Regulation of Stomal Sedoheptulose 1,7-Bisphosphatase Activity by pH and Mg$^{2+}$ Concentration*

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A scheme is proposed for the regulation of stomal sedoheptulose 1,7-bisphosphatase activity which enlarges upon a previously elaborated mechanism (Woodrow, I. E., and Walker, D. A. (1983) Biochim. Biophys. Acta 722, 508–516). The latter involves oxidized (inactive) and reduced (active) enzyme forms. Both the free enzymes and the enzyme-substrate complexes undergo slow oxidation/reduction. This study examines the behavior of the system under pH and Mg$^{2+}$ concentration regimes that are likely to occur in the chloroplast stroma. The control of enzyme activity by pH can be described in terms of each free enzyme and enzyme-substrate complex existing in protonated and nonprotonated forms. The molecular dissociation constants for each protonation reaction were calculated from kinetic data. Mg$^{2+}$ concentration changes modulate these constants. Under conditions that are likely to obtain in the stroma in the dark, the model predicts that approximately 99.1% of the enzyme will be in the inactive forms. Such inactivation is important since it would prevent the reductive pentose phosphate pathway from operating in darkness.

Upon illumination the stromal pH increases by about one pH unit from a near neutral state in darkness (Heldt et al., 1973). The mechanism is believed to involve the “pumping” of protons from the stroma into both the intrathylakoid space (Neumann and Jagendorf, 1964; Trebst, 1974) and the cytosol (Heber and Krause, 1971; Gimmer et al., 1975). The process of altering the pH by using weak acids was employed to investigate the role of stromal pH changes in controlling the flux through the reductive pentose phosphate pathway of photosynthesis during illumination. Where the dissociated and nondissociated forms of weak acids could cross the chloroplast envelope, they constituted a proton shuttle (Pfluger et al., 1978; Heber et al., 1979) and effectively equilibrated the stroma with the surrounding medium (Heber et al., 1979). Addition of weak acids to a medium containing isolated chloroplasts caused an inhibition of CO$_{2}$ fixation and an increase in both the fructose 1,6-bisphosphate and sedoheptulose 1,7-bisphosphate pool sizes (Hiller and Bassham, 1965; Federspiel et al., 1966; Purczeld et al., 1978; Ensers and Heber, 1980; Flügge et al., 1980). The rise in these metabolite levels and the concomitant decline in the carbon flux was interpreted to mean that the activities of fructose bisphosphatase and sedoheptulose bisphosphatase are sensitive to pH changes in the 7–8 range and that, under conditions of declining pH, these enzymes play a significant role in limiting the rate of CO$_{2}$ fixation.

The transfer of protons across the thylakoid membrane is believed to be electrically compensated for by a countertransfer of Mg$^{2+}$ ions (Dilley and Vernon, 1965; Barber et al., 1974; Hind et al., 1974; Krause, 1974; Krause, 1977). Since the chloroplast envelope is relatively impermeable to Mg$^{2+}$ (Pflüger, 1973; Gimmer et al., 1975), this transfer results in an increase in the stromal Mg$^{2+}$ concentration (Hind et al., 1974; Chow et al., 1976). Portis et al. (1977) lowered the stromal Mg$^{2+}$ concentration of illuminated chloroplasts using a divalent ionophore. This effected a decline in the carbon flux and an increase in the sedoheptulose 1,7-bisphosphate and fructose 1,6-bisphosphate levels which were suggested to indicate that the bisphosphatases limited the carbon flux under conditions of declining Mg$^{2+}$ concentration.

In the present report we enlarge upon a previously proposed model for the regulation of sedoheptulose 1,7-bisphosphatase (Woodrow and Walker, 1983) to include the role of stromal pH and Mg$^{2+}$ concentration changes. This unified view of the relationship between enzyme kinetic parameters, the redox state of ferredoxin, and the stromal H$^{+}$, Mg$^{2+}$, and sedoheptulose 1,7-bisphosphate concentrations allows predictions to be made concerning the degree of activation of sedoheptulose 1,7-bisphosphatase under specific conditions. It is probable that enzyme activity in the chloroplast is, under most conditions, related to the light intensity since the latter controls all the factors which regulate sedoheptulose 1,7-bisphosphatase activity. In the extreme case (darkness), it is estimated that less than 1% of the total enzyme is in the active form. Inactivation of sedoheptulose 1,7-bisphosphatase in darkness, therefore, accounts for the cessation of CO$_{2}$ fixation by ribulose 1,5-bisphosphate carboxylase.

**EXPERIMENTAL PROCEDURES**

**Materials**

Wheat (Triticum aestivum L. cv. Sappo) was grown in vermiculite under sunlight and supplementary incandescent lamps. Biochemicals were purchased from Sigma, Munich, F.R.G., auxiliary enzymes from...
addition of tetrathylammonium bromide. The interaction between the latter, sedoheptulose 1,7-bisphosphate and Mg$^{2+}$ is assumed to be negligible. The pH meter was calibrated at 20 °C using 50 mM potassium hydrogen phthalate (pH 4.0) and 50 mM sodium borate (pH 9.22). The titration was repeated at three levels of MgCl$_2$.

**RESULTS**

**Titrations of Sedoheptulose 1,7-Bisphosphate**—The titration curve of sedoheptulose 1,7-bisphosphate over the pH range 4 to 8 shows a single inflection of about pH 6.42. pK$_a$ values of the third (pK$_a$) and fourth (pK$_a$) dissociation constants for sedoheptulose 1,7-bisphosphoric acid at an ionic strength of 0.08 M of 6.02 and 6.92, respectively, were estimated from the pH and slope at the midpoint (Table I) (Martell and Calvin, 1952). The separation of these values is only slightly greater than that expected for identical phosphate groups (Martell and Calvin, 1952).

The ionic species most probably present in the current experiments are related by the following equilibria.

\[
\begin{align*}
H_2SBP^+ & \rightleftharpoons HSBP^- + pK_a^1 \\
K_1 & \rightleftharpoons SBP^- + pK_a^2 \\
K_2 & \rightleftharpoons MgHSBP^+ + pK_a^3 \\
K_3 & \rightleftharpoons MgSBP^2^- + pK_a^4 \\
\end{align*}
\]

The stability constants of the magnesium sedoheptulose 1,7-bisphosphatase complexes are given by $K_1$, $K_2$, and $K_3$. pK$_a$ and pK$_a$ are pH values of the dissociation constants for the MgH$_2$SBP and MgHSBP$^-$ species, respectively.

In the absence of Mg$^{2+}$, the amount of sedoheptulose 1,7-bisphosphate in the tetraanionic state over the pH range used in the kinetic experiments is shown in Table II. Titration in the presence of 2, 10, and 20 mM MgCl$_2$ were also performed to evaluate the other equilibrium constants (Table I). Approximate values for $K_2$ and $K_3$ of 159 M$^{-1}$ and 587 M$^{-1}$, respectively, were calculated using the method described by O'Sullivan and Perrin (1964). The pK$_a$ values of the dissociation constants $K_a$ and $K_a$ are approximately 5.43 and 6.24, respectively. Over the pH range used in the kinetic experiments and in the presence of 10 mM Mg$^{2+}$, most of the sedoheptulose 1,7-bisphosphate occurs in the MgSBP$^2-$ form (Table II). It is, therefore, probable that the latter is a substrate for the catalytic reaction. Nevertheless, formation of species such as MgSBP and Mg(SBP)$^{2-}$ cannot be excluded, especially at higher Mg$^{2+}$ levels.

**Regulation of Sedoheptulose 1,7-Bisphosphatase Activity**—The dependence of the steady state reaction velocity ($V_o$) on Me$^{2+}$ and Mg$^{2+}$ concentration is consistent with the simple dibasic acid model of Michaelis and Davidson (1911). The data were analyzed by plotting the logarithms of the kinetic constants against pH (Dixon, 1953). Fig. 3 shows a plot of log $V$ versus pH. $V$ was calculated from Lineweaver-Burk plots and represents the maximum reaction velocity at given H$^+$ and Mg$^{2+}$ concentrations. Over the pH range likely to occur in the chloroplast stroma, the data are consistent with the occurrence of a single ionization step. The second step of the

**TABLE I**

| [MgCl$_2$] | Middle pH | Slope* |
|-----------|-----------|--------|
| mM       |           |        |
| 0         | 6.42      | -0.98  |
| 2         | 6.35      | -0.95  |
| 10        | 6.03      | -0.87  |
| 20        | 5.78      | -0.80  |

* At the midpoint of the titration curve.
Dependence of the proportion of two ionic species of sedoheptulose 1,7-bisphosphate on pH

| pH  | SBP®* | MgSBP®* |
|-----|-------|---------|
| 7.3 | 77    | 92      |
| 7.5 | 82    | 95      |
| 7.7 | 88    | 97      |
| 8.0 | 94    | 98      |
| 8.4 | 97    | 99      |

*Calculations were made assuming pK₆ values for the third and fourth dissociation constants of 6.02 and 6.82, respectively, and the absence of Mg²⁺.

*Calculations were made assuming pK₅ values for MgHSBP and MgHSBP⁻ dissociation constants of 5.43 and 6.24, respectively, and the presence of 10 mM Mg²⁺.

FIG. 2. Mechanism for the regulation of sedoheptulose 1,7-bisphosphatase activity. The primed and unprimed species represent reduced and oxidized enzyme forms, respectively. R and O are the reductant and oxidant, respectively, k is the rate constant for a given step, Kₛ, K₆, K₇, and K₈ are the molecular dissociation constants which describe the protonation of the enzyme forms. Kₛ, K₆, K₇, and K₈ describe substrate binding to the enzyme forms. It is assumed that only the reduced nonprotonated enzyme form (E') is capable of catalyzing the conversion of substrate (S) to product (P).

Michaelis and Davidsohn (1911) model is negligible over this pH range. Since most of the substrate exists as a single species (MgSBP²⁻) over this pH range, changes in apparent kinetic properties of sedoheptulose 1,7-bisphosphatase do not appear to be due to substrate effects. The plot of log V versus pH was made using both 10 and 2 mM Mg²⁺, and molecular dissociation pK values of 7.67 and at least 8.3, respectively, were recorded for the active enzyme-substrate complex. The plot of log (V/Kₛ) versus pH shown in Fig. 4 gives a pK value for ionization of the free active enzyme of 7.82 (10 mM Mg²⁺).

In both graphs, the slope of the linear portions at the lower pH values is about 1. This probably indicates that one protonation is required to convert the enzyme form predominant over these pH ranges into the active form (Dixon, 1953).

The activation of sedoheptulose 1,7-bisphosphatase was studied under several pH regimes at constant concentrations of substrate, reductant, and Mg²⁺ (Fig. 5). Plots of τ (τ⁻¹ is the apparent rate constant for enzyme activation) versus the H⁺ concentration yielded pK₆ (Fig. 2) values of 8.49 and 8.8 for 10 mM Mg²⁺ and 2 mM Mg²⁺, respectively. The linear relationship between τ and the H⁺ concentration is consistent with the models shown in Fig. 2. The Kₛ value represents the molecular dissociation constant for the inactive enzyme-substrate complex. Graphs of τ versus [sedoheptulose 1,7-bisphosphatase]⁻¹ were made at various pH values. The inverse of the abscissa intercepts of these plots were then plotted against the inverse of the H⁺ concentration (Fig. 6). The linear portion of this graph gave Kₛ and pK₆ values of 69.2 μM and 8.02, respectively (Fig. 2). This method of analyzing the
were functions of $K$, who examined the catalytic and relaxation properties of the nonprotonated reduced form is the active species. The basis can be described by the models presented in Fig. 2.

These measurements were made at a constant pH, and the apparent kinetic constant for protonation of the inactive enzyme ($E$) and the dissociation constant for substrate binding to the inactive enzyme.

results is discussed in the next section.

**Analysis of Sedoheptulose 1,7-Bisphosphatase Activation Kinetics**—The data presented in this study indicate that enzyme species undergo protonation/deprotonation reactions which can be described by the models presented in Fig. 2. The nonprotonated reduced form is the active species. The basis of this model was deduced by Woodrow and Walker (1983) who examined the catalytic and relaxation properties of the system under various substrate and reductant regimes. These measurements were made at a constant pH, and the apparent $K_a$ and $K_d$ for substrate binding to the inactive enzyme form were functions of $K_1$, $K_4$, $K_6$, and $K_8$, and $K_5$, $K_7$, and $K_a$, respectively.

In the present analysis, the protonation/deprotonation and substrate-binding reactions are assumed to be much faster than the oxidation/reduction reactions. This is a reasonable assumption because the latter have half-lives of the order of minutes (Woodrow and Walker, 1983; Woodrow et al., 1983).

It is also assumed that the overall reaction is irreversible, the substrate level remains constant, and there is no product inhibition. Under these conditions, the slowest relaxation will be due to the oxidation/reduction of the enzyme and enzyme-substrate complex and can be described by a single rate constant. The relationship between the latter and the catalytic reaction velocity was derived by Frieden (1970) and is given by

$$v_t = v_f + (v_0 - v_f)e^{-kt}$$  (1)

where $v_t$ is the reaction velocity at time $t$ (which is relative to the change in conditions that initiates the slow relaxation), $v_f$ the final reaction velocity at $t = \infty$, $v_0$ the initial reaction velocity, and $k$ the apparent rate constant describing the transition to the new steady state.

If it is assumed that the concentration of reductant is much greater than that of the enzyme and that the level of reductant ($R$) and oxidant ($O$) remains essentially constant, then the rate constant for activation/inactivation is given by

$$k = \frac{K_d[R](K_hK_a + [S]k_o)}{K_aK_d[H^+] + K_d + K_d[S](K_h[H^+] + K_a)}$$  (2)

If enzyme activation is examined and the amount of oxidant is assumed to remain essentially zero, then the slow relaxation can be described by

$$\tau = \frac{1}{k} = \frac{K_d[R](K_hK_a + [S]k_o) + [S](K_h[H^+] + [H^+])}{K_d[R](K_hK_a + [S]k_o) + K_d[S](K_h[H^+] + K_a)}$$  (3)

As the concentration of substrate is increased and $[S]k_o \gg k_vk_a$, $\tau$ becomes a linear function of $1/[S]$ (assuming a constant $H^+$ and $R$ concentration),

$$\tau = \frac{K_d[R](K_hK_a + K_v)1}{[S]} + K_d + [H^+] / K_d[R]k_o$$  (4)

At very large substrate levels,

$$\tau = \frac{1}{[R]k_o} + \frac{[H^+]}{K_d[R]k_o}$$  (5)

A graph of $\tau$ versus $[H^+]$, under these conditions, intercepts the ordinate axis at $[H^+] = -K_d$.

Plots of $\tau$ versus $1/[S]$ intercept the abscissa at $I = \frac{1}{[S]} = \frac{K_d[R][H^+]}{K_d[R][H^+][S]}$.

And if $[H^+] \gg K_d$, $1/I$ becomes a linear function of $1/[H^+]$,

$$\frac{1}{I} = \frac{K_d[R]}{K_d} + \frac{K_d[R]}{[H^+]}$$  (7)

Equations 6 and 7 allow the determination of the molecular dissociation constants ($K_a$ and $K_d$) and substrate-binding constant ($K_v$) for the inactive enzyme form.

The concentration of individual enzyme species can be described by assuming that all the steps prior to product release are at equilibrium and that the time of measurement is long compared to the time required for adjustment to equilibrium. The concentrations of the species shown in Fig. 2 are given by

$$\frac{[\text{E}' - S]}{E_o} = \frac{[S]A}{K_a}$$  (8)

$$\frac{[\text{E}' - S] + [\text{E}]}{E_o} = \frac{(K_a + [S])A}{K_a}$$  (9)

$$\frac{[\text{E}' - H - S] + [\text{E}' - H]}{E_o} = \frac{[H^+] + [A][S][H^+]}{K_a + K_d[S]}$$  (10)

$$\frac{[\text{E} - S] + [\text{E}]}{E_o} = \frac{[A][O][K_a + K_d[S]]}{K_i}$$  (11)

$$\frac{[\text{E} - H - S] + [\text{E} - H]}{E_o} = \frac{[A][H^+][O][K_a + K_d[S]]}{K_i}$$  (12)

where

$$A = \left[1 + \frac{[H^+]}{K_i} + \frac{[H^+]^2}{K_iK_d[S]} + \left\frac{[S]}{K_a} + \frac{[O]}{K_i} \frac{[K_a + K_d[S] + \frac{[H^+]K_i}{K_d} + \frac{[H^+][S]K_2}{K_d[K_i]}}{K_i} \right]^{-1}$$  (13)

and $E_o$ is the total enzyme concentration.

**DISCUSSION**

The simplest model that is consistent with the measured dependence of the apparent $K_a$, $V_{max}$, and $\tau$ values on proton concentration is shown in Fig. 2. This mechanism is based upon one previously suggested to account for the effect of reductant, oxidant, and substrate on enzyme activity (Woodrow and Walker, 1983; Woodrow et al., 1983).

These mechanisms are based on kinetic evidence and, therefore, may represent simplifications of the actual mechanisms.
Description of the effect of pH as a single protonation reaction is undoubtedly a simplification (Tipton and Dixon, 1980). The mechanism could also conceivably involve oxidation/reduction of the protonated enzyme forms. In this case, activation would also be described by a single first order rate constant. However, to be consistent with the present data the rate constants for reduction of the E·H and E·S·H forms must be much smaller than $k_5$ and $k_6$. It is also possible that the protonated enzyme forms bind substrate. Although this leads to different paths by which the active enzyme-substrate complex may be formed, the interpretation will not be affected if all the steps prior to product release are close to equilibrium.

If the latter is not the case, substrate binding to the protonated enzyme forms would result in extremely complicated kinetics (Laider, 1955; Peller and Alberty, 1963; Stewart and Lee, 1967; Kaplan and Laider, 1967). The inclusion of more than one enzyme-substrate intermediate is also a possibility. However, the number of these intermediates is unimportant in terms of describing the behavior of the system since the constants obtained from the pH dependence of V are average values weighted in favor of the predominant complex (Tipton and Dixon, 1980).

The proton concentration has a multiple role in the present model; it controls the apparent $K_a$ and $V_{max}$ values as well as the total amount of enzyme in the reduced form. Variations in pH will cause a net shift of enzyme from the active to the inactive forms or vice versa. This phenomenon is caused by the differences between $pK_a$ and $pK_b$ (and almost certainly $pK_a$ and $pK_b$) values, $M^2+$ also controls the distribution of enzyme between protonated and nonprotonated and oxidized and reduced forms (Table III). Low levels of $M^2+$ may also affect the system by reducing the proportion of substrate in the MgSBP$^+$ form. Effects of $H^+$ and $Mg^2+$ consistent with the present proposals were also observed by Laing et al. (1981) using a chloroplast extract. The pH for optimal enzyme activity was shifted by changing the $Mg^2+$ concentration. A similar effect was observed by Minot et al. (1982) for stromal fructose 1,6-bisphosphatase. These authors also used a single protonation step to describe the effect of the $H^+$ concentration on enzyme activation.

In the chloroplast, the kinetic properties of sedoheptulose 1,7-bisphosphatase appear to be ultimately controlled by the light intensity. Both the stromal $H^+$ and $Mg^2+$ concentrations are linked to the rate of photosynthetic electron transport.

| Conditions | $E^+$ | $E^+$ | $E^+$ | $E^+$ | $E^+$ |
|------------|-------|-------|-------|-------|-------|
| 10 mM $Mg^2+$, pH 8; $O/R = 1$ | 35.4 | 20.0 | 19.8 | 24.7 | | |
| 10 mM $Mg^2+$, pH 8; $O/R = 0.2$ | 55.0 | 31.1 | 6.1 | 2.8 | | |
| 2 mM $Mg^2+$, pH 7; $O/R = 1$ | 2.1 | 65.0 | 1.2 | 31.6 | | |
| 2 mM $Mg^2+$, pH 7; $O/R = 0.5$ | 0.9 | 28.1 | 2.6 | 68.4 | | |

The abbreviation of enzyme forms is described in the legend to Fig. 1. Calculations of the proportions were made according to the equations described under "Results." In the calculations it was assumed for convenience that $k_5 = 1$ and (sedoheptulose 1,7-bisphosphatase) = 0.1 nM.

It is also possible that a reductant or oxidant is also a possibility. However, the number of these intermediates is unimportant in terms of describing the behavior of the system since the constants obtained from the pH dependence of V are average values weighted in favor of the predominant complex (Tipton and Dixon, 1980).

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