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Ryde-Pettersson, Ulf

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Ulf RYDE-PETTERSSON

Avdelningen för biokemi, Kemicentrum, Lunds universitet, Sweden

A systematic search for possible sources of experimentally observed oscillations in the photosynthetic reaction system has been performed by application of recent theoretical results characterizing the transient-state rate behaviour of metabolic reactions involving two independent concentration variables. All subsystems involving two independent reactants in metabolically fundamental parts of the Calvin cycle and the ancillary pathways of starch and sucrose synthesis have been examined in order to decide on basis of their kinetic and stoichiometric structure whether or not they may trigger oscillations.

The results show that no less than 20 possible oscillators can be identified in the examined reaction system, only three of which have been previously considered as potential sources of experimentally observed oscillations. This illustrates the superiority of the method now applied over those previously used to identify possible two-reactant sources of metabolic oscillations and indicates that there should be no difficulty in complex metabolic pathways to point to a multitude of interactions that may trigger an oscillatory rate behaviour of the system.

Oscillations in the photosynthetic reaction rate were first described in 1938 [1] and have since then been the subject of extensive studies. Several attempts have been made to trace the mechanical origin of the oscillations [2–10]. Such attempts have usually been based on intuitive reasoning and concerned possible oscillatory sources tentatively selected by trial-and-error. No systematic search for potential oscillators in the photosynthetic reaction system has ever been performed and no convincing explanation for the experimentally observed oscillations would yet seem to be available.

Typical oscillations in the rate of photosynthetic carbon dioxide fixation are weakly damped, symmetric and highly sinusoidal with a constant period [3–5, 11–13]. This indicates that the oscillations can be mathematically described by a pair of complex conjugated transient rate parameters with a time constant well separated from the time constants of the other transients governing the kinetics of the system. According to the theory of time hierarchy separation [14–17], therefore, the rate behaviour of the system may be accurately described by a two-variable model over the time scale of the oscillations. It is reasonable then to assume that these variables represent the concentrations of two of the reactants in the system, i.e. that the oscillations are triggered by the kinetic interplay of two reactants. This approach has been frequently used in theoretical treatments as well as in the kinetic modelling of oscillating reactions [15, 17–21]. Its application to biological systems has significantly advanced our understanding of the origin of, for example, the glycolytic oscillations [15, 18–20].

In a recent theoretical study [21] the mechanistic patterns were characterized which may lead to oscillations triggered by kinetic interactions of two reactants in generalized metabolic pathways. The latter study provides the information required to decide if two metabolites in an arbitrary pathway are so kinetically interrelated that they may give rise to oscillations, i.e. information which may be used to search systematically for the presence of potential sources of oscillations in arbitrarily complex metabolic networks. Such a search has now been performed in a reaction system constituted by the Calvin photosynthesis cycle and ancillary pathways of starch and sucrose formation. The results show that there is, in the examined system, a multitude of two-reactant interactions which, in principle, may give rise to oscillations resembling the strongly damped ones observed experimentally in studies of isolated chloroplasts.

RESULTS

Reaction system considered

The reaction system considered in the present investigation is depicted in Scheme 1. It comprises the Calvin photosynthesis cycle and ancillary pathway of starch formation in the stromal solution of the chloroplast, as well as the reactions leading to sucrose synthesis in the cytosol. The light-dependent primary photosynthetic events are not included in Scheme 1. ATP is assumed to be generated through the action of ATP synthetase (step v_{16}) and the concentrations of NADP, NADPH, NAD, NADH, UTP, UDP and CO_2 are treated as fixed reaction parameters.

Several of the enzymic reactions in Scheme 1 have been reported to occur at rates which are modified (activated or inhibited) by metabolites that do not represent a substrate for or product of the reaction. The modifying interactions now considered are listed in Table 1; they do not include reactions involving the phosphate translocator.

Correspondence to U. Ryde-Pettersson, Avdelningen för biokemi, Kemicentrum, Lunds universitet, Box 124, S-221 00 Lund, Sweden
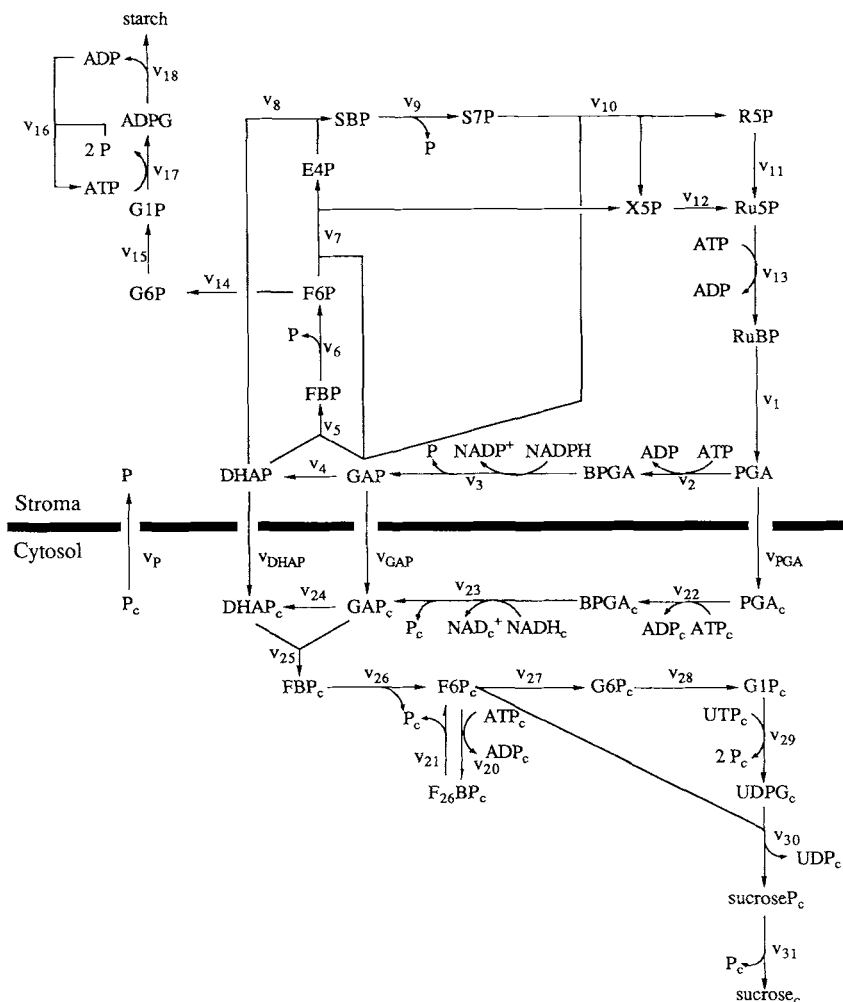
Scheme 1. *The reaction system considered.* A subscript c indicates that the metabolite is located in the cytosol and not in the chloroplast stroma. RuBP, ribulose 1,5-bisphosphate; PGA, 3-phosphoglyceric acid; BPGA, 2,3-bisphosphoglyceric acid; GAP, glyceraldehyde 3-phosphate; DHAP, dihydroxyacetone phosphate; F6P, fructose 6-phosphate; FBP, fructose 1,6-bisphosphate; $F_{26}BP$, fructose 2,6-bisphosphate; E4P, erythrose 4-phosphate; SBP, sedoheptulose 1,7-bisphosphate; S7P, sedoheptulose 7-phosphate; R5P, ribose 5-phosphate; X5P, xylulose 5-phosphate; Ru5P, ribulose 5-phosphate; G6P, glucose 6-phosphate; G1P, glucose 1-phosphate; ADPG, ADP-glucose; UDPG, UDP-glucose; P, inorganic orthophosphate

Table 1. *Reported modifying kinetic interactions for the reactions and reactants in Scheme 1*

RuBP, ribulose 1,5-bisphosphate; PGA, 3-phosphoglyceric acid; BPGA, 2,3-bisphosphoglyceric acid; DHAP, dihydroxyacetone phosphate; F6P, fructose 6-phosphate; FBP, fructose 1,6-bisphosphate; $F_{26}BP$, fructose 2,6-bisphosphate; SBP, sedoheptulose 1,7-bisphosphate; R5P, ribose 5-phosphate; Ru5P, ribulose 5-phosphate; G6P, glucose 6-phosphate

Reaction	Inhibitor	Activator	Reference
v_1	FBP, SBP, P_i, NADPH		[27]
v_4		RuBP, PGA, FBP, P_i	[28]
v_5	RuBP, PGA, ADP		[29]
v_{11}		RuBP	[30]
v_{13}	PGA, FBP, P_i		[31]
v_{17}		PGA, BPGA, FBP, F6P, R5P	[32]
v_{20}	PGA, DHAP, sucrose	P_i	[33, 34]
v_{21}	sucrose	PGA	[33, 35]
v_{24}		PGA, FBP, P_i	[28]
v_{25}	PGA, ADP		[29]
v_{26}	FBP, $F_{26}BP$		[33, 36]
v_{30}	P_i, sucrose	G6P	[35, 37]

Identification of potential oscillators

The metabolic network in Scheme 1 involves 35 non-enzymic reactants participating in a total of 33 reaction steps and 37 modifying kinetic interactions. The stoichiometry of adenylate-dependent steps in the system prescribes that the sum of concentrations of ATP and ADP will remain constant. Due to this adenylate conservation constraint, the concentrations of ATP and ADP become interdependent and it suffices to consider one of them as an independent variable; inhibition of a reaction by ADP is mathematically equivalent to activation of the same reaction by ATP and vice versa. This means that the system in Scheme 1 comprises 528 pairs of concentration variables that may be regarded as independent. The patterns of substrate/product stoichiometry and modifying kinetic interactions characterizing each one of the corresponding 528 pairs of metabolites in Scheme 1 were examined in order to decide whether or not they agree with those that may allow for the appearance of oscillatory transients according to previous theoretical results [21]. By this approach, no less than 19 possible sources of oscillations could be identified in the reaction system examined. Table 2 lists these potentially oscillating two-reactant subsystems.

As has been pointed out elsewhere [22, 23], all carbo-hydrate metabolites participating in the Calvin cycle are subjected to a moiety conservation constraint with phosphate as the conserved moiety. By arguments analogous to those considered in the treatment of oscillations in single-enzyme reactions [24], it can be shown that such a moiety-conserved system constitutes a potential source of oscillations which may give rise to oscillations that, by necessity, are strongly damped. The phosphate conservation constraint characterizing the Calvin cycle, therefore, represents an additional potential source of oscillations in the examined reaction system. From a theoretical point of view the latter source is nearly related to the one discussed by Walker and Giersch [4 − 7] who tentatively attributed the experimentally observed photosynthetic oscillations to a competition for ATP by the two kinases in the Calvin cycle.

Kinetic properties of the ribulose 1,5-bisphosphate/ 3-phosphoglycerate subsystem

Results in Table 2 are of interest because they identify all bireactant subsystems in Scheme 1 that may exhibit oscillatory transient-state kinetics and hence indicate what subsystems should be subjected to further study in order to establish their actual kinetic behaviour under physiological conditions. Such studies may be performed by the mathematical approach described previously [21] and require detailed assumptions as to the rate equations, kinetic parameter values, and reactant concentrations that apply. While it is beyond the purpose of the present investigation to characterize the actual kinetic behaviour of all of the identified potential sources of oscillations in Scheme 1 by this approach, the reaction kinetics of the first subsystem in Table 2 will be examined in full detail in order to illustrate the nature of the approach and of the information one may obtain.

As has been previously reported [9, 23, 25], the available evidence indicates that the steady-state rate equations for reactions catalysed by ribulose 5-phosphate kinase, ribulose 1,5-bisphosphate carboxylase, 3-phosphoglycerate kinase and the phosphate translocator of the chloroplast membrane are given, respectively, by

tone phosphate, FBP, fructose 1,6-bisphosphate, SBP = sedoheptulose 1,7-bisphosphate and Ru5P = ribulose 5-phosphate. Experimentally supported estimates of kinetic parameters (cf. [23]) and steady-state reactant concentrations in Eqns (1−4) are listed in Tables 3 and 4, respectively; the concentrations have been selected to be representative for experiments performed with isolated chloroplasts in a medium containing low concentrations (0.1 mM) of inorganic orthophosphate, a condition known to favour the appearance of oscillatory transients in the photosynthetic CO_2-fixation of isolated chloroplasts [13]. Using these rate equations and parameter values, the transient-state rate behaviour of the first subsystem in Table 2 (involving ribulose 1,5-bisphosphate and 3-phosphoglycerate as kinetically interacting metabolites) was characterized by numerical methods [21] with the assumption that concentrations of other metabolites affecting the behaviour of the subsystem attain the steady-state values indicated in Table 4. The typical results in Fig. 1 illustrate that the examined subsystem under such conditions does exhibit an oscillatory response to perturbations of its steady state of operation [the transient rate parameters are $(6.4 \pm 0.63\sqrt{-1})s^{-1}$]. The period of these oscillations is 10 s which is similar to that observed in experiments with algae [11]. Period times of the order of minutes, as observed in experiments with higher plants [3 − 5, 11, 12], may be obtained with slightly changed parameter values. The theoretically predicted oscillations in Fig. 1 are strongly damped, however, and it seems impossible to find physiological model parameters that yield oscillations as weakly damped as those observed experimentally.

DISCUSSION

Previous attempts to explain the mechanistic origin of the oscillatory behaviour of the photosynthetic reaction system in Scheme 1 have considered two potential sources of such oscillations: the regulatory action of fructose 2,6-bisphosphate on sucrose synthesis [9, 10] (cf. subsystem 15 − 16) and the competition for ATP by the two kinases in the Calvin cycle

$$v_{13} = \frac{V_{m13}[\text{Ru5P}][\text{ATP}]}{\left([\text{Ru5P}] + K_{m131}\left(1 + \frac{[\text{PGA}]}{K_{i131}} + \frac{[\text{RuBP}]}{K_{i132}} + \frac{[\text{P}_i]}{K_{i133}}\right)\right)\left([\text{ATP}] + K_{m132}\left(1 + \frac{[\text{ADP}]}{K_{i135}}\right) + \frac{1 + [\text{ADP}]}{K_{i134}}\right)} \tag{1}$$

$$v_1 = \frac{V_{m1}[\text{RuBP}]}{[\text{RuBP}] + K_{m1}\left(1 + \frac{[\text{PGA}]}{K_{i11}} + \frac{[\text{FBP}]}{K_{i12}} + \frac{[\text{SBP}]}{K_{i13}} + \frac{[\text{P}_i]}{K_{i14}} + \frac{[\text{NADPH}]}{K_{i15}}\right)} \tag{2}$$

$$v_2 = \frac{V_{m2}\left([\text{PGA}][\text{ATP}] - \frac{[\text{BPGA}][\text{ADP}]}{K_2}\right)}{K_{m21}K_{m22}\left(1 + \frac{[\text{PGA}]}{K_{m21}} + \frac{[\text{ATP}]}{K_{m22}} + \frac{[\text{BPGA}]}{K_{m23}} + \frac{[\text{ADP}]}{K_{m24}} + \frac{[\text{PGA}][\text{ATP}]}{K_{m21}K_{m22}} + \frac{[\text{BPGA}][\text{ATP}]}{K_{m23}K_{m24}}\right)} \tag{3}$$

$$v_{\text{PGA}} = \frac{V_{ex}[\text{PGA}]}{([\text{PGA}] + K_{\text{PGA}})\left(1 + \frac{K_{\text{P}_{ic/DHAP}}}{[\text{P}_{ic/DHAP}]}\left(\frac{[\text{P}_i]}{K_{\text{P}_i}} + \frac{[\text{PGA}]}{K_{\text{PGA}}} + \frac{[\text{GAP}]}{K_{\text{GAP}}} + \frac{[\text{P}_{ic/DHAP}]}{K_{\text{DHAP}}}\right)\right)} \tag{4}$$

where RuBP = ribulose 1,5-bisphosphate, PGA = 3-phosphoglyceric acid, BPGA = 2,3-bisphosphoglyceric acid, GAP = glyceraldehyde 3-phosphate, DHAP = dihydroxyace-

[4 − 7]. The present results establish that Scheme 1 includes at least 17 additional subsystems that are equally likely as possible sources of oscillations in the examined system. This illus-

Table 2. *Possibly oscillating subsystems of the reaction system in Scheme 1*

Modifying kinetic interactions necessary for oscillations to occur are indicated by broken arrows. '$+$' and '$-$' means activation and inhibition, respectively. The fluxes v_i are the same as in Scheme 1. The stoichiometric and kinetic structures of the subsystems are categorized according to the nomenclature in [21] as: 3, mixed crosswise coupling; 4, feedback inhibition; 5, branch output activation; 7, branch input inhibition; 8a, substrate inhibition; 9, bimolecular output inhibition; 10, bimolecular branch input activation; 12, bimolecular input cycle; 14, bimolecular branch output inhibition; 16, bimolecular output cycle; cytosol in the last column indicates that the subsystem is, with obvious alterations, also possible in the cytosol. RuBP, ribulose 1,5-bisphosphate; PGA, 3-phosphoglyceric acid; BPGA, 2,3-bisphosphoglyceric acid; GAP, glyceraldehyde 3-phosphate; DHAP, dihydroxyacetone phosp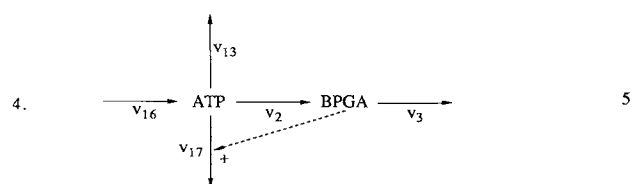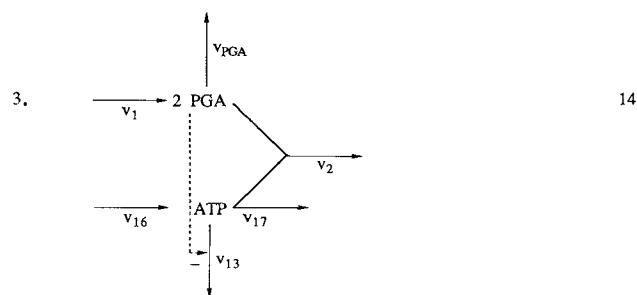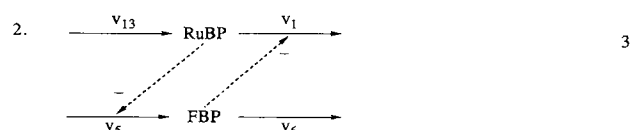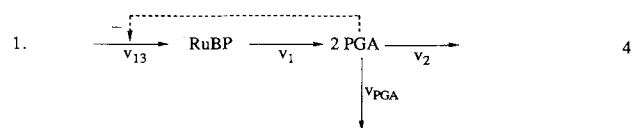hate; F6P, fructose 6-phosphate; FBP, fructose 1,6-bisphosphate; $F_{26}BP$, fructose 2,6-bisphosphate; G6P, glucose 6-phosphate; UDPG, UDP-glucose; P, inorganic orthophosphate
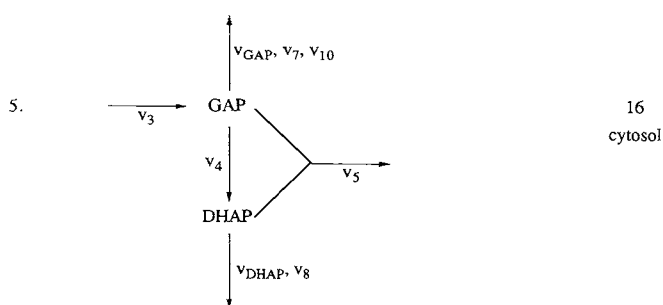
Number	Structure	Category
1.	$\xrightarrow{v_{13}}$ RuBP $\xrightarrow{v_1}$ 2 PGA $\xrightarrow{v_2}$; $\downarrow v_{PGA}$	4
2.	$\xrightarrow{v_{13}}$ RuBP $\xrightarrow{v_1}$; $\xrightarrow{v_5}$ FBP $\xrightarrow{v_6}$	3
3.	$\uparrow v_{PGA}$; $\xrightarrow{v_1}$ 2 PGA ; $\xrightarrow{v_{16}}$ ATP $\xrightarrow{v_{17}}$ $\searrow v_2$; $\downarrow v_{13}$	14
4.	$\xrightarrow{v_{16}}$ ATP $\xrightarrow{v_2}$ BPGA $\xrightarrow{v_3}$; $v_{17} \downarrow$ $+$	5
5.	$\xrightarrow{v_3}$ GAP $^{v_{GAP}, v_7, v_{10}}$; $v_4 \downarrow$ $\searrow v_5$; DHAP $^{v_{DHAP}, v_8}$	16 cytosol
6.	$\xrightarrow{v_3}$ GAP $^{v_{GAP}, v_7, v_{10}}$ $\xrightarrow{v_5}$ FBP $\xrightarrow{v_6}$; $v_4 \downarrow$ $+$	5 cytosol
7.	$\xrightarrow{v_3}$ $\nearrow$ GAP $^{v_4, v_5, v_7, v_{10}}$; $\downarrow v_{GAP}$; P $\xrightarrow{v_{16}}$; $v_{PGA}, v_{DHAP}, v_6, v_9, v_{17}$	12 cytosol
8.	$\xrightarrow{v_5}$ FBP $\xrightarrow{v_6}$; $+$ $+$; $\xrightarrow{v_{16}}$ ATP $\xrightarrow{v_{17}}$; $\downarrow v_2, v_{13}$	3
9.	$\xrightarrow{v_6}$ $\nearrow$ F6P $^{v_7, v_{14}}$; $v_p, v_3, v_6, v_9 \rightarrow$ P $\xrightarrow{v_{16}}$; $+ \uparrow v_{17}$	10
10.	$^{v_{PGA}}$ PGA $\searrow$; $\searrow v_{22}$; ATP$_c$ $\nearrow$; $- \downarrow v_{20}$	14
11.	$\xrightarrow{v_{25}}$ FBP$_c$ $\xrightarrow{v_{26}}$ $-$ F6P$_c$ $\xrightarrow{v_{20}, v_{27}, v_{30}}$; $\uparrow v_{21}$	8a
12.	$\xrightarrow{v_{25}}$ FBP$_c$ $\xrightarrow{v_{26}}$ $-$ P$_c$ $\xrightarrow{v_p}$; $\uparrow v_{21}, v_{23}, v_{29}, v_{31}$	8a

Table 2. Continuation

Number	Structure	Category
13.		5
14.		9
15.		7
16.		7
17.		9
18.		4
19.		4
20.	The moiety conserved Calvin cycle	

Table 3. *Estimates of the kinetic parameters in Eqns (1—4)*
Chl, chlorophyll

Parameter	Value	Reference
K_2	0.00031	[38]
	$\mu mol\ h^{-1}\ (mg\ Chl)^{-1}$	
V_{m1}	340	[39]
V_{m2}	2500	[40]
V_{mx}	250	[41]
V_{m13}	1000	[31]
	mM	
K_{m1}	0.02	[27]
K_{m21}	0.5	[42]
K_{m22}	0.1	[42]
K_{m23}	0.2	[43]
K_{m24}	0.0018	[43]
K_{m131}	0.05	[31]
K_{m132}	0.05	[31]
K_{PGA}	0.25	[44, 45]
K_{GAP}	0.075	[44, 45]
K_{DHAP}	0.077	[44, 45]
K_{P_i}	0.63	[44, 45]
K_{P_ic}	0.74	[44, 45]
K_{i11}	0.84	[27]
K_{i12}	0.04	[27]
K_{i13}	0.075	[27]
K_{i14}	0.9	[27]
K_{i15}	0.07	[27]
K_{i131}	2	[31]
K_{i132}	0.7	[31]
K_{i133}	4	[31]
K_{i134}	2.5	[31]
K_{i135}	0.4	[31]

Table 4. *Estimates of the reactant concentrations in Eqns (1—4)*
RuBP, ribulose 1,5-bisphosphate; BPGA, 2,3-bisphosphoglyceric acid; GAP, glyceraldehyde 3-phosphate; DHAP, dihydroxyacetone phosphate; FBP, fructose 1,6-bisphosphate; SBP, sedoheptulose 1,7-bisphosphate; Ru5P, ribulose 5-phosphate

Reactant	Concentration	Reference
	mM	
BPGA	0.00001	[42]
GAP	0.011	[46, 47]
DHAP	0.25	[46, 47]
FBP	0.3	[46]
SBP	0.15	[46]
Ru5P	0.02	[42]
P_i	2.2	[46]
ATP	0.1	[48]
ADP	0.4	[48]
P_{i_c}	0.1	[46, 47]
NADPH	0.21	[48]

trates the superiority of the systematic method now applied for identification of the subsystems that may trigger photosynthetic oscillations. The method is rapid and of general applicability such that it can be used to identify potential bireactant sources of oscillations in metabolic networks of arbitrary complexity.

Results in Table 2 identify all subsystems that have to be considered in attempts to attribute experimentally observed photosynthetic oscillations to the kinetic interplay of a specific
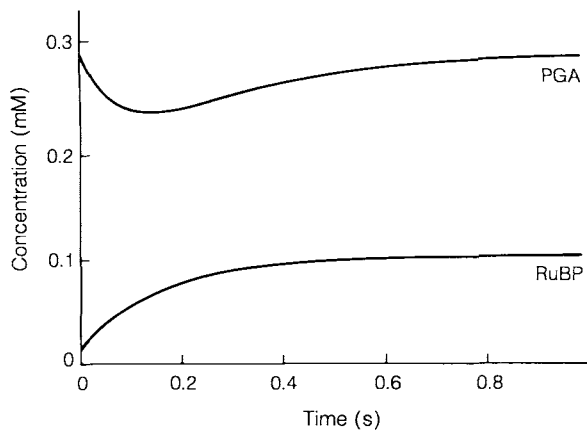
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Fig. 1. *Trajectories for the ribulose 1,5-bisphosphate/3-phosphoglycerate system (subsystem 1).* Time course for reattainment of steady-state conditions following an initial perturbation of the concentration of 3-phosphoglycerate to 10% of its steady-state value. Data calculated by numerical integration using Eqns (1 — 4) and kinetic parameters and concentrations in Tables 3 and 4 respectively. The volume of the chloroplast was assumed to be 33 μl/mg chlorophyll [26]. PGA, 3-phosphoglyceric acid; RuBP, ribulose 1,5-bisphosphate

pair of metabolites in the reaction system defined by Scheme 1. Since the criteria applied for selection of these subsystems do not involve sufficient conditions for the appearance of oscillatory transients, more detailed analyses are required to decide if the subsystems actually do exhibit oscillations under physiological conditions. The present examination of the first subsystem in Table 2 illustrates how such analyses may be performed and provides an example demonstrating that the potential sources of oscillations now identified indeed may exhibit an oscillatory behaviour under physiological conditions. This is consistent with the conclusions drawn from previous analyses of the transient-state kinetic behaviour of a mathematical model considering the competition for ATP by the two kinases in the Calvin cycle [6].

In the latter case (subsystem 20), as well as in the case now examined in full detail (subsystem 1), oscillations predicted by the kinetics of the subsystems were found to be strongly damped. This may well turn out to be a characteristic of many of the potential sources of oscillations listed in Table 2. In any case, the available kinetic theory [21] prescribes that subsystems 5, 7 and 20 may only give rise to strongly damped oscillations. Subsystems 11 and 12, on the other hand, may support weakly damped as well as sustained oscillations.

Results in Table 2, therefore, can be taken to indicate that there should be no difficulty to point to a multitude of possible bireactant sources of the experimentally observed photosynthetic oscillations, at least not of the strongly damped ones that have been detected in experiments performed with isolated chloroplasts [13]. The problem one faces is rather to decide what bireactant source (if any) may be the predominant one. That problem will be considered in a future investigation.

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