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REGULATION OF PHOTOSYNTHESIS IN THE WHOLE PLANT

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ABSTRACT

The article presents the literature review in the field of photosynthesis, photosynthetic carbon metabolism and assimilates transportation in plants in vivo under changing conditions. The sequence of the data presented leads the reader to understanding as to the principle of photosynthesis regulation in the system of the whole plant. The essence of the proposed conception is to coordinate the light stage, during which the energy from sunlight is absorbed and converted to be stored in the form of ATP and NADPH+, and the dark stage, during which (at CO2 fixation) organic acids are formed. Sugars (which are completely exported to the organs-acceptors of photosynthesis product) are formed at a balanced state of these two stages of photosynthesis. If the conditions are changed (reduced illumination, inhibition of sugars outflow from the leaf with a reduction in the mass of the organs-acceptors or an increase in nitrate supply), the export of sugars from the leaf becomes inhibited, and the number of products of the dark stage is relatively greater than that of the light one, then:1) acids accumulate in the mesophyll cell (including resulted from photorespiration and the formation of glycolate with its metabolic products); 2) excess acids come out of the mesophyll and acidify the aqueous medium in the apoplast, which activates apoplast invertase; 3) as a result of hydrolysis of sucrose (from the sucrose molecule → two moles of hexose) osmoticity of the extracellular aqueous medium increases, which increases also due to evaporation of water when moving to the stomata 4) stomata are closed osmotically, the diffusion of CO2 into the leaf and the intensity of photosynthesis decreases. As a result, the disturbed ratio of dark and light processes in chloroplasts is normalized. All these processes in the leaf are changed in the opposite direction in case of an increase in illumination, demand for the products of photosynthesis with the reduction of the leaf surface or nitrate reduction.

INTRODUCTION

The 250th anniversary of the photosynthesis discovery will be celebrated in two years. However, until now the mechanism of photosynthesis regulation in the system of the whole plant under changing conditions is not clear. Why has not this problem (the most important for the production process) been solved yet, despite the development of science and technology? It can be assumed that with the accumulation of information (regardless of the field of science) it becomes increasingly difficult to form an integral view on the whole problem, such as the photosynthesis. At the same time, in the middle of the 20th century, K. I. Popov, the entomologist of Kazan Agricultural Institute, was the first to discover that plants whose leaves are damaged by insects grow faster afterwards (Popov, 1959). Popov was a scientific supervisor of the student work of the author of the present article, who worked over 50 years to bring the idea to the successful conclusion.

To clarify this phenomenon, Popov sent his postgraduate student Yu.S. Karpilov to Kazan State University to get acquainted with the method of photosynthesis measurement using labeled $^{14}CO_2$. The research started with corn, the agricultural plant popular at that time in Russia. As a result of the first experiments, Yu.S. Karpilov discovered (Karpilov, 1960) an unusual composition of primary products of photosynthesis in corn (C-4 type), and all his further efforts were aimed to clarify this phenomenon, and the donor-acceptor relations (DAR) between the leaf and the assimilate-consuming organs were pushed aside. In the same years, the focus of studies on the regulation of photosynthesis moved to particular details of this process for a long time. These studies were very important for understanding photosynthesis (Calvin, Benson, 1948; Mitchell, 1966; Hatch, Slack, 1966, etc.). The most significant from them are: the discovery of the Calvin Cycle, C-4 type of photosynthesis, the mechanism of accumulation of sunlight energy in ATP. But all of them were taken out of the general system of the photosynthetic apparatus of the plant and

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did not provide information to understand the mechanisms of photosynthesis regulation in the system of the whole plant in vivo.

An important stage in the research of the problem of photosynthesis regulation started with the study of the influence of DAR on photorespiration (PR - Warburg effect). It was demonstrated (Lenz 1977; Hall and Brady 1977; Chikov and Isfandiyarov 1978) that the decrease of mass of assimilate-consuming organs (flowers, buds or fruits) causes increase of PR. These findings suggested that photorespiration (generally accepted as a harmful process) is related directly to the regulation of photosynthesis. The studies of the role of the export function of the leaf in the regulation of photosynthesis stopped at this stage. And even meetings (Lenz, 2009; Chikov *et al*., 2009) at joint conferences outside Russia did not initiate such works.

Despite all the obstacles, under the influence of Popov's ideas this problem has been studied purposefully for 40 years in our laboratory in order to clarify the regulation of photosynthesis in vivo. We obtained and published research data on photosynthesis, transpiration and photosynthetic metabolism of ^{14}C-carbon (PSMC) in the leaf, apoplast and the distribution of labeled products of photosynthesis over the organs of the whole plant under changing conditions. The main method of research was a radioactive isotope of ^{14}C carbon. In these experiments, the changes in light conditions and in nitrate supply, as well as the intensity of export of ^{14}C-products of photosynthesis from the leaf were used as the main impacts disturbing photosynthesis in plants. The last factor was changes by the removal of some part of assimilate-consuming organs or mature leaves-donors of photosynthesis products. But photosynthesis was always studied on the native leaf. This mini-review presents the logic of this scientific search, which recently allowed us to propose the concept of photosynthesis regulation in the system of the whole plant in vivo.

Abbreviation: DAR - donor-acceptor relations; ETC - electron transport chai; Fd - ferredoxin; PCM - photosynthetic carbon metabolism; PES - phosphorus esters of sugars; PR - photorespiration; 3-PGA - 3-phosphoglycerate; RuBP - ribulose 1, 5-bisphosphate; RUBISCO - ribulose-1, 5bisphosphate carboxylase/oxigenase; photosynthetic metabolism of ^{14}C-carbon −PSMC.

Content: As the first stage of our DAR research, we used cotton plants (*Gossýpium hirsútum*).This plant has a large number of leaves and fruit elements (balls), the removal of which causes a severe disturbance of DAR. It was found (table. 1) that the inhibition or intensification of assimilates export from the leaf is accompanied by a corresponding change not only in photosynthesis but also in the rate of PR in CO_2-gas exchange of the assimilate donor leaf [Chikov *et al*., 1982; Chikov, 1987]. Inhibition of assimilates outflow from the leaf (removal of fruit elements) increases PR, and its intensification (removal of part of mature leaves) reduces it.

Table 1 The effect of removing leaves or fruit of cotton on photosynthesis and the Warburg effect. (Chikov *et al*., 1982)

Experience option	Photosynthesis (mg CO_2 dc^{-2} h^{-1})		Warburg effect (% to 1% O_2)
	1% O_2	21% O_2	
Control	48,0 ± 1,9	30,0 ± 2,9	37,5 ± 2,4
Removing fruit	15,4 ± 3,7	7,2 ± 1,7	53,2 ± 3,1
Removing leaves	46,5 ± 6,9	35,3 ± 3,7	24,1 ± 2,1

Analysis of distribution of ^{14}C over the products of leaf photosynthesis in the leaves of these variants revealed [Chikov *et al*., 1985; Chikov, 1987) characteristic changes in the ratio of PSMC between sugars and acids, as well as the kinetics of ^{14}C introduction into the products of glycol metabolism. Inhibition of the outflow of assimilates (removal of acceptors or increase of nitrate nutrition) led to a decrease in the ratio of labeled ^{14}C sucrose/hexose, and the inclusion of ^{14}C in the glycolate had two different kinetics of the inclusion of ^{14}C in the glycolate and its metabolic products. In control plants (at CO_2 - 0,03%) ^{14}C enters the glycolate after some delay (20sec). At an increased concentration of CO_2 (0.3%) or inhibition of sugars outflow from the leaf the labeled carbon enters the glycolate immediately, regardless of the export function of the leaf (Fig. 1). This means that there are different sources of glycolate formation, which are activated with different export function of the leaf.

At high concentration of CO_2 we observe not the Warburg effect but Anti-effect (Laisk, 1977), that is, photosynthesis becomes higher at an increase in concentration of oxygen. The Anti-Warburg effect is even greater if the plants are fed with nitrates (Chikov *et al*., m 1998; Chikov, Bakirova, 1999). However, the kinetics of the inclusion of ^{14}C in glycolate in nitrate plants was the same as at CO_2 saturating concentration. These data show (Chikov *et al*., 1985; Chikov, 1987), that in control plants (in stady-state), glycolate is formed mainly via Ribulose biophosphate-oxygenase reaction, and in case of inhibition of the sugars outflow from the leaf (removal of fruits or increase of nitrate nutrition) via a transketolase reaction involving the oxidant formed in the ETC of chloroplasts (Takabe, Asami and Akazawa, 1980).

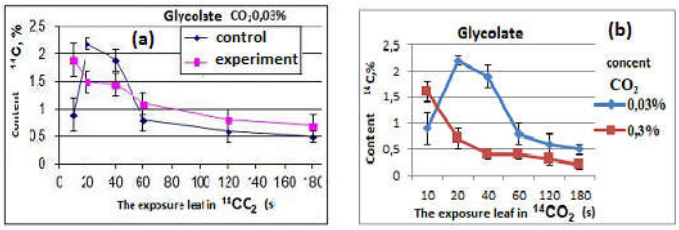

Fig 1 The kinetics of photosynthetic inclusion of ^{14}C in glycolate (% radioactivity of water-ethanol soluble fraction) in leaves of cotton plants. Effect (a) - of removal of fruits and (b) - increasing concentrations of CO_2 (Chikov *et al*., 1985).

In this case, the oxidizer is not the oxygen, but a superoxide radical formed either in the Mehler reaction (Takabe, Asami, Akazava, 1980) or in the nitrite reduction (Chikov and Bakirova, 1999). Even when reducing the oxygen level in the atmosphere of the test leaf to 1% and increasing the carbon dioxide concentration (up to 0.3%), the of glycolate metabolism product formation increases in the plants fed with nitrates, and decreases twofold without nitrates (Chikov *et al*., 1998).

For the formation of labelled ^{14}C-glycolate, the superoxide radical should oxidise the sugar-phosphate formed from the newly labelled ^{14}C of the PGA, and then reduced to ^{14}C-sugar-phosphate. With the oxygenase reaction of glycolate formation, the sugar-phosphate formed from the previously labelled ^{14}C of the PGA should undergo 13 reduction and conversion reactions to obtain the RuBP, which will give the labelled ^{14}C-glycolate. Therefore, in the RuBPo reaction of glycolate formation, the glycolate is labelled with a delay (Fig. 1), because, first of all, all compound pools of the Calvin Cycle should be saturated with the labelled carbon.

Glycolate formation is a regulatory mechanism of photosynthetic function control in case of imbalance between light and dark reactions in chloroplasts. Such mechanism is likely to work in the sheath cells of C-4 type of plants. The researchers did not pay ample attention to this alternative glycolate source and, accordingly, to another aspect of participation of photorespiration in the photosynthesis regulation, despite the long-discovered transketolase mechanism of glycolate formation (Takabe, Asamy and Akazawa, 1980).

Our studies of the PSMC in connection with the study of photorespiration and the nature of the Warburg effect have shown (Chikov *et al*., 1998) that the maximum carbon filling of the glycolate cycle (in ng/cm^2 s) occurs at simultaneously high illumination, concentration of CO_2 and oxygen (Chikov *et al*. 1998). In these circumstances, the delivery of ^{14}C in the glycolate metabolism products is twice as much as at ambient CO_2 concentrations (Chikov *et al*., 1998). This is probably due to the known (Ehleringer, Bjorkman, 1977) electron transport stimulation in chloroplasts with increasing CO_2 concentration. It also shows that the intensity of carbon flow through the glycolate pathway is determined not only by the oxygen and the RuBP/O activity, but also by the presence of superoxide radical, which is involved in the transketolase mechanism of glycolate formation. The oxygen endogenously formed in the chloroplasts or the superoxide radical formed during the nitrite reduction in the ETC are likely to be enough for this. With a decrease in illumination, the ongoing metabolism of glycolate gives a "CO_2-emission" from photorespiration. With a decrease in illumination, the ongoing glycol metabolism produces a CO2 emission from photorespiration.

That is why the Warburg anti-effect is observed at high concentrations of CO_2 (Laysk, 1977; Chikov *et al*., 1998), when the photosynthesis becomes more intense particularly at high concentrations of oxygen, as the intense glycol metabolism eventually is involved in the intensification of the function of the Calvin cycle and the formation of sucrose. Such results were obtained (Chikov *et al*., 1998), when the atmospheric composition in the leaf chamber was changed for the wheat leaf during record of $^{14}CO_2$ only (2 min). All this indicates that, at a high photosynthesis intensity in the steady state, the glycolate cycle is completely closed to the Calvin cycle and promotes the main photosynthetic flow of carbon - to the synthesis of sugars.

Since the glycolate pathway is closed to the Calvin cycle, it can circulate at a high rate exceeding the carbon delivery from the outside. At the ambient concentration of carbon dioxide (0.03%), the Warburg anti-effect was observed only in plants fertilized with nitrates (Chikov, *et al*., 1998), when superoxide radical is formed during the nitrite reduction in chloroplast ETC, and the photosynthetic product export from the leaf is partially carried out in the form of amino acids. This contributes to the partial non-return of carbon to the Calvin cycle and, accordingly, the increase of the photosynthesis intensity.

It should be noted that the phosphoglycolate is the only oxidized compound that comes out of the chloroplasts into the cytoplasm in a mass flow. During its further metabolism, when glycine, serine, oxypyruvate and pyruvate are formed, all of them are concentrated in the cytosol. Therefore, when the PGA reduction to triose in the chloroplasts and its accumulation in the chloroplasts are complicated, the transfer of pyruvate to the chloroplast is blocked. As a result, all these acids are accumulated in the cytoplasm. And this is likely a very sensitive regulatory reaction that reacts to the accumulation of organic acids in the cytoplasm, with pH control of its aqueous medium.

Since the integrated flow of glycolate into the cytoplasm is 20-50% of the photosynthesis, it is too much to allow its accumulation within the photosynthetic cell, so after filling the vacuoles with acids, the extracellular space of the leaf is acidified as well. In turn, this activates the cell-wall invertase that hydrolyses the sucrose. With the sucrose hydrolysis, the osmolarity of the apoplastic fluid is doubled, since two molecules of hexose (glucose and fructose) are formed from one molecule of sucrose. The increased osmolarity of the apoplastic fluid as it moves to the stomatal pore and the evaporation of water increases even more (Polyakov, Karpushkin, 1981), that, in turn, osmotically closes the stomata.

As a result, the feedback of the carbon metabolism of photosynthesis with the light reactions of chloroplasts is carried out, and the formation of the number of photosynthesis products is brought into line with the request from the acceptor organs. When inhibiting the assimilate outflow from the leaf or increasing the level of nitrate supply, the glycolate pathway occurs more open. A part of the glycolate pathway intermediates (in the form of amino acids) can be exported from the leaf through the phloem to the acceptor organs, activating or generating (as with enhanced nitrate nutrition (Chikov, 2012; 2017a) their metabolism in new emerging organs.

The study of the photosynthetic metabolism of carbon (FSMC) under conditions of changing DAR also showed (Chikov *et al*. 1985) the sensitivity of ^{14}C labeled sucrose/hexose ratio to changes of the leaf export function. This evidenced the participation of apoplastic invertase in the photosynthesis regulation (table. 2). The study of gene-modified potato plants with an additional apoplastic invertase gene showed (Chikov *et al*., 2011) that this enzyme is directly involved in inhibiting sucrose outflow thus preventing its export from the leaf. This even increased the death of test-tube plants after their planting in the ground, because the roots received insufficient supply with photosynthesis products.

Table 2 Distribution of ^{14}C [% of the water-etanol-soluble] among labelled products of photosynthesis in leaves and apoplast of top and donor parts of the flax after 5 min of ^{14}C assimilation by a middle part of shoot. (Chikov *et al*., 2001)

Compounds	Top of plant escape		^{14}C-dono-part plant	
	Control (Non-fertilized plants)			
	leaves	apoplast	leaves	apoplast
Sucrose	73,5 ± 0,6	89,7 ± 0,2	60,9 ± 0,5	89,6 ± 0,5
Hexoses	4,8 ± 0,3	0,6 ± 0,3	3,6 ± 0,2	0,7 ± 0,1
Amino acids	10,0 ± 0,6	4,1 ± 0,2	15,1 ± 0,3	3,9 ± 0,4
Malate	3,2 ± 0,2	2,2 ± 0,1	4,0 ± 0,1	2,1 ± 0,1
Other compounds	8,5 ±0,2	3,4 ± 0,8	16,4 ± 0,7	3,7 ± 0,1
Sucrose/hexoses	15,0	149,5	16,9	128,0
	Experiment (N-fertilized)			
Sucrose	61,5 ± 0,3	77,1 ± 0,5	57,1 ± 1,0	76,2 ± 1,1
Hexoses	5,3 ± 0,4	2,1 ± 0,4	4,2 ± 0,2	2,0 ± 0,2
Amino acids	15,7 ± 0,5	11,7 ± 0,5	17,2 ± 0,6	11,1 ± 0,7
Malate	4,7 ± 0,7	3,4 ± 0,4	5,1 ± 0,3	3,7 ± 0,4
Other compounds	12,8 ± 0,7	5,7 ± 0,4	16,4 ± 0,3	7,0 ± 0,4
Sucrose/hexoses	11,6	36,7	13,6	38,1
Sucrose/hexoses (control/experiment)	1,29	4,07	1,24	3,36

The experiments on tomato plants in which, on the contrary, the invertase gene was blocked, showed (Chikov, 2015) that with a sudden reduction of illumination leads to inhibition of photosynthesis and transpiration of the wild type of plants (with normal invertase), and as for gene-modified plants (invertase blocked), their photosynthesis is inhibited, and transpiration increases (table. 3).

Table 3 Effect of irradiance and suppression of the apoplastic invertase gene on leaf physiological characteristics in wildtype tomato plants and in genetically transformed plants (Chikov *et al*., 2015

Characteristic	Wild type	Lin8-RNAi	Wild type	Lin8-RNAi
Photon flux density, µmol/(m2 s)	1556 ± 32		771 ± 58	
Photosynthesis, µmol $CO_2/(m^2$ s)	21.60 ± 0.70	23.49 ± 0.51	17.75 ± 0.56	20.51 ± 0.97
Transpiration, mmol $H_2O/(m^2$ s)	8.08 ± 0.32	8.31 ± 0.36	6.97 ± 0.26	9.44 ± 0.17
Transpiration/photosynthesis ratio	374 ± 7	354 ± 18	393 ± 8	460 ± 37
Stomatal conductance, µmol $CO_2/(m^2$ s)	322 ± 17	303 ± 9	271 ± 12	375 ± 27

This occurs due to the fact that there is no hydrolysis of sucrose in the transformers apoplast, as well as due to successful loading of sucrose into the phloem and, as a result, reducing the osmotic pressure of the aqueous medium surrounding the closing cells of the stomata. The latter results in additional opening of stomata even with a decrease in illumination. All these data allowed us to present (Chikov *et al*., 2015; 2016a; 2016b) the concept of photosynthesis regulation (Fig. 2) in which events occur in the following sequence.

If the light intensity and the export of assimilates (partial defoliation) from the leaf increase: 1) all the fixed carbon is recovered in the chloroplasts to sugar, photorespiration and glycolate metabolism is lowered, and, as a consequence, organic acids are in small amount; 2) pH of apoplast is high, invertase is suppressed, and sugars are exported effectively; 3) the osmotic pressure of the extracellular fluid is low, the stomata is open and photosynthesis is high.

On the contrary, with a decrease in illumination or suppression (removal of a part of the organs consuming products of photosynthesis) of export of assimilates from the leaf: 1) not all the fixed carbon is restored to sugars, the metabolism of glycolate increases (including through transketolase mechanism), and the concentration of organic acids increases, including in apoplast; 2) the activity of invertase increases; 3) hydrolysis of sucrose in apoplast enhances and the osmotic pressure in the aquatic environment increases (two hexoses are formed instead of one sucrose); 4) the stomata close and photosynthesis is reduced. This concept was confirmed in the course of special experiments on the leaves of potato plants at different variations of the illumination received by the plant [Chikov *et al*., 2016a].

Thus, in chloroplasts the light and dark processes ratio is controlled by invertase and stomatal apparatus of the leaf due to the change of the pH of the aqueous medium, first in the mesophilic cells of the leaf, and then in the extracellular space. The interaction of all these processes during the regulation of photosynthesis is shown in figure 2.

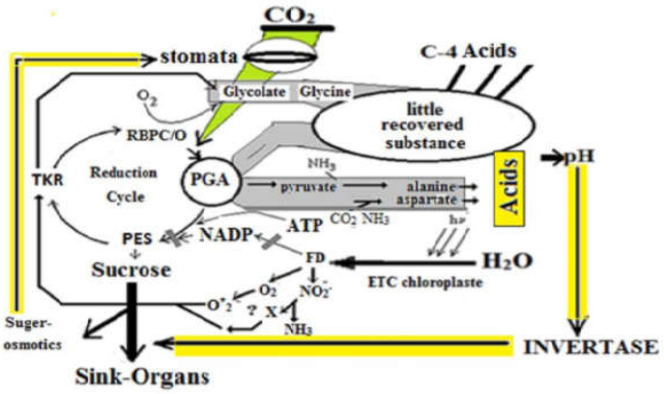

Fig 2 The scheme of photosynthetic carbon metabolism regulation in case of disturbance of dark and light photosynthesis process ratio in the whole plant (Chikov *et al*., 1985; 1987; 1999; 2009; 2016a; 2017b In development).

CONCLUSION

The nature of phenomenon of the plants regrowth after insect damage noted by K. I. Popov is conditioned upon the fact that (Chikov, 2012; 2017a) with the reduction of leaf area the amount of sugar entering the roots decreases. Therefore, nitrates cannot be restored in the roots fully and some of them move up the stem with water into the leaves. As the nitrates move in the stem apoplast, they are non-enzymatically (Neill, Desikan and Hancock, 2003) converted into NO, which expresses more than 200 genes and triggers the formation of the assimilate-accepting shoots. These new acceptors increase efficiency of photosynthesis and promote the shoots growth.

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