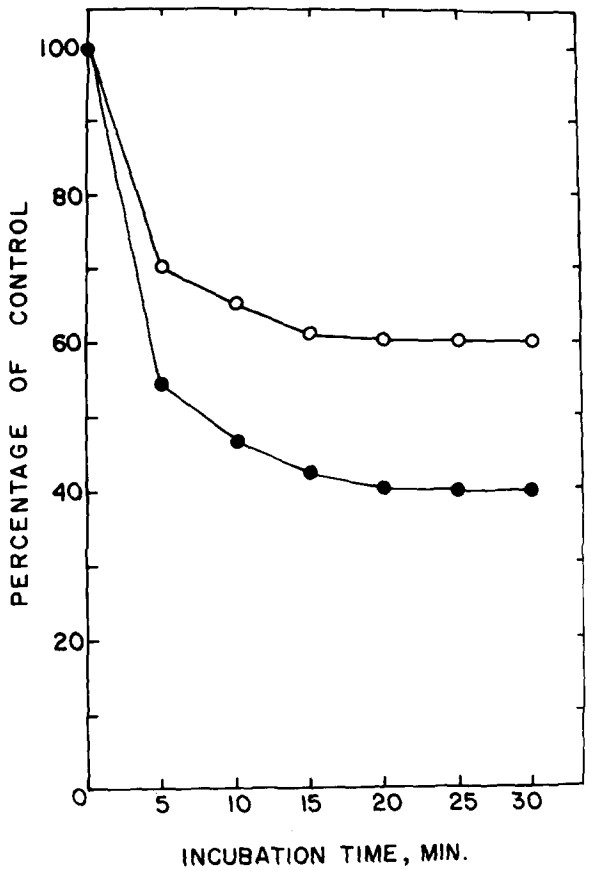


Fig. 2. Time-dependent loss of PS II-mediated DCIP-supported Hill reaction O_2 evolution by two different concentrations of $NiCl_2$. Control rate O_2 evolution (56 μmol/mg Chl per h) was set at 100%. All other details as in Fig. 1. $NiCl_2$ present at: (○——○) 1, (●——●) 2 mM.

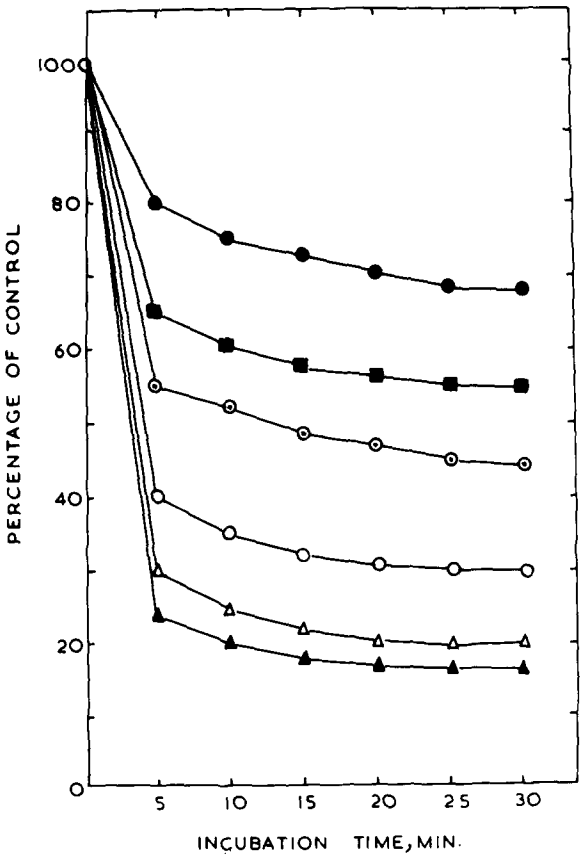


Fig. 3. Effect of addition of various concentrations of $NiCl_2$ on the PS I-mediated ($DCIPH_2 \rightarrow$ methyl viologen) O_2 uptake in barley chloroplasts as a function of time of incubation. 100% rate = 380 μmol/mg Chl per h. Other conditions as in Fig. 1. $NiCl_2$ present at: (●——●) 1, (■——■) 2, (⊙——⊙) 3, (○——○) 4, (△——△) 6, (▲——▲) 8 mM.

Effect of Ni^{2+} treatment on exogenous donor-supported DCIP photoreduction

Fig. 4 compares the extent of inhibition induced by various concentrations of $NiCl_2$ on the whole-chain, PS II- and PS I-mediated electron flow. It is clear that both PS I- and PS II-catalyzed electron flow are inactivated by Ni^{2+}, although that mediated by PS I is comparatively resistant to inactivation at a low concentration (2 mM) of $NiCl_2$. From the above results it is quite clear that Ni^{2+} inhibits photosyn-

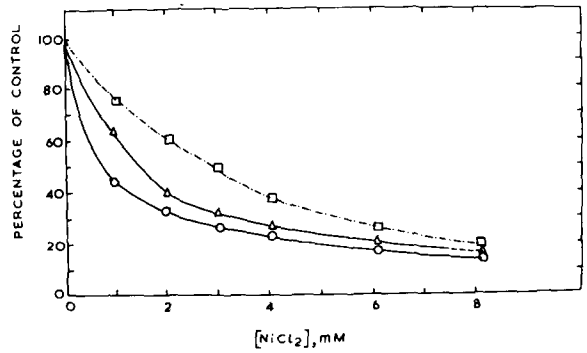


Fig. 4. Effect of varying concentrations of $NiCl_2$ on the whole-chain, PS II-dependent and PS I-dependent electron transport processes in isolated barley chloroplasts. Chloroplasts were incubated for 10 min before assay. Other details as in Figs. 1–3. (○——○) $H_2O \rightarrow$ methyl viologen, (△——△) $H_2O \rightarrow$ DCIP, (□·–·–·–□) $DCIPH_2 \rightarrow$ methyl viologen.

thetic electron transport mediated by both PS II and PS I although PS II is much more sensitive to Ni^{2+} inhibition than PS I. To locate the possible site of inhibition of the PS II reaction, DCIP photoreduction supported by various exogenous electron donors which feed electrons to different sites on the oxidizing side of PSII was measured. The supply of saturating amounts of exogenous electron donors such as $MnCl_2$ (0.3 mM), benzidine (0.5 mM) and NH_2OH (5 mM) to barley chloroplasts preincubated with 2 mM $NiCl_2$ for 15 min could not restore the ability of chloroplasts to photoreduce DCIP (data not shown).

Effect of Ni^{2+} treatment of Chl a fluorescence yield of chloroplasts

Changes in Chl *a* fluorescence intensity are intimately associated with PS II activity and they reflect the redox states of the primary acceptor of PS II [15]. Fig. 5 shows that incubation of chloroplasts with $NiCl_2$ lowers the steady-state level of Chl *a* fluorescence intensity measured at 686 nm (F_{686}). Treatment of chloroplasts with 1 mM $NiCl_2$ lowered the Chl *a* fluorescence level by approx. 60%. There was a very rapid drop in fluorescence level by approx. 60%. This rapid decrease in fluorescence intensity occurred within 1 min of addition of $NiCl_2$ to chloroplast suspensions and any further increase in the incubation period caused only a slight increase in the lowering of fluorescence intensity. Fig. 5A shows that about 35% of the total fluorescence intensity remained unquenched even after long periods (30 min) of incubation with a high concentration (4 mM) of $NiCl_2$. Again, addition of exogenous electron donors, such as $MnCl_2$ and NH_2OH, to Ni^{2+}-treated chloroplasts could not restore the loss of Chl *a* fluorescence intensity to the initial untreated control level (Fig. 5B).

Ni^{2+} also suppressed the delayed light emission which is a good diagnostic indicator of PS II photochemistry [17]. The delayed light emission spectrum did not change upon addition of Ni^{2+} and only the intensity of delayed light emission was lowered; with 0.5 mM $NiCl_2$ the 2 ms delayed light intensity decreased by 71% and with 1 mM $NiCl_2$ the intensity was lowered to 86% of that of the untreated sample. The suppression of delayed light emission suggests that Ni^{2+} affects the back recombinations between

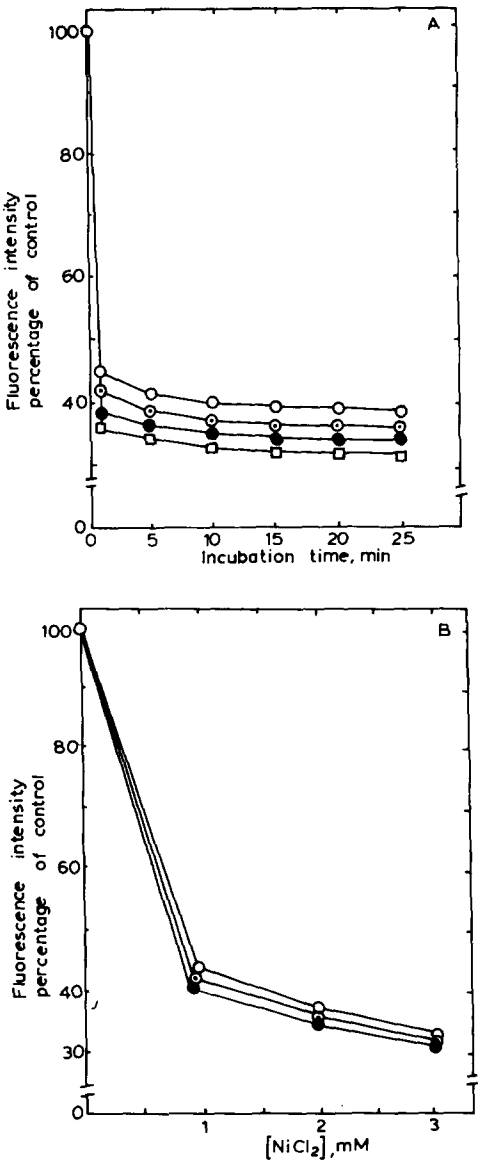
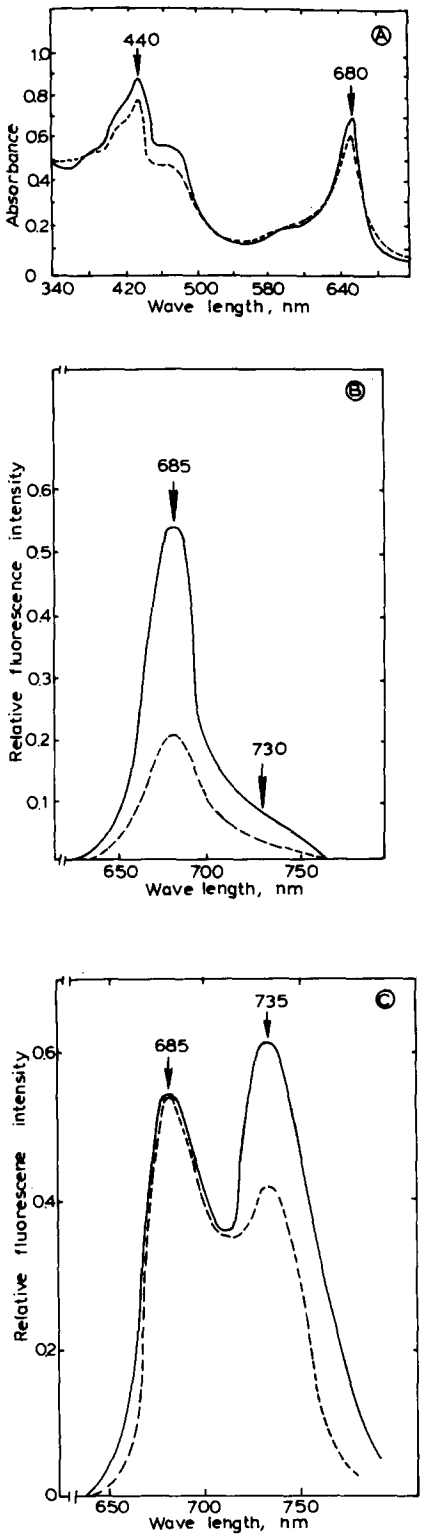


Fig. 5. Effect of Ni^{2+} treatment on Chl *a* fluorescence intensity of barley chloroplasts in the presence and absence of PS II electron donors. (A) Lowering of Chl *a* steady-state fluorescence level as a function of time of incubation with varying concentrations of $NiCl_2$. Chloroplasts were incubated with varying concentrations of $NiCl_2$ for specified periods before measurements. Controls were incubated without Ni^{2+} for the same periods of time for comparison. $NiCl_2$ present at: (o——o) 1, (o——o) 2, (•——•) 3, (□——□) 4 mM. (B) Lowering of Chl *a* fluorescence level in the presence and absence of exogenous donors. Chloroplasts were treated with $NiCl_2$ for 5 min before steady-state Chl *a* fluorescence measurements: (o——o) 0.3 mM $MnCl_2$, (o——o) 5 mM NH_5OH, (•——•) no addition.



the primary oxidized donor and reduced acceptor of PS II [18].

Changes in Chl a fluorescence emission induced by Ni^{2+}

The measurements of absorption spectra of chloroplasts in the prescence and absence of $NiCl_2$ (2 mM) showed only minor suppression of the red absorption band of the chloroplast absorption spectrum (Fig. 6A). However, Ni^{2+} not only severely depressed the room temperature Chl *a* fluorescence yield as shown in Fig. 6B, but also reduced changes in Chl *a* fluorescence emission characteristics. The room temperature emission peak (F_{685}) of the spectrum was reduced by 60% upon treatment with $NiCl_2$. Furthermore, the ratio of F_{685} to F_{730} increased from 5.6 in the case of the untreated sample to 6.0 in Ni^{2+}-treated chloroplasts which suggests that the F_{730} band, which mostly arises from PS I [15,16], was also suppressed by Ni^{2+}. Fig. 6C shows the Chl *a* fluorescence emisssion spectra of chloroplasts measured at 77 K in the presence and absence of $NiCl_2$. It is clear that both F_{685} and F_{730} bands were suppressed by Ni^{2+}, but the F_{735} band was much more suppressed than the F_{685} band in the presence of Ni^{2+}. Also the ratio of F_{685} to F_{735} increased from 0.88 in the control to 6.0–6.4 on treatment with Ni^{2+}.

Effect of glutaraldehyde fixation on Ni^{2+}-induced damage to chloroplast function

Glutaraldehyde fixation is known to protect against the damage to chloroplast function caused by some heavy metal ions [11]. We have thus measured the DCIP photoreduction and 90° light-scattering changes of chloroplasts fixed with glutaraldehyde in the presence and absence of Ni^{2+}. Glutaraldehyde fixation of chloroplast structure could not provide significant protection against the Ni^{2+}-induced loss of O_2-evolving activity of chloroplasts although it

Fig. 6. Effect of addition of $NiCl_2$ on the absorption and Chl *a* fluorescence emission spectra of isolated spinach chloroplasts. (A) Absorption spectra; (B) room temperature emission spectra; (C) 77 K emission spectra. Chloroplasts were treated with 2 mM $NiCl_2$ for 10 min before measurements. Excitation slit width 1 mm, emission slit width 1.5 mm. Other details as in Materials and Methods. (———) Untreated, (- - - - -) treated.

did arrest the salt-induced volume changes due to addition of Ni^{2+} (data not shown).

Effect of washing of chloroplasts after Ni^{2+} treatment

To ascertain if Ni^{2+} inhibition of photosynthetic electron transport in barley chloroplasts is reversible, $NiCl_2$ (1–3 mM)-treated chloroplasts were washed three times with isolation buffer. Ni^{2+} incubation with chloroplasts was carried out for 15 min and then the chloroplasts were washed with isolation buffer three times and their activity measured for O_2 evolution with DCIP as an electron acceptor. The control sample was also kept in the dark for 15 min and washed three times and assayed for activity. The washing of Ni^{2+}-treated chloroplasts with buffer could only slightly (10%) relieve the inhibition. Addition of $MnCl_2$ to Ni^{2+}-treated and subsequently washed chloroplasts has also no effect on relieving the Ni^{2+} inhibition.

Discussion

The results presented in this paper demonstrate that the Ni^{2+}-induced inhibition of the photosynthetic electron-transport processes of isolated barley chloroplasts is distinctly different from the inhibitory effect of other heavy metal ion-induced losses of chloroplast activity. Pb^{2+}, Cd^{2+} and Zn^{2+} have been shown to inhibit electron transport by blocking the flow of electrons to PS II at the water-splitting side [10,13]. Ni^{2+} inactivates PS II activity at millimolar (4 mM) concentrations and inactivates PS I activity at still higher concentrations (Figs. 1 and 4).

The results obtained on Chl *a* fluorescence yield changes indicate that Ni^{2+} suppressed the variable Chl *a* fluorescence yield due to loss of chloroplast ability to photoreduce Q, the primary acceptor of PS II (Fig. 5A). Even the addition of NH_2OH failed to reduced Q, the primary acceptor of PS II in the light (Fig. 5B). Ni^{2+} inhibition of the PS II reaction could not be by-passed by the supply of exogenous electron donors such as $MnCl_2$, benzidine or NH_2OH which feed electrons to PS II. In this respect, Ni^{2+} inhibition of the PS II reaction is different from that of Zn^{2+} or Pb^{2+} which can be by-passed by the supply of artificial PS II electron donors [2,11]. These results suggest that the inhibition of electron transport by Ni^{2+} must be due to either inactivation of PS II reaction centres or alteration of membrane structure of the photosynthetic apparatus. Furthermore, we note that the Ni^{2+} inhibition of PS II activity cannot be easily removed by washing out Ni^{2+} from the chloroplast suspension. Immobilization of chloroplast structure by glutaraldehyde fixation also did not arrest the loss of PS II-dependent electron flow. The change in the room temperature emission spectrum and the suppression of delayed light emission indicate that Ni^{2+} mostly inactivates PS II activity. The presence of Ni^{2+} caused lowering of both the F_{685} band, which originates from Chl *a* associated with light-harvesting Chl *a* linked to PS II [16,18], and the F_{730} band, which originates mostly from Chl *a* linked to PS I [16,19]. However, the extent of quenching was more extensive for the PS I emission band F_{730} than for the associated F_{685} band (Fig. 6B). This is quite evident from the emission spectrum of Chl *a* fluorescence measured at 77 K (Fig. 6C) which shows that the F_{730} band is extensively quenched in the presence of Ni^{2+}: the increase in the F_{685}/F_{730} ratio of the emission bands induced by Ni^{2+} may not be due only to suppression of energy transfer from PS II to PS I by divalent cations [16,19,20]. It is likely that the suppression of the F_{730} band is due partly to some structural alterations of chloroplast membranes by Ni^{2+} resulting in inactivation of PS I activity (Fig. 3) and paramagnetic quenching.

In summary, Ni^{2+} brings about some irreversible inactivation of PS II-catalyzed O_2 evolution by inflicting some changes on the chloroplast membrane structure, and this damage cannot be prevented by immobilization of chloroplast membranes with glutaraldehyde [11,19]. The irreversible loss of PS II activity and also possible associated changes in the energy transfer from PS II to PS I [19, 20], as revealed by changes in Chl *a* emission induced by Ni^{2+}, are quite distinct from other metal ion-induced inhibitory effects on PS II photochemistry [2,6,10]. Ni^{2+} also affects PS I activity but at a higher concentration (Fig. 3). The actual mode of inactivation of PS II photochemistry by alteration of chloroplast protein/lipid structure by Ni^{2+} remains to be investigated.

Acknowledgements

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