Phosphoryl Group Exchange between ATP and ADP Catalyzed by H\(^+\)-ATPase from Oat Roots

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ATP-ADP exchange was estimated in the presence of plasma membrane H\(^+\)-ATPase of oat (Avena sativa) roots partially purified with Triton X-100 by measuring \( ^{32}\)P\( \beta\)P formation from \(^{32}\)P\( \alpha\)P. Most studies were done at 0°C. At pH 6.0 the exchange showed: (a) Mg\(^2+\) requirement with a biphasic response giving maximal activity at 152 \( \mu\)M and (b) insensitivity to ionic strength, [Na\(^+\)], and [K\(^+\)]. ATP and ADP dependence were analyzed with a model in which nucleotide-enzyme interactions are at rapid-random equilibrium, whereas E,ATP \( \leftrightarrow \) E-P,ADP transitions occur in steady state. The results indicated competition between ADP and ATP for the catalytic site, whereas ATP interaction with the ADP site was extremely weak. At 0°C the exchange showed a 3-fold pH increase, from pH 5.5 to 9.0. At an alkaline pH the reaction was not affected by sodium azide and carbonyl cyanide p-trifluomethoxyphenyl-hydrazone, had a biphasic response to Mg\(^2+\) (maximal at 513 \( \mu\)M), and was insensitive to ionic strength. At 20°C ATP-ADP exchange was pH insensitive. At both temperatures ATP hydrolysis displayed a bell-shaped response, with a maximum around pH 6.0 to 6.5. Because no adenylate kinase activity was detected under any condition, these results demonstrate the existence of an ATP-ADP exchange reaction catalyzed by the plant H\(^+\)-ATPase.

The PM H\(^+\)-ATPase from higher plants belongs to the family of (E-P)ATPases, an ATP synthesis resulting from the interaction of ADP with some form of E-P has been well characterized (Andersen, 1989; Beaugé and Glynn, 1979). Likewise, this has also been observed with the synthesis of ATP, starting with the interaction of the enzyme with Pi, or ATP-Pi exchange, in the PM H\(^+\)-ATPase from yeast (Malpartida and Serrano, 1981a, 1981b; de Meis et al., 1987). ATP-Pi exchange requires the interaction of ADP with the phosphoenzyme; however, we are not aware of any report of a phosphoryl group exchange between ATP and ADP catalyzed by any plant H\(^+\)-ATPase, the existence of which has been suggested by Briskin and Poole (1983). In the present work we describe and characterize, for the first time to our knowledge, an ATP-ADP exchange reaction catalyzed by the PM H\(^+\)-ATPase from higher plants.

MATERIALS AND METHODS

Source of Enzyme

Seeds of oat (Avena sativa L. Seagram var) were obtained commercially. Oat roots were grown hydroponically for 7 d in deionized water at 20°C in the dark. For the preparation of the enzyme, the method of Vara and Serrano (1982) was followed with some modifications. All of the operations were carried out at 4°C. Oat roots (100 g) were cut and homogenized in 150 mL of a medium containing Suc 30% (w/w), 250 \( \mu\)M Tris-HCl, pH 8.5, 25 \( \mu\)M EDTA, 2.5 \( \mu\)M DTT, and 8.1 mg mL\(^{-1}\) PMSF. The homogenate was passed through four layers of cheesecloth and the filtrate was centrifuged for 25 min at 6,000g. The pellet was discarded and the supernatant, containing the microsomal fraction, was centrifuged at 85,000g for 30 min. The pellet (microsomal fraction) was resuspended in GTED 20 (20% glycerol, 10 \( \mu\)M Tris-HCl [pH 7.6 at room temperature], 1 \( \mu\)M EDTA-Tris, and 1 \( \mu\)M dithiothreitol) and applied to a discontinuous Suc gradient (33–46%, w/w) with TED (10 mm of Tris-HCl [pH 7.6 at room temperature], 1 mm of EDTA-Tris, and 1 mm of DTT). After centrifugation for 120 min at 85,000g, the interface fraction enriched in PM was removed, washed according to Hodges and Leonard (1974), resuspended in GTED 20, and stored at −20°C for 4 mg total protein mL\(^{-1}\). For Triton X-100 treatment 1.5 mg mL\(^{-1}\) of the PM fraction was incubated for 10 min at 0°C with 3.7 mg mL\(^{-1}\) of the detergent in 0.5 M (final concent...
tation) KCl (Serrano, 1988). After centrifugation at 85,000g for 45 min in the cold, the pellet was resuspended in GTED 20 at a final protein concentration of 4 to 6 mg mL⁻¹. Aliquots of 100 μL of this enzyme suspension were stored at −20°C until use.

**Biochemical Determinations**

ATP hydrolysis was determined by following the [³²P]Pi released from [γ-³²P]ATP of known specific activity by isobutanol benzene extraction (de Meis and Carvalho, 1974). The total amount of hydrolysis never exceeded 2 to 4%; this means that even at 0°C there is still a substantial overall cycle of ATP hydrolysis. Therefore, in each experimental condition, ATPase activity was simultaneously determined and the rate of exchange was corrected for ATP hydrolysis according to Beaugé and Glynn (1979). The ATP-ADP exchange rate was determined from the [¹⁴C]ATP formed from [¹⁴C]ADP (Beaugé and Campos, 1986). The nucleotides were separated on Dowex 1 × 8-400 resin columns. The total eluent volumes passed were 7 mL of 10 mM HCl, 30 mL of 20 mM HCl-γ-HCl, and 15 mL of 250 mM HCl. In all of the cases the exchange fraction never exceeded 10% of the expected equilibrium fraction. To reduce the fractional ATP breakdown most experiments were performed at 0°C; however, some studies on the pH effects were also carried out at 20°C. Solutions contained 50 mM Mes-Tris, pH 6.0, or Tris-HCl, pH 9.0, 0.5 mM EGTA, 0.16 mM ammonium molybdate, 1 mM EDAC (1-ethyl-3-[3-dimethylamino-propyl] carbodiimide), and 5 mg mL⁻¹ oligomycin. ATP, ADP, Mg²⁺ concentrations, and other modifications are indicated in the figure legends. Before starting the reaction by the addition of the nucleotides, the enzyme was preincubated 12 min in the reaction medium without the nucleotides. Except when ATP and ADP dependent were investigated, the concentrations routinely used were 3 mM ATP and 2 mM ADP. Total protein concentration ranged from 0.05 to 0.5 mg mL⁻¹ in a reaction medium of 100 μL.

**Protein Determination**

Total protein concentration was determined by the method of Bradford (1976) and modified by Read and Northcote (1981) using BSA as a standard.

**Solutions**

All solutions were made with Milli-Q water (Millipore) and the reagents were of an analytical grade. Vanadium-free ATP and ADP was from Boehringer Mannheim. Ionized Mg²⁺ concentrations were estimated with the Maxchelator Program (Hopkins Marine Station, Pacific Grove, CA) and dissociation constants were corrected for temperature, ionic strength, and pH. [γ-³²P]ATP was enzymatically labeled by the method of Glynn and Chappell (1964), as modified by de Meis (1972). [¹⁴C]ADP was from DuPont-New England Nuclear and [³²P]Pi was purchased from the Comisión Nacional de Energía Atómica (Buenos Aires, Argentina).

**RESULTS**

**Mg²⁺ Dependence**

The presence of Mg²⁺ ions is an absolute requirement for the activity of all transport ATPases, including the plant PM H⁺-ATPase (Brooker and Slanyman, 1983; Serrano, 1984). On the other hand, in the Na⁺,K⁺-ATPase, the optimal free Mg²⁺ is much higher for the overall ATP hydrolysis (about 1 mM) than for the ATP-ADP exchange (about 20 μM) (data calculated from Beaugé and Glynn, 1979; Beaugé and Campos, 1986). Therefore, we started by exploring the Mg²⁺ dependence of both reactions in the plant H⁺-ATPase. These results are illustrated in Figure 1, A and B. For the H⁺-ATPase activity (Fig. 1A) the Mg²⁺ dependence follows a Michaelian function with a Kₘ of 120 ± 5 μM. Figure 1B shows that at pH 6.0 the response of the exchange reaction to [Mg²⁺] is biphasic, with an optimum at 150 μM. On the other hand, the 21% inhibition observed at 4.2 mM Mg²⁺ is less marked than that seen with the Na⁺,K⁺-ATPase (Beaugé and Glynn, 1979).

![Figure 1](https://www.plantphysiol.org/)

Figure 1. H⁺-ATPase activity (A) and ATP-ADP exchange (B) at different [Mg²⁺] in H⁺-ATPase from oat root PM treated with Triton X-100. H⁺-ATPase activity was calculated from the [³²P]phosphate released from [γ-³²P]ATP. The exchange rate was estimated on the basis of the [¹⁴C]ATP formed from [¹⁴C]ADP. The H⁺-ATPase activity (A) is stimulated by Mg²⁺ following a Michaelian function with a Kₘ of 120 ± 3 μM Mg²⁺. On the other hand, a biphasic response can be observed for the ATP-ADP exchange (B) with the peak stimulation at 150 μM Mg²⁺; higher [Mg²⁺]s are slightly inhibitory. Each point is the mean ± SE of triplicate determinations. See text for details.
The Mg\(^2+\) dependence of the ATP-ADP exchange rate was also explored at pH 9.0 (see below). At this stage we wish to point out that the response to [Mg\(^{2+}\)] was also biphasic, but with a maximum at 510 \(\mu\)M Mg\(^{2+}\). The highest [Mg\(^{2+}\)] investigated, 3.4 mM, produced a 27% inhibition, which is not very different from that seen at pH 6.0 (not shown).

The possible effects of the Na\(^+\) and K\(^+\) ions on H\(^+\)-ATPase and ATP-ADP exchange activities were also studied at 0°C at concentrations between 0 and 100 mM. On the whole, and except for an inhibition of H\(^+\)-ATPase activity by [K\(^+\)] above 40 mM, no other significant effect was observed (not shown).

**Dependence of ATP and ADP Concentrations**

We next studied the dependence of this ATP-ADP exchange reaction on the concentrations of ATP and ADP. Two series of experiments were done, all at 0°C, pH 6.0, and 152 \(\mu\)M free Mg\(^{2+}\). In the first experiment (Fig. 2A), the concentration of ATP was varied between 0.05 and 3 mM at two fixed concentrations of ADP, 0.2 and 2 mM. In the second experiment (Fig. 2B), the concentration of ADP was varied between 0.05 and 2 mM at two fixed ATP concentrations, 0.3 and 3 mM. The points in the figures correspond to the mean ± SE of triplicate determinations. The ATP and ADP dependence were analyzed on the basis of a simplified kinetic model (Fig. 3) with the following assumptions: (a) ATP can compete with ADP for E\(_P\), but it does not affect E\(_P\) dephosphorylation; (b) ADP can compete with ATP at a single catalytic site, but it does not phosphorylate E\(_I\); (c) ATP and ADP unions are in rapid equilibrium; (d) the E\(_I\),ATP ↔ E\(_P\),ADP transitions are at steady state; and (e) ATP hydrolysis is not included in this scheme; however, exchange estimations were always corrected for the simultaneous ATPase activity. The model, solved with the King-Altman approach as modified by Cha (Segel, 1975), gave the following equation:

\[
v = \frac{k_fk_{-2}D[EH]}{k_{-1}D(K'_T + T) + k_{1}T(K'_D + D)}
\]

where E\(_T\) is the total enzyme; \(k_f\) is the forward rate constant for the E\(_I\),ATP-E\(_P\),ADP transition (the rate constant for enzyme phosphorylation); \(k_{-1}\) is the backward rate constant for the E\(_I\),ATP-E\(_P\),ADP transition (the rate constant for ATP synthesis); T = \(\mu\)mol ATP; D = \(\mu\)mol ADP; \(K_s\) is the dissociation constant for the E\(_I\),ATP complex; \(K_s\) is the dissociation constant for the E\(_I\),P,ADP complex; \(K'_{s}\) is the dissociation constant for the E\(_I\),ATP-E\(_P\),ADP transition (inhibition constant for ADP); and \(K_{s}\) is the dissociation constant for the E\(_I\),P,ATP complex (inhibition constant for ATP).

The curves through the points (in Fig. 2, A and B) are the simultaneous best fit of all of the data to Equation 1 done with the Scop Program (Simulation Resources, Inc., Berrien Springs, MI) using the \(\chi^2\) criterion. As this figure illustrates, a good fit was observed. Note that the actual fitting parameters are six because the apparent affinity constants are fully determined by the dissociation and inhibition constants. The number of data points taken was 78; this means 13 points per parameter, a more than reasonable ratio for an adequate fitting. The values of the different constants are given in Table I. Their implications will be addressed in “Discussion.”

**Effect of Proton Concentration**

Previous works on the pH profile of the H\(^+\)-ATPase activity, assayed at 20°C and in the absence of ADP, showed that it is bell-shaped with a maximal rate at 6.5 (Serrano, 1990; Roberts et al., 1991). The left side of Figure 4 describes experiments at 0°C analyzing the pH effects on ATPase (A) and ATP-ADP exchange (B) reactions in the presence of 3 mM ATP and 2 mM ADP. The H\(^+\)-ATPase activity displayed an approximately bell-shaped behavior with a maximum at pH 6.0 and decreasing to zero at pH 7.0.
9.0. On the other hand, the exchange reaction remained practically unaffected from pH 5.5 to 7.0, whereas from that value it sharply increased to reach a 3-fold factor at pH 9.0. In the absence of any bound ligand, the conformation equilibrium of ATPases is strongly temperature dependent. In Na+,K+-ATPase at 0°C about 40% is E, that percentage value it sharply increased to reach a 3-fold factor at pH 9.0. On the other hand, the exchange reaction remained practically unaffected from pH 5.5 to 7.0, whereas from that value it sharply increased to reach a 3-fold factor at pH 9.0.

Table 1. Values for ATP- and ADP-enzyme dissociation and inhibition constants and forward and backward rate constants for the E1,ATP-E1,ADP transition

<table>
<thead>
<tr>
<th>Type of Constant</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unidirectional rate</td>
<td></td>
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<tr>
<td>$k_1$</td>
<td>3.6 ± 0.7 min$^{-1}$</td>
</tr>
<tr>
<td>$k_{-1}$</td>
<td>6.1 ± 1.2 min$^{-1}$</td>
</tr>
<tr>
<td>True dissociation</td>
<td></td>
</tr>
<tr>
<td>$K_{S_{D}}$</td>
<td>792 ± 158 μM</td>
</tr>
<tr>
<td>$K_{S_{T}}$</td>
<td>564 ± 133 μM</td>
</tr>
<tr>
<td>True inhibition</td>
<td></td>
</tr>
<tr>
<td>$K_{I_{D}}$</td>
<td>2993 ± 599 μM</td>
</tr>
<tr>
<td>$K_{I_{T}}$</td>
<td>$4 \times 10^9$ ± 0.8×10^9 μM</td>
</tr>
<tr>
<td>Apparent dissociation</td>
<td></td>
</tr>
<tr>
<td>$K_{D_{0.3}}$</td>
<td>792 ± 158 μM</td>
</tr>
<tr>
<td>$K_{D_{3}}$</td>
<td>792 ± 158 μM</td>
</tr>
<tr>
<td>$K_{T_{0.2}}$</td>
<td>601 ± 120 μM</td>
</tr>
<tr>
<td>$K_{T_{2}}$</td>
<td>941 ± 186 μM</td>
</tr>
</tbody>
</table>

*The meaning of the symbols is in text except: $K_{D_{0.3}}$, apparent dissociation constant for the E1,ATP complex at 0.3 mM ATP; $K_{D_{2}}$, apparent dissociation constant for the E1,ATP complex at 3 mM ATP; $K_{T_{0.2}}$, apparent dissociation constant for the E1,ATP complex at 0.2 mM ADP; and $K_{T_{2}}$, apparent dissociation constant for the E1,ATP complex at 2 mM ADP.

Figure 3. Simplified model for the ATP-ADP exchange reaction catalyzed by PM H+-ATPase from higher plants. Shaded regions belong to rapid equilibrium segments, and the rest belongs to the steady-state segment. The details of the model are given in the text.

Figure 4. pH effect on ATPase activity (A–C) and ATP-ADP exchange (B–D) catalyzed by the H+-ATPase from oat root PM treated with Triton X-100. The experiments were performed at 0°C (A and B) and 20°C (C and D) between pH 5.5 and 9.0 in media of the following composition: 3 mM ATP; 50 mM Mes-Tris, pH 5.5 and 6.0; 50 mM Tris-HCl, pH 7.0, 8.0, and 9.0; 0.5 mM EGTA; 1 mM EDTA; 0.16 mM ammonium molybdate; 5 mg mL$^{-1}$ oligomycin; and 8 mM MgSO$_4$. The incubation time was between 10 and 30 min at the different pHs and temperatures. Note that at 0 and 20°C the H+-ATPase activity displays bell-shaped behavior with a maximum at pH 6.0 and nil at pH 9.0 (A–C), whereas the exchange rate at 0°C increases 3-fold from pH 7.0 to 9.0 (B), and at 20°C the pH shows no stimulation (D). Each point is the mean ± SE of triplicate determinations. See text for details.

Figure 5. $[^{14}C]$ labeling of ATP in the presence of cold ATP and $[^{14}C]$ADP catalyzed by H+-ATPase preparation from oat root PMs treated with Triton X-100 at pH 6.0 and 9.0 at 0°C and in the presence and absence of A_{P, A}. The reaction was determined in 3 mM ATP, 2 mM $[^{14}C]$ADP, 50 mM Mes-Tris, pH 6.0, or 50 mM Tris-Cl, pH 9.0, 0.5 mM EGTA, 1 mM EDTA, 0.16 mM ammonium molybdate, 5 mg mL$^{-1}$ oligomycin, and 1 or 4 mM MgSO$_4$ at pH 6.0 and 9.0, respectively, and in the presence/absence of 0.2 mM A_{P, A}. The incubation time was 25 min at pH 6.0 and 15 min at pH 9.0. Observe that the inhibitor has no effect on the $[^{14}C]$ATP labeling. Each bar is the mean ± SE of triplicate determinations. See text for details.
production in this preparation was the simultaneous presence of ATP and ADP, and the rate of ATP hydrolysis was about 20-fold higher than that observed at 0°C. On the other hand, ATP-ADP exchange, which increased 8-fold over the maximum at 0°C, was completely insensitive to pH.

Specificity of the Exchange Assays

A major problem with the determination of [14C]AMP production in this preparation was the simultaneous presence of an adenylate kinase activity, particularly efficient at alkaline pH. This enzyme catalyzes the reaction of two ADP molecules, leading to the synthesis of one molecule of ATP and the release of one AMP. Several experiments were done to investigate this point using 200 μM of the specific adenylate kinase inhibitor AP5A; note that at 1 μM this compound produces 98% inhibition of the rabbit muscle enzyme (Lienhard and Secemski, 1973). Figure 5 shows that there is no effect of AP5A on the rates of ATP-ADP exchange either at pH 6.0 or 9.0. Figure 6 summarizes the results at pH 6.0 (A) and pH 9.0 (B) on the appearance of [14C]AMP, or its net synthesis, and on the production of [14C]ATP when the enzyme preparation was incubated with 2 mM [14C]ADP in the presence and absence of ATP. It can be shown that: (a) with [14C]ADP and ATP, the appearance of [14C]ATP is the same without and with the inhibitor (it concurs with Fig. 5). In addition there is no production of [14C]AMP in any case; and (b) with [14C]ADP alone there is no net synthesis of either ATP or AMP in the absence or presence of AP5A. The facts that (a) AP5A has no effects at concentrations expected to be more than saturating, and (b) that ADP alone does not induce net synthesis of ATP, clearly indicate that in our preparation there is no detectable adenylate kinase activity that could bias the ATP-ADP exchange results.

We also ruled out any effect due to contamination by mitochondrial H+-ATPase. At pH 6.0 and 9.0 the ATPase activity and the ATP-ADP exchange rate were not affected by sodium azide and FCCP (carbonyl cyanide p-trifluomethoxyphenyl-hydrazone) (data not shown).

DISCUSSION

The work presented here shows that the plant H+-ATPase enzyme can catalyze a sizable phosphoryl group exchange between ATP and ADP. The existence of this reaction is predicted from the overall cycle suggested earlier for this enzyme (Briskin, 1990) and outlined in Scheme I, but up to now it had never been experimentally verified. The two main results we present have to do with the nucleotide requirements and interactions and the effects of pH.

The model in Figure 3, which concentrates on the phosphoryl group-exchange part of the ATPase cycle, can adequately account for the nucleotide dependence of the exchange process. It could be argued that this approach is an oversimplification, particularly since it does have the two simultaneous ATP-binding sites postulated for this enzyme (Roberts et al., 1991, 1995). In our view the simplification is justified because leaving out the overall ATPase cycle, it is unlikely that the regulatory site (or role) of ATP will come into play. Some of the conclusions that can be drawn from the fitting parameters (see Table I) are indeed very interesting. On the one hand, there is a similar true affinity of the catalytic site for both nucleotides (about 40% smaller for ADP); this means that ADP can effectively compete with ATP for that site. On the other hand, the affinity for ATP of the ADP-binding site in E,P is so low that in practice ATP does not influence ADP binding and dephos-
phorylation. These two characteristics have also been observed in the Na⁺,K⁺-ATPase (Beaugé and Glynn, 1979; Klodos and Norby, 1988).

The fact that high pH completely inhibits ATP hydrolysis while it enhances ATP-ADP exchange (at 0°C) or does not affect this reaction (at 20°C) indicates that, whatever step is involved in ATPase inhibition, it cannot be due to stabilization of any given complex. The reason is that stabilization would stop not only ATP hydrolysis, it would halt the exchange reaction as well; i.e. the stable state would behave as a sink. Good examples can be found with the Na⁺,K⁺-ATPase. In that enzyme extracellular Na⁺, acting with intermediate affinity, stabilizes E₃P, whereas extracellular K⁺, following dephosphorylation at low ATP concentrations, does so with E₄(K); in both cases ATP hydrolysis and ATP-ADP exchange are inhibited (Beaugé and Glynn, 1979; Beaugé and Campos, 1986). On the other hand, N-ethylmaleimide and oligomycin block the E₃P-E₄P transition and inhibit ATP hydrolysis, but increase ATP-ADP exchange (for references, see Beaugé and Glynn, 1979). To account for our observations, alkalinization must retard or block some forward transition(s) following E₃P (inhibition of ATPase activity), while accelerating some backward steps starting at E₄P without removing enzyme units from the reaction pathway. In yeast H⁺-ATPase, at 35°C, alkalinization inhibits ATP hydrolysis while enhancing, by about 4-fold, ATP-Pi exchange (de Meis et al., 1987). ATP-ADP and ATP-Pi exchanges share the initial partial reactions of the cycle (see Scheme I); ATP-ADP exchange ends at E₃P, whereas ATP-Pi exchange goes as far as E₄. This indicates that high pH halts the overall cycle at the E₃-E₄ transition, and it is consistent with our observations provided some backward rate(s) starting at E₃P, which are limiting at 0°C but not at 20°C, are accelerated when pH is increased. Other comparisons with the ATP-Pi exchange data are difficult because of (a) the large ADP concentration differences, and (b) the very low rates of ATP formation from Pi (0.21 nmol min⁻¹ mg⁻¹ at 35°C) compared with those obtained in our ATP-ADP exchange experiments (12 and 45 nmol min⁻¹ mg⁻¹ at 0 and 20°C, respectively). Incidentally, in the Na⁺,K⁺-ATPase it has been proposed that alkalinization slows the forward E₃P-E₄P transition in the phosphorylation step (Forbush and Klodos, 1991). The pH effects on the plant H⁺-ATPase cannot be the same because a reduction in the phosphorylation reaction should lead to an inhibition, not an activation, of the ATP-ADP exchange. A complete understanding of the mechanism will require the knowledge of all of the intermediates and unidirectional rate constants involved.

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ATP-ADP Exchange by Plant H⁺-ATPase


