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The influence of sugar synthesis and transport rates on bioenergetics and kinetics of higher plant photosynthesis

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Abstract

We have obtained the theoretical dependences of stromal metabolite steady-state concentrations on external inorganic phosphate (P_i) concentration. For this purpose, the theoretical model of photosynthesis, earlier described in [Ann. Appl. Biol. 138 (2001) 117], was modified to account for the regulation of starch formation by 3-phosphoglycerate (PGA) to P_i ratio. When the rate constant of starch synthesis is taken to be independent on PGA/P_i ratio, the steady-state concentrations of Calvin cycle metabolites and starch were found to change insignificantly as external P_i concentration increases in wide range. However, as external P_i range exceeds a critical value, the steady-state concentrations of all metabolites change abruptly. If the rate constant of starch synthesis depends on PGA/P_i ratio, the steady-state concentrations of stromal metabolites change qualitatively in the same way with the increase of external P_i. However, no abrupt changes of metabolite and starch steady-state levels at high concentration of P_i are observed. These results testify that the control of starch synthesis by PGA/P_i ratio makes the photosynthetic system more stable in wide range of external P_i concentrations. © 2002 Published by Elsevier Science B.V.

Keywords: Starch; Inorganic phosphate; Phosphate translocator; Theoretical model

1. Introduction

Calvin cycle activity is regulated in answer to the physiological needs of photosynthesising cell. Inorganic phosphate (P_i) and triose phosphate levels play an important role in this regulation due to the work of phosphate translocator (TPT) [2]. TPT provides the inorganic phosphate balance inside and outside the chloroplast. A change in inorganic phosphate level indirectly influences the carbon fixation activity through the variation of Calvin cycle intermediate concentrations in the chloroplast [3]. If triose phosphates (TP) exit from the chloroplast via TPT due to high concentration of external orthophosphate, then a smaller portion of TP is used for ribulose bisphosphate (RuBP) regeneration. Ribulose bisphosphatase (RuBPase) activation takes time and hence the rate of CO_2 fixation decreases [2,4]. Thus, high concentrations of inorganic phosphate in cytosol may limit the photosynthesis rate. This limitation can be diminished by 3-phosphoglycerate (PGA) or TP addition due to TPT function in the chloroplast envelope [5]. An increased availability of exported products of photosynthetic metabolism (photosynthates) in the cytosol does not decrease the net Calvin cycle activity, but redirects the reaction flux to starch production [6]. The starch is a basic supplying substance of plant cell, which is formed and accumulated in the chloroplast. ADP-glucose pyrophosphorilase (AGPase) is a key enzyme of starch synthesis in the chloroplast stroma. The studies of starch deficient mutants show that starch level is directly correlated with AGPase activity, which is the required PGA for maximal activity and is inhibited by inorganic phosphate [7]. Many works [6,8] contain theoretical models comprising starch synthesis, but they do not account for the regulatory role of PGA/P_i ratio in starch synthesis. In the present work, we calculate and compare the dependences of stromal metabolite steady-state concentrations on the concentration of external P_i in a theoretical model of photosynthesis with and without taking into account the regulation of starch synthesis rate constant on PGA/P_i ratio.

2. Methods

We have used a theoretical model of photosynthesis including light absorption, charge separation, linear and cyclic electron transfer between the photosystems, main reactions of Calvin cycle and TPT, earlier described in

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Ref. [1]. We have extended the model to include the starch synthesis and degradation. In the modified model, the starch is obtained from TP in a single reaction where two inorganic phosphate molecules form. For starch synthesis regulation by PGA/P_i ratio, the rate constant of the starch synthesis was taken to be proportional to PGA/P_i ratio. The regime with the inorganic phosphate lack was used in our calculations in order to increase the system sensitivity to the inorganic phosphate concentration alterations in the cytosol. The calculations were conducted with the help of a home-made Fortran 5.0 program. Standard program Merson was used to solve the system of ordinary differential equations consisting the model under consideration.

3. Results and discussion

Theoretical dependences of Calvin cycle intermediate steady-state concentrations on external P_i concentration in the regime with P_i lack are represented in Figs. 1 and 2. We can see that PGA concentration decreases, concentrations of glyceradehyde 3-phosphate (G3P), ATP and RuBP do not alter significantly, concentrations of diphosphoglycerate (DPGA), starch and external trioses increase with the increase of external phosphate concentration. As external P_i level exceeds a critical value, steady-state concentrations of all the above-mentioned metabolites change abruptly. These results may be explained by the supposition that while external concentration of P_i is lower than the critical one, the system successfully processes the entering phosphate; it is utilized in ATP formation or exchanged for TP via TPT. Triose leak from the chloroplast can be compensated by their synthesis in Calvin cycle. When the critical concentration of P_i is reached, TP flow to the cytosol exceeds the rate of its formation inside the chloroplast,

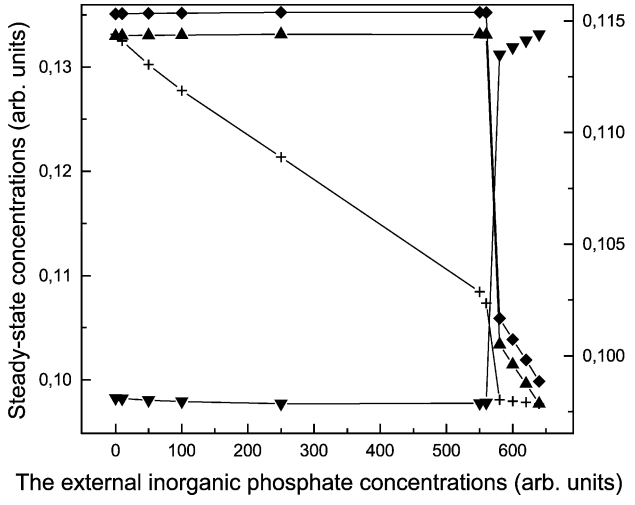

Fig. 1. The dependence of steady-state concentrations of PGA (+), RuBP (▲), G3P (♦/◇) and ATP (▼) on external orthophosphate concentration without tacking into account the starch synthesis rate dependence on the PGA/P_i ratio.

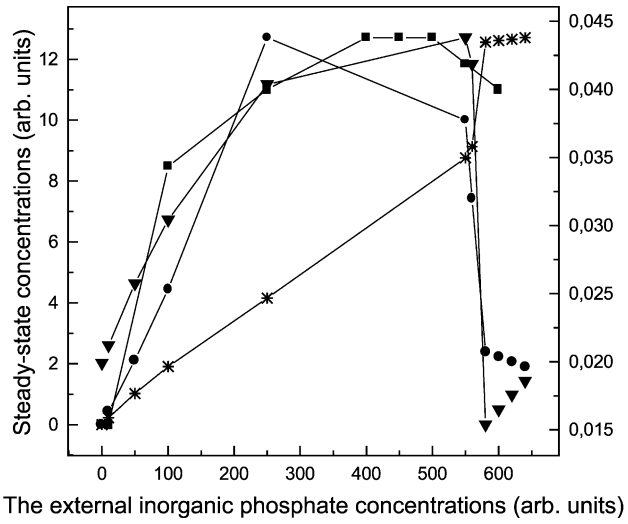

Fig. 2. The dependences of steady-state concentrations of DPGA (●), starch (■), external trioses (∗) and internal orthophosphate (▼) on external orthophosphate concentration without tacking into account the starch synthesis rate dependence on the PGA/ P_i ratio.

trioses begin to exit rapidly to the cytosol and to join partially the starch production pathway. These processes result in the decrease of RuBP, PGA and DPGA levels and increase in external triose and starch levels. As TP is actively exported, orthophosphate almost does not exit from the chloroplast, but is used for ATP synthesis. ATP consumption for RuBP and DPGA formation decreases due to low substrate levels in these reactions. The inclusion of internal P_i into ATP formation and diminished ATP expenditure in Calvin cycle reactions result in an increase of steady-state ATP concentration. ATP is produced faster than consumed, hence, the concentrations of substrates for ATP-consuming reactions decrease; G3P exits to the cytosol for sucrose synthesis.

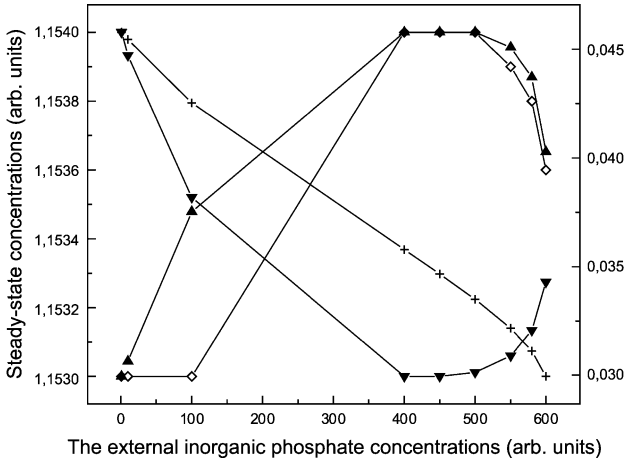

Fig. 3. The dependence of steady-state concentrations of PGA (+), RuBP (▲), G3P (♦/◇) and ATP (▼) on external orthophosphate concentration with tacking into account the starch synthesis rate dependence on the PGA/ P_i ratio.

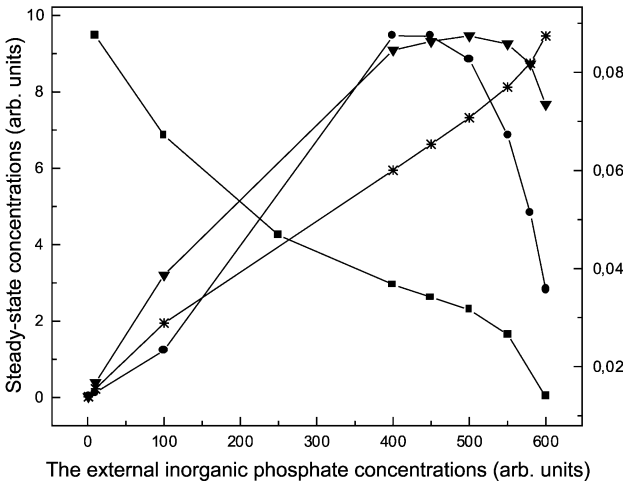

Fig. 4. The dependences of steady-state concentrations of DPGA (●), starch (■), external trioses (∗) and internal orthophosphate (▼) on external orthophosphate concentration with tacking into account the starch synthesis rate dependence on the PGA/P_i ratio.

The steady-state Calvin cycle intermediate, ATP and starch concentrations versus external phosphate plots for a model with starch synthesis rate constant depending on PGA/P_i ratio are presented in Figs. 3 and 4. First of all, it can be noted that the steady-state concentration of starch decreases insignificantly while external P_i concentration increases (Fig. 4). It can be explained as follows. If the external P_i concentration increases, more trioses will flow from chloroplast to cytosol in exchange for inorganic phosphate. There will be less PGA and more P_i, hence, the PGA/P_i ratio will decrease. AGPase will be inactivated and starch synthesis will slow down. Figs. 3 and 4 show that, as in the model with starch synthesis independent of PGA/P_i ratio, PGA concentration is diminished, G3P and RuBP concentrations almost do not alter, internal P_i, DPGA and external trioses are accumulated, ATP concentration decreases insignificantly with the increase of external P_i. However, unlike the previous case, no abrupt changes of Calvin cycle metabolite concentrations are observed. Most likely, as P_i concentration increases, the ratio PGA/P_i and hence starch level in the chloroplast decline and triose synthesis proceeds more efficiently. These results testify that the control of starch synthesis by PGA/P_i ratio has made the system more stable in wide range of external P_i concentrations.

4. Conclusion

We have obtained theoretical dependences of steady-state concentration of stromal metabolites on the concentration of P_i in cytosol in two cases with PGA/P_i dependent starch production and without this dependence. The results obtained have been discussed. Our theoretical investigates lead to the conclusion that the steady-state levels of Calvin cycle intermediates are controlled by the external level of inorganic phosphate.

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