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AN APPROACH TO THE STUDY OF PHOTOSYNTHESIS*

— Kinetics of an analogon of Calvin cycle —

Investigations of the kinetics of photosynthesis have been mainly based upon registration of the actual course of photosynthetic production, or intermediate processes, of plants under experimental conditions. It has become a matter of custom to search for a definite agent or partial cause in order to explain this or that type of, say, functional dependence of oxygen evolution upon illumination regime and/or other factors. Much important work on induction phenomena, intermittent light photosynthesis, etc. has been done along these cause-tracing lines.[1]

On the other hand, thorough biochemical studies have led to, at least qualitative, modelling of photosynthetic processes. Such models as Calvin carbon reduction cycle[2], and Arnon's scheme of *sensu-stricto*-photosynthesis sequencies[3], based upon more experimental evidence, and less hypothetism, than anything before in the field, make a grateful basis for a different approach to the kinetic studies — for kinetic investigation of models and analogues, having in view their subsequent (or intermittent) comparison with performancies of the actual plant mechanisms. The least such an approach could bring would be a dissaproval of the proposed models. Otherwise, such a study may help to elucidate those features of the process which inevitably follow from the given (i. e. adequately modelled) structure. So the search for relatively independent agents could be balanced by an axiomatic treatment of the problem, i. e. revealing of inherent properties of the photosynthetic system.

Aronoff[4] proposed a mathematical model based on Calvin cycle. Although the individuality as well as the actual number of intermedients of carbon reduction have been neglected in this model, it is of value as a step towards *quantitative* modelling and quantitative model investigation of the carbon cycle. Aronoff's model had to be „compartmental", since the formal mathematical solution he adopted was practically inapplicable to systems of many differential equations. Further

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complication of the model, and its connection to other functionally related structures, would make it's use even more difficult, along this way.

Yet adequately constructed and used electronic analogues, based on extensive mathematical models, and „non-mathematical" analogue elements, could do more and better, than is acheavable by classical methods. In this paper an attempt is described of use of an analogon of the Calvin cycle.

1. The model and the analogue

The carbon-reduction cycle, according to Calvin and co-workers, is represented in *Fig.* 1. Corresponding mathematical model is given as a system of differential equations:

$$(1) \quad \frac{dA}{dt} = 2P_3CO_2k_7 - Ak_1;$$

$$(2) \quad \frac{dT_1}{dt} = Ak_1 + T_2k'_{10} - T_1(k_{10} + T_2k_2 + H_1k_3 + Qk_2 + Sk_5);$$

$$(3) \quad \frac{dT_2}{dt} = T_1k_{10} - T_2(k'_{10} + T_1k_2);$$

$$(4) \quad \frac{dH_1}{dt} = T_1T_2k_2 - H_1(k_8 + T_1k_3);$$

$$(5) \quad \frac{dH_2}{dt} = H_1k_8;$$

$$(6) \quad \frac{dQ}{dt} T_1H_1k_3 - QT_1k_4;$$

$$(7) \quad \frac{dS}{dt} QT_1k_4 - ST_1k_5;$$

$$(8) \quad \frac{dP_1}{dt} = ST_1k_5 + P_2k'_9 - P_1k_9;$$

$$(9) \quad \frac{dP_1}{dt} = ST_1k_5 + P_1k_9 - P_2(k_6 + k'_9);$$

$$(10) \quad \frac{dP_3}{dt} = T_1H_1k_3 + P_2k_6 - P_3CO_2k_7.$$

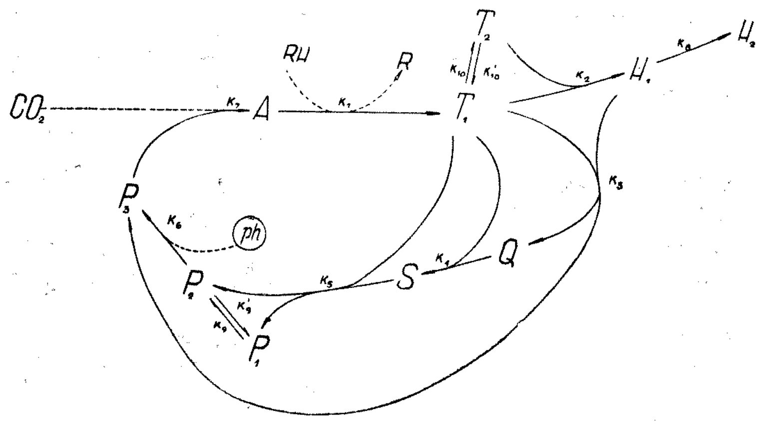

Fig. 1. Calvin cycle. A — PGA; T — triose-phosphates; H— hexose-phosphates; Q — tetrose; S — sedoheptulose-phosphate; P_1 — ribose-phosphate; P_2 — ribulose monophosphate; P_3 — ribulose diphosphate.

Based on this model, an electronic analogue was put together, according to the bloc-scheme given in *Fig.* 2. An *RR* repetitive diferential analyzer was used.

As can be seen, the analogue is a combination of standard elements, except for the synchronized electronic switch (SES), which has been specially desinged* to control „reduction" of *A* to T_1. The „on" position of the switch is analogous to the presence of „reducing power" with an intensity well above limiting, and the „off" position is analogous to it's absence. Work of the SES is equivalent to control of intermittent „reduction" of *A*.

For the purpose of present experiments, all the constants have been kept equal, except for k_7; implying that CO_2 concentration is constant, the composite constant CO_2k_7 was made limiting („bottle-neck").

2. »CONSTANT ILLUMINATION« EXPERIMENTS

These experiments are analogous to constant illumination experiments with plants, after a long period of darkness. Therefore the following initial conditions were given:

$$A_0 = 1 ; T_{1_0} = T_{2_0} = H_{1_0} = H_{2_0} = Q_0 = S_0 = P_{1_0} = P_{2_0} = P_{3_0} = 0$$

The course of functions $A, T_1, T_2, H_1, H_2, Q, S, P_1, P_2,$ and P_3 is given in *Fig.* 3 (a, b, c, d, e, f, g, h, i, j).

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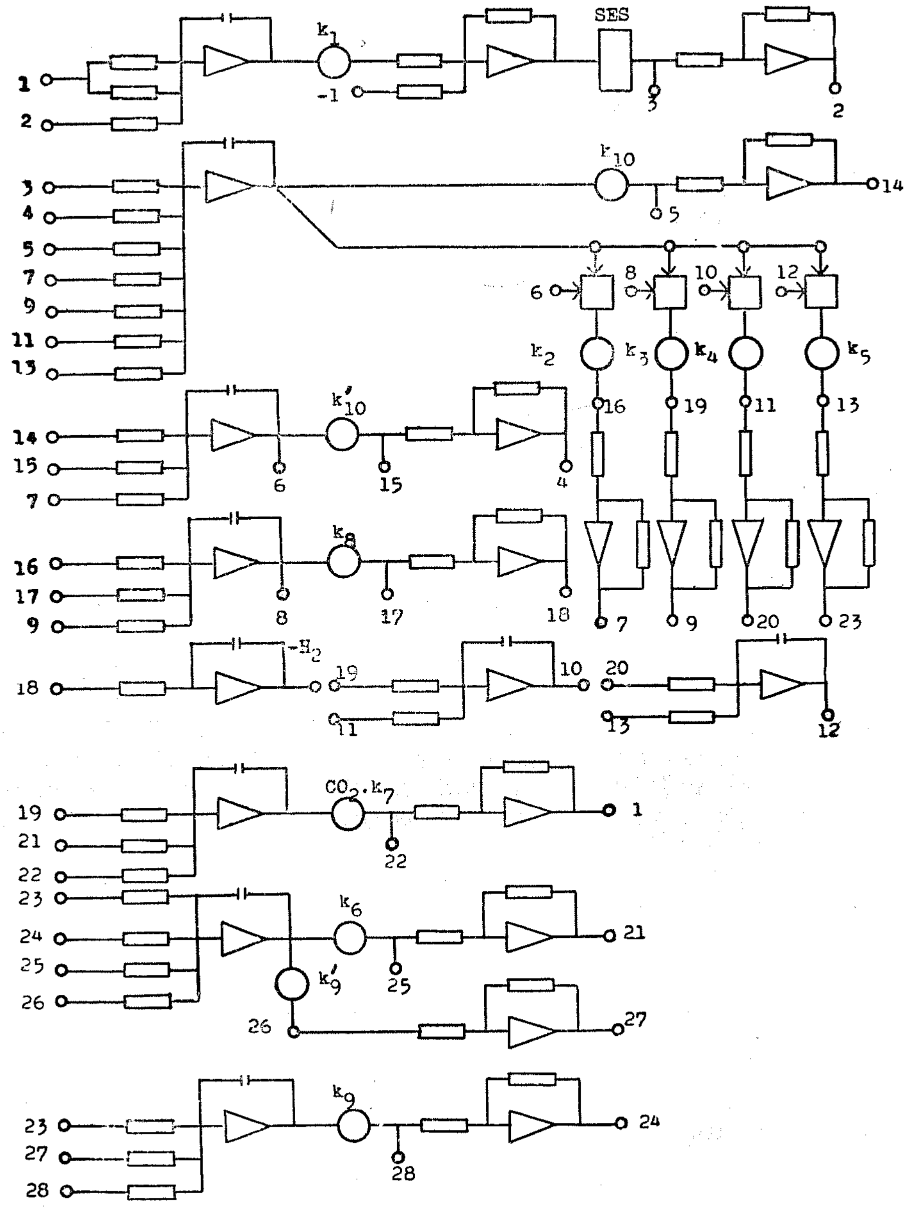

Fig. 2. Bloc-scheme of the electronic analogue of Calvin cycle. Explanation in text.

It can be seen that, in general, the change of respective values with time is compatible with the results of corresponding experiments with plant material[5]. This can be taken as a strong indication of ade-

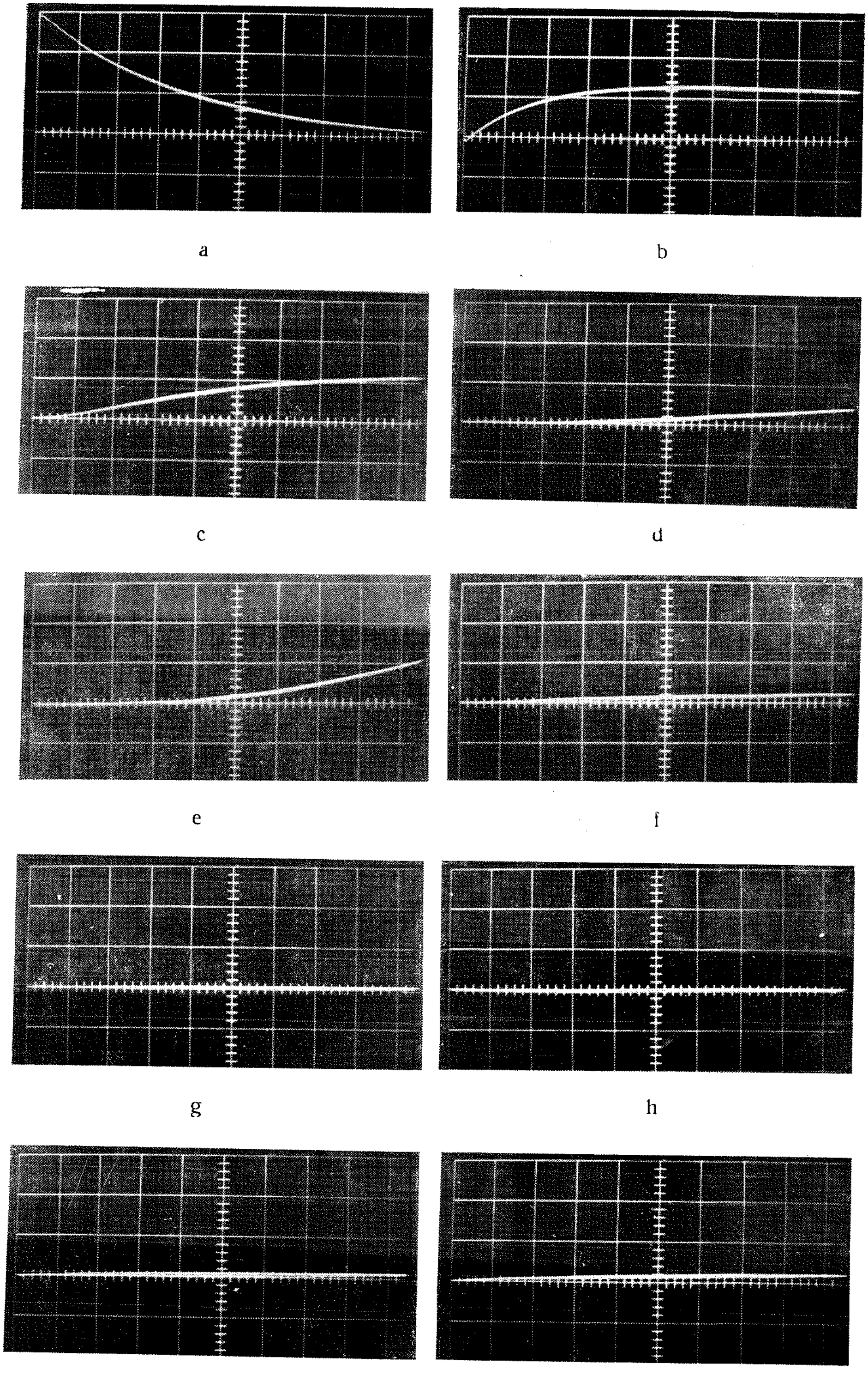

Fig. 3. The course of functions: A (a); T_1 (b); T_2 (c); H_1 (d); H_2 (e); Q (f); S (g); P_1 (h); P_2 (i); P_3 (j). Explanation in text.

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Rezime

JEDAN PRISTUP PROUČAVANJU FOTOSINTEZE

— kinetika jednog analogona Kalvinovog ciklusa —

Ispitivanja kinetike fotosinteze su, uglavnom zasnivana na registrovanju stvarnog toka fotosintetičke produkcije, ili intermedijernih procesa, u biljaka pod eksperimentalnim uslovima. Uobičajeno je da se traži određeni uzročnik ili parcijalni uzrok, da bi se objasnila ovakva ili onakva funkcionalna zavisnost, recimo, evolucije kiseonika od svetlosnog režima i (ili) drugih faktora. U ovom duhu je mnogo rađeno na fenomenima indukcije, fotosinteze pri intermitentnom osvetljavanju, itd.

S druge strane, biohemijska istraživanja su dovela do takvih modela fotosintetičkih procesa, kao što je Kalvinov ciklus, ili Arnonova shema. Ovi modeli čine zahvalnu osnovu za drugačiji pristup kinetičkim studijama, tj. za kinetičko ispitivanje modela i analoga, sa njihovim naknadnim (ili intermitentnim) upoređivanjem sa stvarnim biljnim mehanizmima. Takva studija može pomoći da se osvetle inherentna svojstva fotosintetičkog sistema i, tako, potraga za nezavisnim agensima uravnoteži aksiomatskim tretiranjem problema.

Aronofljev matematički model redukcije ugljenika u fotosintezi interesantan je kao korak ka kvantitativnom modeliranju ovog procesa. Ali, formalno matematičko rešavanje odgovarajućeg sistema diferencijalnih jednačina pruža ograničene mogućnosti.

Adekvatno konstruisani i korišćeni elektronski analogi, zasnovani na ekstenzivnim matematičkim modelima, kao i »ne-matematičkim« elementima, mogu doprineti više, nego što se može postići klasičnim metodima.

U ovom članku je opisan jedan pokušaj upotrebe elektronskog analogona Kalvinovog ciklusa.

Kalvinov ciklus je predstavljen sistemom od 10 diferencijalnih jednačina. Na osnovu tog modela, sastavljen je analogni elektronski sistem, u koji je uključen i jedan automatski elektronski prekidač, čije je uključivanje i isključivanje analogno redukciji, odnosno otsustvu redukcije fosfoglicerinske kiseline u fotosintezi.

Vršene su dve serije eksperimenata: prva, analogna ispitivanju fotosinteze pri kontinualnom osvetljenju, i druga, analogna ispitivanju fotosinteze u uslovima intermitentnog osvetljavanja.

Ponašanje analogona je slično ponašanju biljne ćelije, u pogledu promena koncentracije »intermedijenata« u vremenu. Eksperimenti indiciraju (1) postojanje *osnovnog indukcionog perioda,* nezavisno od eventualnog efekta inhibitora, i (2) kinetički efekat intermitentnog osvetljavanja na fotosintetički prinos, nezavisno od efekta zaostale »redukcione rezerve« u mračnim intervalima.

Nagoveštava se dalje istraživanje zavisnosti dodatnog prinosa pri intermitentnom osvetljavanju od učestanosti intermitencije, kao i dalja razrada metodike.

Ovaj članak je zasnovan na referatu održanom pred naučnom sekcijom Srpskog biološkog društva.