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EFFECTS OF MAGNESIUM AND CHLORIDE IONS ON LIGHT-INDUCED ELECTRON TRANSPORT IN MEMBRANE FRAGMENTS FROM A BLUE-GREEN ALGA*

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SUMMARY

The effects of magnesium and chloride ions on photosynthetic electron transport were investigated in membrane fragments of a blue-green alga, *Nostoc muscorum* (Strain 7119), noted for their stability and high rates of electron transport from water or reduced dichlorophenolindophenol to $NADP^+$. Magnesium ions were required not only for light-induced electron transport from water to $NADP^+$ but also for protection in the dark of the integrity of the water-photooxidizing system (Photosystem II). Membrane fragments suspended in the dark in a medium lacking Mg^{2+} lost the capacity to photoreduce $NADP^+$ with water on subsequent illumination. Chloride ions could substitute, but less effectively, for each of these two effects of magnesium ions. By contrast, the photoreduction of $NADP^+$ by $DCIPH_2$ was independent of Mg^{2+} (or Cl^-) for the protection of the electron transport system in the dark or during the light reaction proper. Furthermore, high concentrations of $MgCl_2$ produced a strong inhibition of $NADP^+$ photoreduction with $DCIPH_2$ without significantly affecting the rate of $NADP^+$ photoreduction with water. The implications of these findings for the differential involvement of Photosystem I and Photosystem II in the photoreduction of $NADP^+$ with different electron donors are discussed.

INTRODUCTION

Of the inorganic ions that may play a role in photosynthesis, chloride and magnesium have received the greatest attention. In experiments with isolated chloroplasts, chloride ion, now known to be a micronutrient essential for plant growth [1, 2] was found to be a cofactor required for the photooxidation of water [3–11]. The presence of chloride was also needed to protect isolated chloroplasts against

Abbreviations: DCMU, 3-(3,'4'-dichlorophenyl)-1,1-dimethylurea; DCIP, $DCIPH_2$, oxidized and reduced forms of 2,6-dichlorophenolindophenol, respectively.

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photoinactivation that resulted from illumination in the absence of an electron a ceptor [12].

With regard to magnesium ions, much interest has centered on their effect o fluorescence of chloroplasts. Homann [13] observed a magnesium induced increase i chloroplast fluorescence yield which he correlated with oxygen evolution. The findin of Murata [14] that Mg^{2+} increased the fluorescence yield of Photosystem II an decreased the fluorescence yield of Photosystem I led him to postulate that Mg^2 controls the partition of energy between Photosystem I and Photosystem II, a concep that has received considerable attention from other investigators [15–25]. Othe investigations have also linked Mg^{2+} with energy conservation [26, 27] and membran structure [28–30]. In some instances, however, it is difficult to ascribe a specific effec to Mg^{2+} because similar effects were produced by other divalent cations (e.g., Ca^{2+} Mn^{2+}) that are normal constituents of chloroplasts [28, 15, 17, 25].

In contrast to the more frequent investigations of the role of Mg^{2+} and Cl^- i chloroplasts, there are relatively few studies on the role of these ions in light reaction of membrane fragments of blue-green algae. Moreover, some of the observations o algal fragments seem at variance with those in chloroplasts. Thus, Susor and Krog mann [31] found that $MgCl_2$ was essential for high rates of photooxidation of wate but, since NaCl was ineffective as a substitute, the effect appeared to be due solely t Mg^{2+} and not to involve Cl^-. $MgCl_2$ also strongly stimulated the rate of $NADP^+$ reduction by algal fragments with either water or reduced indophenol dye as the electron donor [32], whereas in chloroplasts Mg^{2+} increased the rate of light-induced electron flow from water but decreased the rate of $NADP^+$ photoreduction by a reduced indophenol dye [14].

This paper reports an investigation of the effects of magnesium and chloride ions on the light-induced electron transport in membrane fragments of a blue-green alga, with $NADP^+$ as the electron acceptor and with either water or reduced dichlorophenolindophenol ($DCIPH_2$) dye as the electron donor. The algal membrane fragments consisted of Fraction C from *Nostoc muscorum* (Strain 7119), a preparation noted for stability and high light-induced activity of electron transport from water or $DCIPH_2$ to $NADP^+$ [33, 33a].

Some of the Mg^{2+} and Cl^- effects previously observed in chloroplasts and algal preparations have been confirmed, and some new aspects of the influence of these ions have been revealed. Magnesium ions were found to be required not only for light-induced electron transport from water to $NADP^+$ but also for the maintenance in the dark of the integrity of the water-photooxidizing system (Photosystem II). Membrane fragments suspended in the dark in a medium lacking Mg^{2+} lost the capacity to photoreduce $NADP^+$ with water on subsequent illumination. Chloride ions could substitute, but less effectively, for each of these two effects of magnesium ions. By contrast, the photoreduction of $NADP^+$ by $DCIPH_2$ was independent of Mg^{2+} (or Cl^-) for the protection of the electron transport system in the dark or during the light reaction proper. Furthermore, high concentrations of $MgCl_2$ produced a strong inhibition of $NADP^+$ photoreduction with $DCIPH_2$ without significantly affecting the rate of $NADP^+$ photoreduction with water. The implications of these findings for the differential involvement of Photosystem I and Photosystem II in the photoreduction of $NADP^+$ with different electron donors are discussed.

METHODS

The membrane fragments used in these experiments were prepared from *Nostoc muscorum* (Strain 7119) cells grown in an N_2-CO_2 atmosphere with N_2 serving as the sole source of nitrogen [33]. Fraction C was prepared as previously described [33] except that the Fraction C pellet was suspended in a $MgCl_2$-free solution (0.5 M sucrose; 50 mM Tricine buffer, pH 7.7) and $MgCl_2$ or others salts were immediately added to this suspension, depending on the nature of the experiment (see Results).

Photoreduction of $NADP^+$ was measured by monitoring absorbance changes at 340 nm as described by McSwain and Arnon [34]. Chlorophyll *a* was determined [35] and ferredoxin and ferredoxin-$NADP^+$ reductase were isolated and purified from spinach leaves by procedures previously reported from this laboratory [36, 37].

RESULTS

Effect of Mg^{2+} and Cl^- ions on the photoreduction of $NADP^+$ with water

Low concentrations of $MgCl_2$ gave striking increases in the rates of $NADP^+$ photoreduction with water; maximum rates of electron transport from water to $NADP^+$ were attained at concentrations of $MgCl_2$ of about 20 μequiv./ml (Fig. 1). Higher concentrations of $MgCl_2$ did not inhibit electron transport. [Salt concentrations are expressed as microequivalents (μequiv.) to facilitate comparisons of effects of monovalent and divalent ions.]

The striking activation by $MgCl_2$ of electron flow from water to $NADP^+$ could not be attributed exclusively to unique effects of Mg^{2+}. Cl^-, when supplied as salts of monovalent cations, also increased the rate of $NADP^+$ photoreduction by water but much higher concentrations were needed for maximum activity. NaCl con-

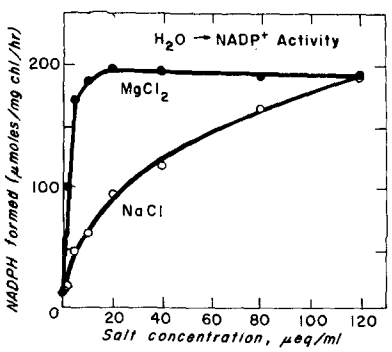

Fig. 1. Effect of Mg^{2+} and Cl^- on photoreduction of $NADP^+$ with water by *Nostoc* membrane fragments. Membrane fragments (Fraction C pellet suspended in the $MgCl_2$-free solution as described in Methods) were immediately after preparation assayed for their ability to photoreduce $NADP^+$ with water in the presence of $MgCl_2$ or NaCl. Aside from Mg^{2+} or Cl^- (at the concentrations indicated on the abscissa) the reaction mixture contained (per 1.0 ml) membrane fragments equivalent to 50 μg of chlorophyll *a* and the following: Tricine [*N*-Tris(hydroxymethyl)methylglycine] buffer (pH 7.7), 50 μmol; ferredoxin, 0.01 μmol; $NADP^+$, 2 μmol; and saturating amounts of ferredoxin $NADP^+$ reductase. Wide-band red illumination ($6.0 \cdot 10^5$ ergs/cm^2/s) was provided by light from a 1200-watt DHT projection lamp filtered through a waterbath and Corning 2-58 and 1-69 filters. Gas phase, air; temperature, 20 °C.

TABLE I

EFFECT OF INORGANIC IONS ON PHOTOREDUCTION OF $NADP^+$ WITH WATER

20 μequiv./ml of Mg^{2+}, Cl^-, Na^+, or K^+ was added, as indicated. Other conditions were as in Fig. 1 (Q_{NADP^+} = μmol $NADP^+$ reduced/mg chlorophyll *a*/h).

Mg^{2+} effect		Cl^- effect		Na^+ or K^+ effect	
Salt added	Q_{NADP^+}	Salt added	Q_{NADP^+}	Salt added	Q_{NADP^+}
$MgCl_2$	250	NaCl	140	$NaNO_3$	43
$Mg(CH_3COO)_2$	200	KCl	88	$Na(CH_3COO)$	22
$Mg(NO_3)_2$	153			KNO_3	22
		None	13	$K(CH_3COO)$	22

TABLE II

EFFECT OF INORGANIC IONS ON PHOTOREDUCTION OF $NADP^+$ WITH $DCIPH_2$

The reaction mixtures contained (per 1 ml) ascorbate, 10 μmol, DCIP, 0.1 μmol, DCMU, 0.001 μmol, and 20 μequiv. of Mg^{2+}, Cl^-, Na^+, or K^+. Other conditions were as in Fig. 1.

Mg^{2+} effect		Cl^- effect		Na^+ or K^+ effect	
Salt added	Q_{NADP^+}	Salt added	Q_{NADP^+}	Salt added	Q_{NADP^+}
$MgCl_2$	320	NaCl	400	$NaNO_3$	380
$Mg(CH_3COO)_2$	330	KCl	360	$Na(CH_3COO)$	350
$Mg(NO_3)_2$	350			KNO_3	400
		None	330	$K(CH_3COO)$	360

centrations of about 100 μequiv/ml were required to produce a rate of $NADP^+$ reduction equal to that given by 10 μequiv./ml of $MgCl_2$ (Fig. 1).

At a concentration of 20 μequiv./ml, $MgCl_2$, which supplied both Mg^{2+} and Cl^- ions, gave the highest rates of electron transport from $NADP^+$ but high rates have also resulted from the addition of Mg^{2+} without Cl^-, i.e., from the addition of magnesium acetate or magnesium nitrate (Table I). By contrast, sodium and potassium acetate were largely ineffective. In the absence of Mg^{2+} ions, only sodium or potassium chloride produced appreciable stimulation of electron flow from water to $NADP^+$ (Table I).

Whereas Mg^{2+} or Cl^- were required for the photoreduction of $NADP^+$ with water, they were not required for the photoreduction of $NADP^+$ with $DCIPH_2$. Magnesium, sodium or potassium salts of chloride, acetate or nitrate (at a concentration of 20 μequiv./ml) did not significantly increase the already high rates of photoreduction of $NADP^+$ with $DCIPH_2$ in the absence of these salts (Table II).

Protective effects of Mg^{2+} and Cl^- on the stability of light-induced electron transport activity

The usual procedure for the preparation of *Nostoc* membrane fragments included, at all stages, the presence of $MgCl_2$ (20 μequiv./ml) in the suspending solution [33]. Membrane fragments so prepared (Fraction C) could be frozen and stored

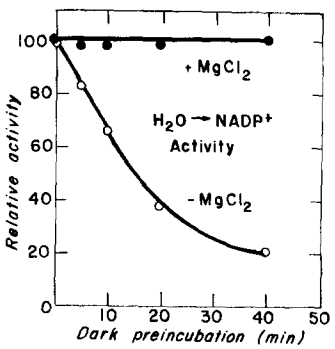

Fig. 2. Effect of incubation of *Nostoc* membrane fragments in the dark with or without $MgCl_2$ on subsequent photoreduction of $NADP^+$ with water. Membrane fragments (Fraction C pellet suspended in the $MgCl_2$-free solution as described in Methods) were divided into two portions. $MgCl_2$ (10 μmol/ml) was immediately added only to the "$+MgCl_2$"portion and it, as well as the "$-MgCl_2$" portion, was preincubated at 3 °C in the dark for the time interval indicated on the abscissa. At the end of the incubation period, a 0.05-ml aliquot from each portion (containing 50 μg of chlorophyll *a*) was assayed for $NADP^+$ photoreduction in a reaction mixture that contained 10 μmol/ml of $MgCl_2$ and the other components listed in the legend to Fig. 1. Wide-band red illumination ($4.0 \cdot 10^5$ ergs $\cdot$ $cm^{-2} \cdot s^{-1}$) was provided by light from a 150-watt FCS projection lamp filtered through Corning 2-58 and 1-69 filters. Other conditions were as in Fig. 1.

for a month or more at −20 °C without losing (upon thawing) their capacity to photoreduce $NADP^+$ at high rates with either water or $DCIPH_2$ [33]. However, as shown in Fig. 2, 40 min of dark preincubation in a suspending solution lacking $MgCl_2$ resulted in an irreversible and almost complete loss of the capacity of membrane fragments to photoreduce $NADP^+$ with water. This loss occurred even though $MgCl_2$ was present in the reaction mixture during the subsequent illumination period at a concentration sufficient for maximum activity of membrane fragments that were not exposed to an incubation period without $MgCl_2$ (Fig. 1). That activity was not

TABLE III

PROTECTIVE EFFECTS OF DIFFERENT SALTS DURING DARK INCUBATION OF MEMBRANE FRAGMENTS ON THEIR SUBSEQUENT ABILITY TO PHOTOREDUCE $NADP^+$ WITH WATER

To *Nostoc* membrane fragments (Fraction C pellet suspended in the $MgCl_2$-free solution as described in Methods) was immediately added one of the salts indicated below, and the suspension was incubated in the dark at 3 °C for 50 min. The final concentration of Mg^{2+}, Cl^-, Na^+, or K^+ was 20 μequiv./ml. At the end of the incubation period an 0.05-ml aliquot (containing 50 μg of chlorophyll *a*) from each suspension was assayed for $NADP^+$ photoreduction in a reaction mixture containing 10 μmol/ml of $MgCl_2$. Other conditions were as in Fig. 2.

Dark incubation with:	Q_{NADP^+}	Dark incubation with	Q_{NADP^+}	Dark incubation with	Q_{NADP^+}
$MgCl_2$	207	NaCl	55	$NaNO_3$	0
$MgSO_4$	103	KCl	44	Na_2SO_4	0
$Mg(NO_3)_2$	98			KNO_3	0
$Mg(CH_3COO)_2$	76	None	0	$K(CH_3COO)$	0

restored even when the concentration of $MgCl_2$ during illumination was increased 4 fold, to 120 μequiv./ml.

The damage to the photosynthetic apparatus from preincubation in the medium lacking $MgCl_2$ was greater than that caused by Tris treatment [38]. Tris-treated membrane fragments, like chloroplasts, were unable to photooxidize water but were able to photoreduce $NADP^+$ with artificial electron donors for Photosystem II, such as 1,5-diphenylcarbazide or hydroquinone [38]. By contrast, membrane fragments incubated in a medium lacking $MgCl_2$ were unable to use these substitute electron donors. The inactivation of the photoreductive capacity of Photosystem II caused by preincubation of membrane fragments in the absence of $MgCl_2$ was independent of the electron acceptor: it was also observed when $NADP^+$ was replaced by ferricyanide or DCIP.

As shown in Table III, $MgCl_2$, which provided both Mg^{2+} and Cl^-, had the greatest protective effect during the dark incubation period. Without Cl^- ions, Mg^{2+} ions supplied by magnesium sulfate, nitrate, or acetate were less effective. A smaller but significant protective effect was also provided by Cl^- (added as sodium or potassium salts) in the absence of Mg^{2+}. Without either Mg^{2+} or Cl^- ions no protection was observed from the addition of sodium, potassium, nitrate, sulfate, acetate, or other ions (Table III).

Inhibition by Mg^{2+} ions of the photoreduction of $NADP^+$ with $DCIPH_2$

In the experiments presented so far, low concentrations of Mg^{2+} ions or high concentrations of Cl^- ions greatly increased the rates of $NADP^+$ photoreduction with water but had no effect on the rates of photoreduction of $NADP^+$ with $DCIPH_2$ (Fig. 1 and Table II). Other experiments revealed yet another difference between the two $NADP^+$ systems. Fig. 3 shows that the maximum rate of $NADP^+$ reduction with water, which was obtained with 10 μequiv./ml of $MgCl_2$, remained the same when the concentration of $MgCl_2$ was increased 12-fold, to 120 μequiv./ml. By contrast, the high rate of $NADP^+$ photoreduction with $DCIPH_2$, which was in the main independent of low concentrations of $MgCl_2$, began to decline sharply at higher con-

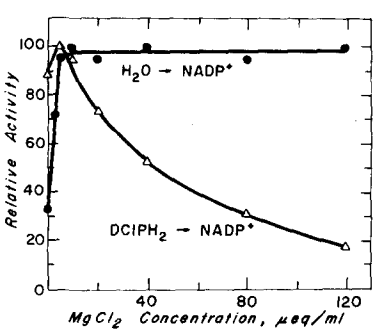

Fig. 3. Contrasting effects of $MgCl_2$ concentration on photoreduction of $NADP^+$ by *Nostoc* membrane fragments with water or $DCIPH_2$ as the electron donor. All reaction mixtures contained, aside from the indicated concentration of $MgCl_2$, the other components given for Fig. 1. In addition, the $DCIPH_2 \rightarrow NADP^+$ system contained (per 1.0 ml): ascorbate, 10 μmol; DCIP, 0.1 μmol; and DCMU, 0.001 μmol. Relative activity of 100 corresponds to a Q_{NADP^+} of 300 for the $DCIPH_2 \rightarrow NADP^+$ system and a Q_{NADP^+} of 200 for the $H_2O \rightarrow NADP^+$ system.

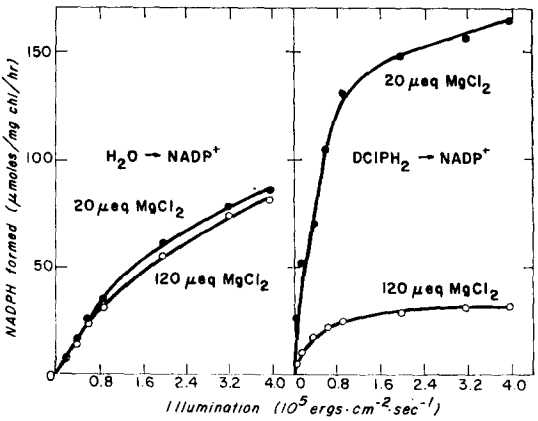

Fig. 4. Effect of high concentration of $MgCl_2$ at different light intensities on photoreduction of $NADP^+$ by *Nostoc* membrane fragments with water or $DCIPH_2$ as the electron donor. Reaction mixtures and conditions (except for variable light intensity and $MgCl_2$ concentration) were as described in Fig. 3.

centrations of the salt, the decline amounting to over 80 % at a $MgCl_2$ concentration of 120 μequiv./ml (Fig. 3).

The inhibitory effect of high concentrations of $MgCl_2$ on the photoreduction of $NADP^+$ with $DCIPH_2$ but not on the photoreduction of $NADP^+$ with water was observed over a wide range of light intensities, from limiting to saturating light (Fig. 4). The marked inhibitory effect of high concentrations of $MgCl_2$ was also observed with high concentrations of magnesium sulfate or acetate and thus appears to be due to Mg^{2+} ions. High concentrations of sodium and potassium chloride or of sodium and potassium acetate gave only a slight inhibition of $NADP^+$ photoreduction with $DCIPH_2$ (Table IV).

The depressing effect of high concentrations of Mg^{2+} on the photoreduction of $NADP^+$ by Photosystem I was most pronounced with $DCIPH_2$ as the electron

TABLE IV

EFFECT OF HIGH CONCENTRATIONS OF Mg^{2+}, Cl^-, AND OTHER IONS ON THE PHOTOREDUCTION OF $NADP^+$ WITH $DCIPH_2$

Experimental conditions were as described in Fig. 3 for the $DCIPH_2 \rightarrow NADP^+$ system.

Salt added	Relative rates of $NADP^+$ reduction (% of no-salt control)	
	20 μeq/ml	120 μeq/ml
$MgCl_2$	100	20
$MgSO_4$	106	34
$Mg(CH_3COO)_2$	113	42
NaCl	112	100
KCl	104	87
$Na(CH_3COO)$	111	87
$K(CH_3COO)$	120	87

TABLE V

EFFECT OF HIGH CONCENTRATIONS OF Mg^{2+} AND Cl^- ON PHOTOREDUCTION OF $NADP^+$ WITH ARTIFICIAL ELECTRON DONORS

The concentration of Mg^{2+} or Cl^- was 120 μequiv./ml. Other conditions were as described in Fig. 1 for the $DCIPH_2 \rightarrow NADP$ system except that DCIP was replaced in one case by 1.0 μmol of *p* phenylenediamine and in the second case by 0.1 μmol of 2,3,5,6-tetramethyl-*p*-phenylenediamine

Salt added	e^- donor:	Q_{NADP^+}		
		Asc+DCIP	Asc+*p*-phenylenediamine	Asc+2,3,5,6-tetramethyl-*p*-phenylenediamine
None		273	87	196
NaCl		240	98	207
$MgCl_2$		55	55	98

donor but was also appreciable (about 50 %) with other Photosystem I electron donors, i.e., *p*-phenylenediamine and 2,3,5,6-tetramethyl-*p*-phenylenediamine. Here again, the effect appeared to be due to Mg^{2+} and not to Cl^- ions (Table V).

DISCUSSION

The results of this investigation show that in *Nostoc* membrane fragments the nature of the electron donor determined the contrasting effects that Mg^{2+} had on the photoreduction of $NADP^+$. Mg^{2+} was not required for the photoreduction of $NADP^+$ with electron donors to Photosystem I but was required for the photooxidation of water and for the preservation of the Photosystem II activity in membrane fragments kept for relatively short periods of time in the dark. Following such dark storage, in the absence of Mg^{2+} *Nostoc* membrane fragments were unable when illuminated and supplied with Mg^{2+} to photoreduce $NADP^+$ with water or even with artificial Photosystem II electron donors that were effective substitutes for water in Tris-treated preparations. Membrane fragments stored in the presence of Mg^{2+} retained their Photosystem II activity and on illumination gave good rates of $NADP^+$ photoreduction with water when Mg^{2+} was present in the reaction mixture. Low concentrations of Mg^{2+} were sufficient to produce these effects and high concentrations were not inhibitory.

By contrast, Mg^{2+} ions were required neither for the preservation of the Photosystem I activity of *Nostoc* membrane fragments kept in the dark nor for the light reaction proper when $NADP^+$ was being photoreduced with $DCIPH_2$ or other Photosystem I electron donors. Another important difference was that, at high concentrations, Mg^{2+} severely inhibited the photoreduction of $NADP^+$ with $DCIPH_2$ and similar donors but did not affect the photoreduction of $NADP^+$ with water.

In their protective effect on Photosystem II during dark storage and in their role in stimulating the photooxidation of water, Mg^{2+} was replaceable by Cl^- but at considerably higher concentrations. None of the other cations and anions tested proved to be effective substitutes for Mg^{2+}. Only with respect to the inhibition of the photoreduction of $NADP^+$ by $DCIPH_2$ and similar Photosystem I electron donors did Mg^{2+} appear to be specific, at least within the limits of the concentrations tested.

The contrasting effects of Mg^{2+} observed here invite comparison with the findings of Rurainski and Hoch [39, 40] that $MgCl_2$ increased the light-induced rate of electron flow from water to $NADP^+$ but decreased the rate of light-induced electron flow through *P*-700. The authors concluded that, contrary to the currently popular series scheme, the photoreduction of $NADP^+$ with water and the photoinduced electron flow through *P*-700 are parallel photoacts [39, 40]. A similar concept, based on different considerations, was put forward from this laboratory [41–43]. The contrasting effects of Mg^{2+} observed in this study are also consistent with the view that the photoreduction of $NADP^+$ with $DCIPH_2$ involves a Photosystem I photoact that is not a component of the overall electron transport pathway from water to $NADP^+$.

In summary, the presented data do not support the concept that the photoreduction of $NADP^+$ by $DCIPH_2$ which is inhibited by Mg^{2+} represents a segment of an overall electron transport chain from water to $NADP^+$ that is stimulated by Mg^{2+}. The inhibitory effect of Mg^{2+} on the $DCIPH_2$ to $NADP^+$ pathway is being further investigated but one possibility, i.e., that Mg^{2+} may have inhibited electron transfer from $DCIPH_2$ to *P*-700, is ruled out by results to be presented elsewhere.

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