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Research Article

THE PARTICIPATION OF PHOTORESPIRATION IN THE REGULATION OF PHOTOSYNTHESIS

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ABSTRACT

The results of long-term studies of photorespiration are summarized and the unsuccessful attempts to increase productivity by suppressing this process are shown. It has been shown that photorespiration and glycolate metabolism are involved in the regulation of the relationship between light processes in chloroplasts and the dark reactions of carbon dioxide assimilation. The studies were conducted on plants in vivo and were associated with the activity of the apoplastic invertase enzyme, affecting assimilate transport. In violation of donor-acceptor relations between photosynthetic and plant-assimilating organs (removal of part of organs-consumers of assimilates or leaves, increase in nitrate nutrition), the kinetics of inclusion of ¹⁴C in glycolate was changed. This is due to the strengthening of the role of the transketolase mechanism of its formation. The study of genetically transformed plants, in which either an additional apoplastic invertase gene was introduced, or the existing gene was blocked and did not act, showed a different change in the ratio of ¹⁴C-labeled sucrose / hexose and the transpiration response to reduced light. In this connection, the concept of the mechanism of photorespiration interaction with apoplastic invertase and stomatal apparatus of the leaf is proposed when the ratio of light and dark reactions of photosynthesis or assimilate transport is changed.

The essence of the concept is that when the ratio of light and dark processes is disturbed, the concentration of organic acids changes first in mesophilic cells (mainly by photorespiration), and then in the extracellular space. It changes the activity of apoplastic invertase, which hydrolyzes sucrose and prevents it from being exported from the leaf. Hydrolysis of sucrose increases the osmoticity of the aquatic environment of the apoplast, which increases with movement to the stomata. The changed osmoticity of the environment around the stomatal guard cells changes the resistance of CO₂ diffusion into the leaf. This normalizes the ratio of light and dark processes in the sheet. Therefore, when illumination decreases, nitrate nutrition increases or difficulties arise with the use of photosynthesis products in acceptor organs, the ratio of ¹⁴C-labeled sucrose / hexose decreases, and the stomata close. With increasing illumination, reverse events occur.

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INTRODUCTION

It is known that respiration - the process of absorption of oxygen and the release of carbon dioxide is an attribute of both animals and plants. Photosynthesis is the opposite of respiration. In the process of photosynthesis, oxygen is released and carbon dioxide is absorbed. It is carried out in plants, algae and photosynthetic microorganisms. The process of photosynthesis is accompanied by less known, so-called photo-oxidative processes that directed oppositely to photosynthesis and affect both the exchange of oxygen and carbon dioxide in the plant (Chikov,1996). Thus, simultaneously with photosynthesis (absorption of carbon dioxide and oxygen release), release of carbon dioxide and absorption of oxygen

occurs in the leaf. We call this photorespiration, although there may be controversy over the name. Abbreviation: ETC – electron transport chain; 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/oxygenase; (PES) – phosphoric esters of sugars.

Whereas the intensity of "dark respiration" is usually 5-7% of photosynthetic gas exchange, the intensity of photorespiration is about half. In the 70-80s of the last century, the attention of many plant physiologists was fixed to this phenomenon. Disputes between representatives of different (sometimes opposite) points of view boiled. But then everything calmed

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down and, although in the last two decades there are publications related to photorespiration (Betti, Bauwe, Busch *et al.*, 2016; Walker, Van Looke, Bernacchi *et al.*, 2016), they also tried to find a place for photorespiration by manipulating individual particulars of this process. And the main focus is still on the Rubisco enzyme (Anderson, 2008) or attempts to find genotypes with different photorespiration (Aliyev, 2012). However, it is obvious that the role of photorespiration is more significant (considering its intensity) and it must be tested at the organism level, since for the regulation of such a process as photosynthesis it is necessary to have a factor equal to it in power. At the same time, it is not clear how photorespiration is involved in the regulation of photosynthesis and plant productivity.

Manifestation of Photorespiration in the Plant Gas Exchange

The first signs of photorespiration were discovered a long time ago. Back in 1920, the German scientist Otto Warburg remarked (Warburg, 1920) that the intensity of algae photosynthesis increases if the oxygen concentration in the environment is reduced. This meant that simultaneously with photosynthesis some oxidative reactions occur, accompanied by the release of CO₂ and reducing photosynthesis (absorption of CO₂). Subsequently, this phenomenon was called the Warburg effect. With the creation of highly sensitive and fast equipment (polar graphs, infrared optical-acoustic gas analyzers, mass spectrometers), other manifestations of photorespiration were also detected.

Photorespiration is especially noticeable in the leaf gas exchange as it shifts from light to dark. If one turns off the illumination of the leaf during the automatic measurement in the flow system of the intensity of photosynthesis as carbon dioxide absorption, the characteristic kinetics of gas exchange could be seen. This is done as follows. The air with a natural concentration of carbon dioxide (0.03%) is blown through a sealed transparent chamber containing a leaf. A strong decrease in carbon dioxide concentration in the air emerging from the leaf chamber will be observed in the light due to photosynthesis. This is recorded on the recorder chart (Fig. 1) as the absorption of carbon dioxide - "apparent" photosynthesis. Why "apparent"? Yes, because the actual absorption of carbon dioxide is much more intense, but it is underestimated, since at the same time CO₂ is released in other reactions. The active absorption of carbon dioxide observed in the light ceases after the light has been switched off (Laisk, 1977), and the chart recorder pen, quickly crossing the zero line (both visible CO₂ absorption and emission are absent), indicates intense CO₂ emission (Fig. 1).

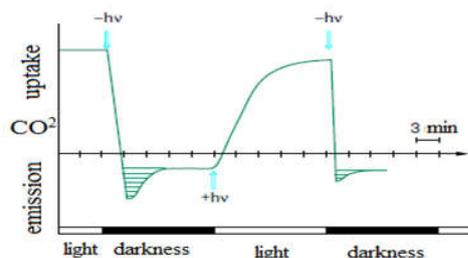


Fig. 1. Change in the leaf CO₂ gas exchange after switching the light off and on (shown by the symbols - hv ↓ and + hv, respectively). the intensity of absorption or release of carbon dioxide is plotted against the y-axis. The shaded part is the pool of oxidized substances in the cell after turning off the light (Chikov, 1996).

Since in the dark the leaf cells respire, a weak emission of carbon dioxide corresponding to the dark respiration should gradually be established. However, in reality, the gas analyzer registers something else: immediately after the light is turned off, a significantly more intense release of carbon dioxide is observed than later on, when only dark respiration remains (see Fig. 1). Researchers have called this phenomenon the carbon dioxide burst. It usually lasts 3-5 minutes. Intensive emission of carbon dioxide immediately after turning off the light indicates the presence of some substance formed in the light, but quickly oxidized in the dark.

This conclusion was confirmed by the fact that the burst size depended on the duration of the preliminary illumination of the photosynthesizing object, CO₂ concentration, and other conditions. The pool of this oxidized substance corresponds to the area of the plotted "post-illumination CO₂ burst" (the shaded part in Fig. 1). If after the "post-illumination CO₂ burst" has been registered on the record chart and dark respiration has been established, one turns the light on again and repeat the procedure with turning off the light, then the intensity of photosynthesis and repeated "burst" will depend on the duration of the leaf illumination between the two "bursts" (see Fig. 1).

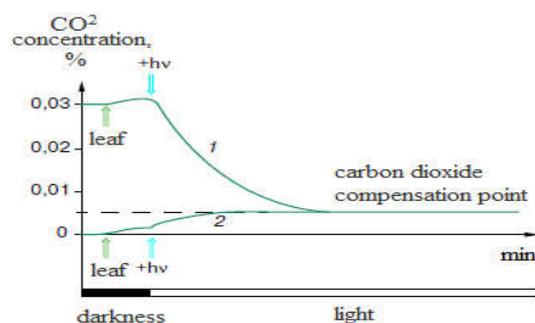


Fig 2 Changes in CO₂ concentration in a closed chamber containing a leaf in the dark and in the light (Chikov, 1996). The initial CO₂ concentration is 0.03% (1) or 0.0% (2).

If the repeated illumination is very short and the oxidizable substance accumulates only a little, then there may be no "burst" of carbon dioxide at all. Photorespiration also reveals itself when one studies the dependence of the intensity of photosynthesis on carbon dioxide concentration. A leaf placed in the light in an enclosed space begins to intensely absorb carbon dioxide from it, and the concentration of CO₂ rapidly decreases (Fig. 2, curve 1). However, most plant species cannot absorb CO₂ completely, since simultaneously with CO₂ absorption, it is released during dark respiration and photorespiration.

Therefore, there always remains a certain level of carbon dioxide, which the plant cannot absorb. The concentration of carbon dioxide, at which no visible photosynthesis is observed (there is no absorption or release of carbon dioxide), is called a carbon dioxide compensation point. Typically, this concentration is about 5-10 thousandth of a volume percent of CO₂ (50-100 ppm CO₂). Depending on the conditions (temperature, light, oxygen concentration, level of nitrogen nutrition, moisture supply, etc.), the value of the CCP is different.

Interestingly, if in the dark the chamber containing a leaf is blown with air that does not contain carbon dioxide, then CO₂ will be released, which is formed during respiration. Under the same conditions in the light, CO₂ will be released from the leaf at a higher rate equal to the sum of the rates of dark respiration and photorespiration (Fig. 2, curve 2). This can continue without much damage to the photosynthetic cell for quite a long time, probably, until the pool of sugars in the cell has been exhausted. But if the leaf is placed in an atmosphere not containing carbon dioxide or oxygen (for example, that of nitrogen), then the illumination will result (and the brighter it is, the faster) in damages to the photosynthetic apparatus of the plant (photodestruction). It follows from this that photorespiration is a necessary, useful process.

Chemical Mechanism of the of Carbon Dioxide Assimilation And Photorespiration

Carbon Dioxide Fixation. It should be noted that the active study of photorespiration was carried out in the period when the biochemical mechanism of carbon dioxide assimilation, the so-called Calvin-Benson cycle, was already known (Calvin, Benson, 1948). With the discovery of this cycle, the mechanism of the binding of carbon dioxide molecule and the regeneration (reproduction) of its acceptor ribulose bisphosphate (RuBP), which initially adds CO₂, became clear. There was little information about the fate of individual participants in this process outside the CO₂ recovery cycle. It has been shown (Kursanov, 1976) that during photosynthesis, sucrose is synthesized from CO₂, which is transported to organs (roots, fruits, growth points) consuming products of photosynthesis.

In sink organs, a variety of substances needed by these tissues is synthesized from sucrose carbon. It was also found that the enzyme catalyzing the reaction of the addition of carbon dioxide is the most wide-spread protein in nature. More than half of the soluble proteins in the plant leaves is represented by an enzyme that fixes carbon dioxide, ribulose-bisphosphate carboxylase (RuBP carboxylase).

Since the first product of the assimilation of CO₂ in most plant species is the three-carbon compound -3-phosphoglyceric acid (PGA), this type of photosynthesis was called the C-3 type. The other, C-4 type of photosynthesis will be described below. The resulting PGA is then reduced to three carbon sugars (triosophosphates), whose carbon, having passed a series of transformations through various phosphoric esters of sugars (PES), is used in part to regenerate the CO₂ acceptor molecule (RuBP) (highlighted in red in Fig. 3), but mainly to form sucrose as the major transport compound in most plant species.

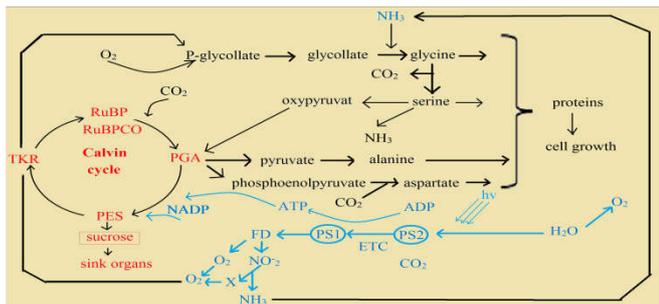


Fig 3 A scheme of CO₂ assimilation during photosynthesis (the Calvin cycle) and photorespiratory glycolate metabolism (Chikov, Bakirova, 1999).

It should be remembered that photosynthesis itself consists of two stages (Fig. 3): the light stage, which includes photophysical and photochemical reactions of absorption and storage of the photon energy, and the dark reaction of carbon dioxide assimilation. The light stage (highlighted in blue in Fig.3) results in the formation of a strong reducing agent—reduced nicotinamide adenine dinucleotide phosphate (NADPH) and energy-rich adenosine triphosphate (ATP). Formed during photochemical light reactions, NADPH and ATP are also called the “assimilatory force” of chloroplasts, since these substances are used in the course of dark biochemical reactions for the assimilation of CO₂ and the formation of sugars. The building of an “assimilatory force” is associated with electron transfer in the electron transport chain (ETC) of chloroplasts, when a chlorophyll molecule excited by photons generates an electron flow from water (which decomposes with the formation of oxygen) to NADP (Fig. 3) through the ETC. As a result, NADP is reduced, and ATP is formed from adenosine diphosphate (ADP) in the process of photophosphorylation coupled with the electron flow. ETC consists of a series of components, differing in their redox potentials.

The mechanism of carbon dioxide and oxygen binding. As it turned out, the CO₂ binding enzyme has a dual function (Fig. 4). It can carry out both the carboxylation reaction (carbon dioxide addition to the five-carbon compound ribulose bisphosphate), followed by the formation of a six-carbon compound, which breaks down into two molecules of the three-carbon PGA and the oxygenation reaction (the addition of an oxygen molecule with the formation of only one PGA molecule and one two-carbon glycolic acid phosphate molecule). Accordingly, this enzyme is usually designated as RuBP carboxylase/oxygenase or Rubisco (ribulose bisphosphate carboxylase / oxygenase).

Special studies have shown (Bowers *et al.*, 1971) that initially the carbon dioxide acceptor RBP “sits down” at the active site of the Rubisco enzyme, and then either CO₂ or O₂ can be bound and either carboxylation or oxygenation is performed (Fig. 4). As a result, there is a competition between oxygen and carbon dioxide for the active center of the enzyme. The ability of this enzyme to bind carbon dioxide is significantly higher than oxygen. Therefore, with natural atmospheric concentrations of these gases (21% oxygen, and 0.03% carbon dioxide), the latter has significant advantages and the proportion of photorespiration in the leaf photosynthetic gas exchange under these conditions is only 25-30%.

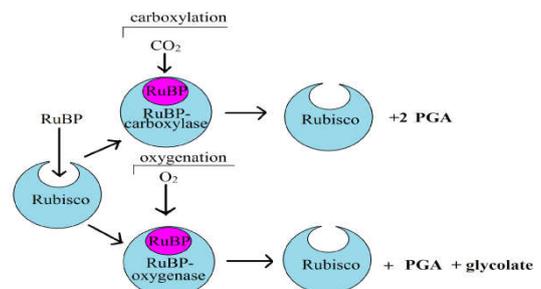


Fig 4 The mechanism of the carboxylase and oxygenase reactions implemented by the enzyme RuBP carboxylase/oxygenase (Rubisco) (Chikov, 1996)

However, if the concentration of carbon dioxide decreases and that of oxygen increases, then the competitiveness of oxygen grows and the role of photorespiration in the leaf gas exchange increases. In an extreme situation (complete absence of carbon dioxide at a natural oxygen concentration), photorespiration exceeds photosynthesis, and during the measurement of the leaf gas exchange in the light, carbon dioxide is not absorbed but released (see Fig. 2, curve 2). In fact, under natural conditions, both release and absorption of CO₂ and O₂ occur, since both processes occur simultaneously, but release of O₂ is more intense than its absorption.

Glycolic acid Transformations. Studies of the further fate of phosphoglycolate carried out with the help of labeled atoms showed (Tolbert, 1979) that after removal of the phosphate residue glycolic acid (glycolate) is transferred from chloroplasts to the cytoplasm, where it is first oxidized to glyoxylic acid in special cellular structures (peroxisomes and mitochondria), and then is converted into the amino acid glycine by amination (Fig. 3). In the mitochondria, a three-carbon amino acid serine is formed from two glycine molecules; at the same time one molecule of carbon dioxide is released.

Reactions of the glycolate formation and its further transformation proceed in the dark. Therefore, after turning off the light, when the process of carbon dioxide absorption and the restoration of its primary fixation products ceases, the formation and metabolism of glycolate continue, and the carbon dioxide resulting from the conversion of glycine to serine can still be released from the photosynthetic object. This is the very same CO₂ burst that occurs after turning off the light. In the light, CO₂ released during photorespiration reduces the observed photosynthetic rate, and at low carbon dioxide concentrations is the cause of the CCP existence.

Serine, which is formed during glycolate metabolism, is either used in the synthesis of proteins, or, after passing a series of biochemical reactions and losing the amino group, is converted into phosphoglyceric acid, which, in the fully grown leaves in light is usually involved in the photosynthetic reduction process in chloroplasts to form sugars (Chikov, Bakirova, 1999). Thus, as it can be seen in the diagram (Fig. 3), the reactions of glycolate formation and further conversion, associated with photorespiration, allow bypassing the photosynthetic carboxylation reaction in the Calvin cycle, and the cycle can function without CO₂ absorption. This was the basis for the emergence of the first and most widely recognized hypothesis explaining the physiological meaning of the photorespiration existence.

Physiological Essence of Photorespiration

Initially it was assumed that the role of photorespiration is only to use the products of the light phase of photosynthesis in the absence of CO₂. If the products of the light phase cannot be used to reduce carbon dioxide (in the absence of CO₂), then photo-destruction of the photosynthetic apparatus occurs. Simply put, certain structures of chloroplasts are destroyed, which leads to their inability to carry out the process of photosynthesis. The most favorable conditions for photodestruction are high illumination in the absence of both oxygen and carbon dioxide (Simpson and Bagar, 1976). If under these condition oxygen appears in the atmosphere

surrounding the leaf, then the glycolate formation is triggered. But this requires a sufficiently high (close to natural) oxygen concentration. Glycolate carbon (Fig. 3), after going through a cycle of transformations before the formation of PGA, is partially released as CO₂ and returns to the Calvin cycle, where it is reduced in the usual way using the “assimilation force” of chloroplasts (NADPH and ATP).

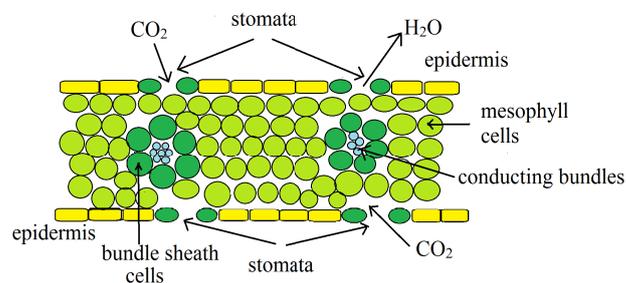


Fig 5 Schematic anatomy of the maize (C4-plant) leaf cross section (Chikov, 1996)

As a result, in the course of photorespiration, a partial “burning” of sugars occurs, carbon dioxide is released and the products of photochemical reactions are consumed. The photosynthetic apparatus seems to be running free (without absorbing external carbon dioxide), but at the same time the structures of the chloroplasts remain in an operable state. Such a situation usually occurs under drought, when, due to moisture deficiency, the stomata, which are the main channels letting carbon dioxide into the leaf and water vapor out of the leaf (Fig.5), are closed. In accordance with this concept, photorespiration, useful under drought, becomes a harmful, parasitic process under optimal conditions.

Search for Ways of Reducing Photorespiration Intensity in Order to Increase Plant Productivity

The discovery of such a powerful process, which decreases the photosynthetic rate, and hence the productivity of plants, led to the emergence of a number of research directions, the main task of which was if not to eliminate this process then to minimize its activity. Work was carried out in several directions (Chikov, 1996).

1. Obtaining mutants and studying them to find forms with defects related to photorespiration biochemistry.
2. Searching for substances able to block photorespiration.
3. Searching for plants with reduced photorespiration.
4. Development and creation of new methods and methodological approaches for a deeper study of the photorespiration phenomenon.

All these areas have been intensively developed. Work was particularly active in the 60s, 70s and the first half of the 80s. Numerous conferences, symposia and workshops were held on these issues. However, it must be noted that the task (increasing productivity by suppressing photorespiration) was not fulfilled. And the reason is not that they could not solve any of the problems that have arisen, but that this task did not have a positive solution. But let's sort these questions in order.

Getting Mutants Deficient in Photorespiration. Much work has been done in this direction, and such forms have been obtained (Zelitch, 1976). The reactions related to glycolate transformations were blocked in these mutants. As a result,

such plants turned out to be non-viable under the usual oxygen concentration in ambient air and could exist only at low oxygen concentration (less than 2%).

Searching for substances that inhibit glycolate metabolism and photorespiration. This direction was developed very intensively, since such inhibitors would allow to study deeper the very processes of photosynthesis and photorespiration. Such substances have been found (for example, glycidic acid) (Zelitch, 1978). Plants treated with this preparation, reacted less to a decrease in oxygen concentration. In some cases, they turned out to have higher photosynthesis, but their growth was suppressed and they had low productivity.

Searching for plants with reduced photorespiration. A long search has not resulted in detecting species with reduced photorespiration among C3 plants, but the fact that there exist plants with a different type of photosynthesis was established. It turned out that the vast majority of plant species assimilate carbon dioxide along the so-called C3 path of photosynthesis, but not all plant species. There is a group of plants assimilating carbon dioxide by another mechanism. In these plants, another carbon dioxide acceptor is used — the three-carbon compound phosphoenolpyruvate (PEP), and the primary product of carbon dioxide assimilation are the four-carbon compounds. The primary product of carbon dioxide fixation in these plants is oxaloacetic acid (OAA), but this compound is unstable and quickly turns into another four-carbon compound, usually either malic acid or aspartic amino acid. Accordingly, this type of photosynthesis was called the C-4 type (Fig. 6).

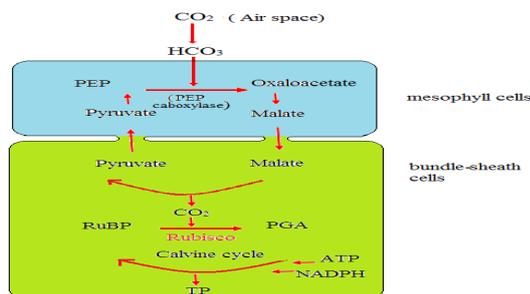


Fig 6 Scheme of C-4 type photosynthesis (Chiko, 1996). PEP - phosphoenolpyruvic acid, Rubisco - ribulose biphosphate carboxylase / oxygenase.

There are more than a thousand of such plant species. Among them are many tropical cereals (including corn, sugar cane, sorghum), the amaranth family, and some plant species from other families. Plants were also found with an intermediate type of photosynthesis, in which C-3 photosynthesis is observed under certain conditions, and C-4 photosynthesis reveals itself under others (most often under unfavorable (drought) conditions). The discovery of the C-4 type of photosynthesis strongly activated investigations of photorespiration, because C-4 plants did not show pronounced photorespiration.

The specific feature is that chloroplasts containing chlorophyll in these plants are not only in the leaf mesophyll (the main photosynthetic tissue), but also in the so-called bundle sheath cells that surround the phloem vessels transporting photosynthetic products from the leaf to the consuming organs. In the mesophyll cells of these plants (Fig. 6), CO₂ is assimilated with the formation of four-carbon compounds

(carboxylation process), which are then transferred to the bundle sheath cells.

In bundle sheath cells, these compounds (malic or aspartic acid) undergo decarboxylation (the process of CO₂ release that is reverse to carboxylation). The released carbon dioxide is reabsorbed with the help of Rubisco, since the normal Calvin-Benson cycle functions in the bundle sheath cells. This shows that in plants with the C-4 type of photosynthesis, the processes of the CO₂ carbon binding and its reduction to sugars are separated in space. In the mesophyll cells, CO₂ absorption takes place, and in the bundle sheath cells it is reduced to sugars, which pass into conducting vessels for export to the consuming organs.

CO₂ binding in the mesophyll occurs with the help of phosphoenolpyruvate carboxylase, which has a high affinity for CO₂. Therefore, it can absorb it even at very low concentrations. Since the product of CO₂ fixation (malic or aspartic acid) is transferred into the bundle sheath cells by active transport across the cell membranes, CO₂ seems to be pumped into the bundle sheath cells. Here, CO₂ is assimilated by the usual mechanism incident to C-3 type plants, but occurs already at an elevated concentration of CO₂, formed by decarboxylation of malic or aspartic acid. This explains the lack of visible photorespiration in C-4 plants, since near Rubisco the concentration of CO₂ is significantly higher than in the ambient air and oxygenase reaction is suppressed, although the formation and metabolism of glycolate in these plants exist.

Thus, none of the directions in the search for ways to reduce photorespiration did not result positively in increased plant productivity. Moreover, it appeared that the conditions suppressing photorespiration also reduce the productivity of plants. These efforts show that in any case, it is impossible to interfere with the evolutionarily established process without careful analysis of the purpose for which it was created by nature. Further sections of this article are devoted to this issue.

It should be noted that the understanding of the role of photorespiration in the plant productivity among plant biologists has not changed almost since the 80s of the twentieth century. New publications that have appeared [Rakhmankulova, 2018; Betti *et al.*, 2016; Walker *et al.*, 2016, and others.] are dedicated to particular issues and continue to manipulate photorespiration in order to force productivity by suppressing this process. All recent reviews on photorespiration ignored the publications in which transketolase pathway was shown as a way of glycolate formation (alternative to Rubisco) by ¹⁴C kinetic experiments (Chikov, 1987; 2017). In the case of the formation of glycolate through the transketolase mechanism, a superoxide radical is required, which is formed in connection with the flow of electrons in the electron transport chain of chloroplasts. It is this mechanism that integrated photorespiration into the general regulation of photosynthesis in the whole plant system.

Photo-Oxidative Processes and the use of Assimilates in the Whole Plant

Unsuccessful attempts to find a way to reduce photorespiration and thus increase plant productivity, however, had a positive consequence. Data has accumulated to understand the role of this process in the regulation of metabolism, not only in chloroplasts, cells, organs, but also in the whole plant. There

appeared new methods, new approaches for the analysis of this interesting phenomenon.

In the process of study of photosynthetic gas exchange and glycolate metabolism under various conditions it was found that photo-oxidative processes depend on the ratio between the mass of the produced photosynthetic products and the capacity of the consuming organs, that is on the intensity of photosynthetic product export from the leaf to the sink organs. If we reduce the number of fruit organs by removing some flowers or fruits, the proportion of the Warburg effect in leaf gas exchange increases (Lenz, 1977; Chikov, 1987). In this case, a larger amount of absorbed CO₂ is spent on the synthesis of amino acids, but not sugars, and the number of photosynthetic products used for the growth of the leaf itself increases. Thus, photorespiration is enhanced under conditions when many carbohydrate photosynthetic products are formed, and the transport systems and the consumption of sucrose by sink organs cannot cope with their export from the cell. Under these conditions, "excess" sugars begin to undergo oxidation with the formation of organic and amino acids.

Photorespiration and photosynthetic carbon metabolism. Interest in the photorespiratory process has been enhanced by the studies of the relationship between photosynthetic carbon metabolism (PCM) and transport of labeled assimilates from the leaf. It was established (Chikov, 1987; Chikov, 1988) that under the action of any photosynthesis suppressing factor, the export of assimilates from the leaf decreases and the non-carbohydrate orientation of the PCM increases. This phenomenon is especially pronounced under the action of nitrate nitrogen (Chikov, Batasheva, 2012), the removal of some of the sinks for assimilates, or when comparing leaves of different ages (Chikov, 1987). The degree of closure of the glycolate cycle on the Calvin cycle and the source of glycolate formation change (Chikov, 1987; Chikov, Bakirova, 1999).

This was confirmed by kinetic experiments on the incorporation of ¹⁴C into glycolate. When studying the dynamics of incorporation of ¹⁴C labeled carbon into photosynthetic products in leaves of plants in different physiological states, for example, after removing of fruits or increasing the level of nitrate nutrition (Chikov *et al.*, 1985; Chikov, 1987), there is a difference in the kinetic curves of ¹⁴C incorporation into glycolate. At an early stage (a few seconds in ¹⁴CO₂), the kinetic curves for the label incorporation into glycolate (Chikov, 2017) in different variants run in opposite directions (Fig. 7). In the case of the glycolate formation through Rubisco (steady state of control plants), the label content in glycolate increases up to 20 seconds and then decreases. With other sources of glycolate formation (at removal of assimilate acceptors or increase in CO₂ concentration), the maximum label incorporation into glycolate is noted in the very first seconds, and then the label content rapidly decreases.

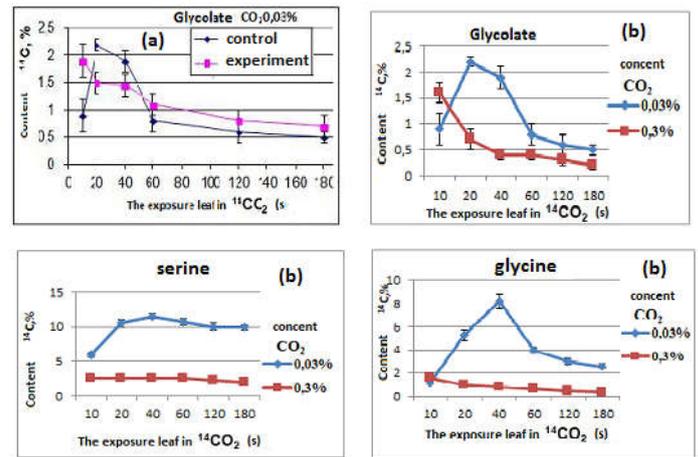


Fig 7 The kinetics of ¹⁴C introduction into some products of photosynthesis (% radioactivity of water-ethanol soluble fraction) in leaves of cotton plants (Chikov *et al.*, 1985). Effect of removal of fruits (a) and increasing concentrations of CO₂ (b).

Transketolase reaction in the Calvin cycle may be another (apart from RuBPO) possible glycolate source (Takabe, Asamy, 1980). In this case, the oxidizer is not the oxygen, but a superoxide radical formed either in the Mehler reaction (Takabe, Asami, 1980) or in the nitrite reduction (Chikov *et al.*, 1998). 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 ¹⁴C-glycolate, the superoxide radical should oxidise the sugar-phosphate formed from the newly labelled ¹⁴C of the PGA, and then reduced to ¹⁴C-sugar-phosphate. With the oxygenase reaction of glycolate formation, the sugar-phosphate formed from the previously labelled ¹⁴C of the PGA should undergo 13 reduction and conversion reactions to obtain the RuBP, which will give the labelled ¹⁴C-glycolate. Therefore, in the RuBPO reaction of glycolate formation, the glycolate is labelled with a delay (Fig. 7), 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, 1980).

Our studies of the photosynthetic carbon metabolism in connection with the study of photorespiration and the nature of the Warburg effect have shown (Chikov *et al.*, 1998; 1999) that the maximum carbon filling of the glycolate cycle (in ng/cm² s) occurs at simultaneously high illumination, concentration of CO₂ and oxygen (Chikov *et al.* 1998). In these circumstances, the delivery of ¹⁴C in the glycolate metabolism products is twice as much as at ambient CO₂ concentrations (Chikov *et al.*, 1998). This is probably due to the known (Ehleringer, Bjorkman, 1977) electron transport stimulation in chloroplasts with increasing CO₂ concentration. It also shows that the

intensity of carbon flow through the glycolate pathway is determined not only by the oxygen and the Ru BPO 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.

That is why the Warburg anti-effect is observed at high concentrations of CO₂ (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 ¹⁴CO₂ 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, 2017) their metabolism in new emerging organs.

The regulatory significance of the ratio of labeled sucrose to hexoses. Another important indicator of changes in PCM and export of leaf photosynthetic products is the ratio of ¹⁴C labeled sucrose to hexoses (glucose and fructose). At any decrease in the intensity of photosynthesis and export of leaf assimilates, the ratio of ¹⁴C labeled sucrose to hexoses decreased. For the photosynthetic transport compound (sucrose) to be loaded into the phloem, it must leave the mesophyll cells for the extracellular space of the leaf (apoplast), where it will be loaded into the leaf phloem vessels by specific energy-dependent carrier proteins. But in the apoplast there is an enzyme, invertase, hydrolyzing sucrose to glucose and fructose (Kursanov, 1984). The optimum activity of invertase is in the acidic pH range (Kursanov, 1984). By changing the pH of the extracellular fluid, it is apparently possible to influence the process of sucrose hydrolysis in the apoplast, and hence its export to the plant sink organs.

We tested this working hypothesis in special experiments. Bean plants grown in small plastic vessels were placed under a glass bell jar, as shown in fig. 8, where either a solution of hydrochloric acid or ammonia was placed on a Petri dish. Water served as control. NH₃ dissolves in the leaf apoplastic water, binds H⁺ ions and causes rapid alkalization as a direct result of NH₄⁺ formation (Husted and Schjoering, 1996).

As it was shown by experiments, acidification of the medium inhibited photosynthesis, and labeled assimilates accumulated in the apoplast. Alkalization led to the opposite effects (Fig. 8). The opposite effects of HCl and NH₃ vapors on photosynthesis and ¹⁴C content in the apoplast suggests that the key factor for the sucrose loading into phloem terminals is the pH of the apoplast medium, which affects the activity of invertase.

Stimulation of photosynthesis under the NH₃ treatment is impossible without the successful export of assimilates from the leaf. Intensive synthesis of sucrose in the leaf must inevitably lead to its accumulation in the apoplast. However, this did not happen. It means that this intermediate compartment was successfully passed by the assimilates. Accordingly, with two-fold inhibited photosynthesis (under the action of HCl), when there is a shortage of assimilates, their accumulation in the apoplast is difficult to explain without recognizing the fact of a decrease in the sucrose export from the leaf through the phloem.

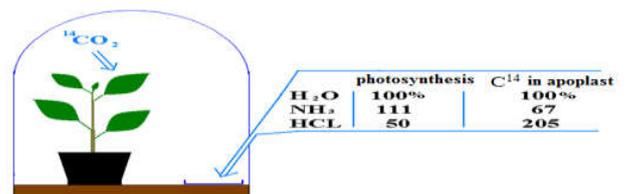


Fig 8 Effect of acidification or alkalization of the apoplast of a bean plant on photosynthesis and ¹⁴C content in leaf apoplast (Chikov, 2008).

It is characteristic that in this experiment, the acidity of the extracellular medium drastically changed the ratio of labeled products of photosynthesis (Chikov, 1987). Excessive concentration of HCl (from an acidified solution used to displace $^{14}\text{CO}_2$ from $\text{NaH}^{14}\text{CO}_3$ in a gas-holder), caused (Chikov, 2008) a decrease in the ^{14}C incorporation into sucrose and an increase in the label content in hexoses (Table 1). By the way, a decrease (by acidification of the gaseous environment around the leaf) of ^{14}C in phosphoric esters of sugars (PES) suggests that their conversion to sucrose was not suppressed. The formation of other labeled compounds also changes only a little. All this suggests that the main changes in the incorporation of labeled carbon into sucrose and hexose occurred as a result of stimulation of invertase and hydrolysis of sucrose in the apoplast.

To check *in vivo* whether the activity of the invertase enzyme itself affects PCM, we investigated genetically transformed plants with decreased or increased activity of apoplastic invertase. Experiments with potato plants, in which an additional gene for yeast apoplastic invertase was introduced, have shown (Chikov *et al.* 2011) that additional invertase significantly reduces photosynthesis and the sucrose to hexoses ratio (especially under limiting light). Test-tube transformed plants rooted worse and, due to the shortage of photosynthetic products in the roots, were more likely to die when they were planted in the soil.

On the contrary, experiments with tomato plants (Table 2), in which the expression of apoplastic invertase in leaves was suppressed using RNA interference, showed (Chikov *et al.* 2015) that invertase suppression increases photosynthesis (measured using $^{14}\text{CO}_2$) by 30-40%, but only in young plants, which have not yet exhausted the mineral nutrition fund in their pots. Two months later, when the mineral nutrition in the pot ended, the advantages of the transformant turned into a disadvantage. The photosynthesis of plants during this time decreased two- to three-fold, but it was 25% lower in transformed plants than in control plants.

Table 1 The effect of HCl concentration (%) in a gasholder on the ^{14}C incorporation (% radioactivity of the water-ethanol soluble fraction) into some soluble products of 3-minute photosynthesis in cotton leaves (Chikov, 1987)

Labeled compounds	HCl concentration (%)	
	0.3-0.5	2.0-2.5
PES	19.1	4.4
Sucrose	48.7	10.5
Hexoses	0.9	50.9
Alanine	6.8	8.3
Other compounds	24.5	25.9
Sucrose/hexoses	54.1	0.21

From this it follows that apoplastic invertase is involved in the regulation of photosynthesis in the whole plant system, but to influence its activity, a regulatory change in the pH of the extracellular fluid is necessary. The question arises, how does this happen?

Table 2 Effect of suppression of the apoplastic invertase activity on leaf photosynthesis (kBq / cm^2 min) in wild-type and transformed (Lin8RNAi) tomato plants of different ages (Chikov *et al.*, 2015).

Plant type	Plant age		The ratio of the young to the old
	Young (30 days)	Old (60 days)	
Wild type	10.2 ± 0.6	5.6 ± 0.3	1.82
Lin8RNAi	14.1 ± 1.4	4.2 ± 0.2	3.36
Lin8RNAi/wild type	1.38	0.75	-

This became clear after gasometric studies. The turning point in understanding of the mechanism of photosynthesis regulation and the role of photorespiration in this regulation was the simultaneous measurement of water vapor and CO_2 gas exchange in tomato plants under changing light (Chikov *et al.*, 2015).

Table 3 Physiological parameters of leaves of wild type tomato plants and tomato transformants (Lin8-RNAi) with decreased apoplastic invertase activity under varying illumination (Chikov *et al.*, 2015)

Parameters	Wild type	Lin8-RNAi	Wild type	Lin8-RNAi
Photon flux density* ($\mu\text{mol}/(\text{m}^2 \text{ s})$)	1556 ± 32		771 ± 58	
Photosynthesis, $\mu\text{mol CO}_2/\text{m}^2 \text{ s}$	21.6 ± 0.7	23.5 ± 0.5	17.7 ± 0.6	20.5 ± 1.0
Transpiration, $\mu\text{mol H}_2\text{O}$	8.1 ± 0.3	8.3 ± 0.4	7.0 ± 0.3	9.4 ± 0.2
Stomatal conductance, $\mu\text{mol CO}_2/(\text{cm}^2 \text{ s})$	322 ± 17	303 ± 9	271 ± 12	375 ± 27

In plants grown in direct sunlight, photosynthesis and transpiration were measured simultaneously using a gasometric system Walz GFS-300 (Germany), which allowed calculation of the stomatal conductance for CO_2 diffusion. The results of the experiments showed (Chikov *et al.*, 2015) that, in the steady state, photosynthesis of transformants was only 9% higher than that of the wild type (Table 3). At the same time, transpiration and stomatal conductance did not differ significantly.

But if the illumination was reduced by half (using gauze), the photosynthesis of Lin8-RNAi plants decreased to a lesser extent (and was 16% higher than that of the wild type plants). It is noteworthy that after reducing the illumination, leaf transpiration in the wild type tomato decreased significantly (by 14%), while in the transformant it increased (by 13%). As a result, stomatal conductance in the wild type decreased (by 16%), and in transformed plants increased (by 24%). A similar connection between the stomata and mesophyll chloroplasts was also shown in potato plants (Chikov *et al.*, 2016a) and later in maize plants (Chikov *et al.*, 2016b) under a rapid change in illumination.

Thus, after a decrease in light stomata closed in the wild type tomato plants (as it usually happens in all plants), but became even more opened in the transformant Lin8-RNAi. From this it follows that with a decrease in illumination, the reduction of the CO_2 fixation product (phosphoglyceric acid) to sugars decreased. Unreduced acids began to accumulate first in chloroplasts, and then in the cytosol and vacuole. Then an increase in the concentration of acids occurs in the apoplast, which activates the invertase. Increased hydrolysis of sucrose in the extracellular space increases the osmolarity of the aqueous medium (two molecules of hexoses are formed from one molecule of sucrose). The solution with increased osmolarity moves towards the stomata and due to the evaporation of water its concentration (and osmolarity) increases even more. And stomata close, leading to a decrease in transpiration and photosynthesis. This happens in in wild-type tomato plants.

In the transformed plants, invertase is suppressed, and sucrose is not hydrolyzed. Under these conditions, the loading of sucrose into the phloem continues, but its formation (due to a decrease in illumination) decreases. As a result, the concentration of sucrose in the extracellular solution is reduced. The osmolarity of the aqueous environment around

the stomata is reduced, and the turgor of the stomatal guard cells increases. And in this case, they open even more. Accordingly, the leaf photosynthesis in Lin8-RNAi tomato plants became higher compared to the wild type plants after a decrease in illumination, since CO₂ diffusion into the leaf, and therefore its absorption increased.

CONCLUSION

The above discussion of the results obtained with genetically transformed plants allows us to give the following explanation for the involvement of photorespiration and glycolate metabolism in the general regulation of photosynthesis in the whole plant system. But, in order to go directly to the mechanism of regulation of photosynthesis using photorespiration, we first recall what photosynthesis is in the whole plant system. This is a four-stage process.

First stage. Biochemically, photosynthesis is a carboxylation reaction, i.e. the formation of the acid carboxyl group (-COO⁻) in the CO₂ acceptor. Regardless of the type of photosynthesis and CO₂ acceptor, an acid is always formed when a carbon dioxide molecule is attached to an organic compound.

Second stage. Using the absorption of photons and the formation of the "reducing power" of chloroplasts (ATP and NADPH), the appeared acid is reduced to sugars.

Third stage. Transport of the formed photosynthetic products (in most plant species, it is sucrose) into sink organs, with sucrose entering the apoplast and encountering invertase. Depending on the activity of invertase, sucrose export from the leaf occurs to a greater or lesser extent. Hydrolysis of sucrose increases the osmolarity of the apoplastic fluid, which affects the degree of stomatal opening. The time of filling the space from the leaf chloroplasts to the apoplast with acids is the time of stomatal lag in response to exposure. It is likely that the role of each of the compartments can be divided kinetically into individual components all this way from chloroplasts to the stomatal guard cells.

Fourth stage. From the transport products of photosynthesis, either new shoots, leaves, or fruit elements (fruits, ears or roots) are formed, which are the final consumers of the photosynthetic products and the goal of growing agricultural plants.

A part of the photosynthetic products formed will be spent on symbiosis with soil microorganisms, which will provide the plant with additional resources (primarily with nitrogen absorbed from air and biologically active substances). And these microorganisms (consumers of photosynthetic products) enter into a competition for assimilates with other sink organs in the whole plant (Chikov, 1984).

And this process can probably also be regulated to the benefit of human beings. But in each of these competitions, the relationship between the source and the sink is harmonious. Microorganisms will not be able to give the plant what it cannot possibly use (so far) in its metabolism. If there are all the conditions favourable for the growth and development of the plant, then the decrease in the hydrolysis of sucrose stimulates the export of sucrose from the leaf and the plant productivity. And the transformation of the very operation of the photosynthetic apparatus will gradually occur.

Intensification of the export function (partial removal of leaves or a decrease in illumination) leads to the stimulation of photosynthesis (Mokronosov, 1983).

If there are no conditions for using photosynthetic products, then nothing can help photosynthesis to be active. The plant always forms its full copy in accordance with the available resources. As a result, in the absence of a request for assimilates under high illumination and the absence of external oxygen, photorespiration can be provided by oxygen formed endogenously in chloroplasts and photo destruction will be delayed. But with a significant violation of sink-source relations between photosynthetic and consuming organs in the plant (removal of all mature source leaves while all sink organs are present), chloroplast photodestruction occurs (Shabashvilly, Chikov, 1992). But this situation is not lethal for the plant. The enhancement of the non-carbohydrate orientation of photosynthesis is accompanied in the leaf by metabolization of the Calvin cycle sugar phosphates through the shikimate pathway with the formation of precursors of hormonal substances. The flow of hormones through the phloem activates the formation of new sink organs (Chikov *et al.*, 2016a; Chikov, 2017) and the steady state is preserved.

Each of these four steps has its own regulatory mechanisms that harmonize all biochemical reactions in accordance with the available resources. At the level of chloroplasts, where the main two stages of photosynthesis converge, the decrease in illumination, as already mentioned, will immediately decrease the reduction of the CO₂ fixation product and lead to the accumulation of acids. An increase in the acidity of the extracellular medium activates apoplastic invertase and all subsequent events involving stomatal regulation of the CO₂ flow into the leaf. The stomata close, and the light and dark processes in the chloroplasts are balanced.

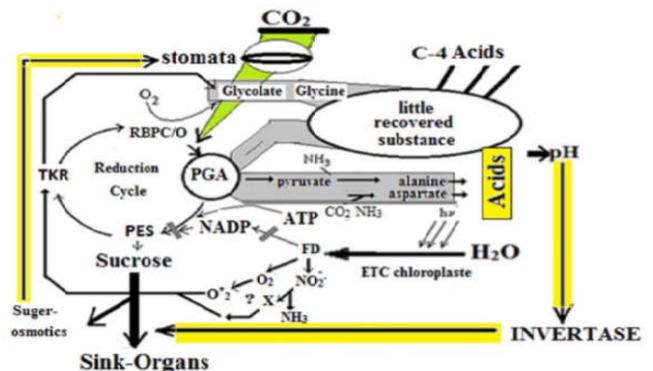


Fig 9 The scheme of photosynthetic carbon metabolism regulation in case of disturbance of dark and light photosynthesis process ratio in the whole plant (Chikov *et al.*, 1985; 1987; 1999; 2016 In development).

Similar events develop with other changes in the conditions of plant existence. For example, at plant nutrition with nitrates. When nitrates enter the leaf, non-enzymatic formation of nitric oxide occurs (Neil, Desikan, 2003), which triggers the expression of many genes, and induces the formation of callose, which clogs the pores in the sieve plates of phloem tubes, delaying the transport of sucrose along the phloem to sink organs. At the same time, in chloroplasts, nitrate ions begin to compete for electrons of the chloroplast electron transport chain with other consumers. In this process, superoxide is formed, which together with transketolase will produce

glycolate from already labeled ^{14}C Calvin Cycle sugar phosphates. Thereby, more acids are formed, which will lead to the triggering of the invertase mechanism of stomatal regulation of CO_2 flow into the leaf. And the disturbed balance between light and dark processes in chloroplasts will be restored. In this process, photorespiration and glycolate metabolism play a key role. Thus, photorespiration and glycolate metabolism are involved in the regulation of the ratio (sought by the plant) between the nitrogen- and carbon-containing products of photosynthesis, as well as between light and dark processes, creating a general harmony of metabolism in the whole plant. The scheme of this regulation is presented in Figure 9.

If, at the Steady-State state, the formation of NADPH exceeds the export capacity of sugars, then the formation of superoxide radical and the synthesis of glycolate through the transketolase reaction (TKR) is enhanced. With an increase in the level of nitrate nutrition, NO^- formed in the apoplast of the stem contributes to the closure of pores in the transverse partitions of phloem tubes and inhibits the outflow of sugars from the leaf. This reduces the recovery of organic acids and the formation of new sugars, which reduces the use of NADPH. All this enhances glycolate metabolism, which closes the flow of the glycolate cycle to the Calvin cycle. The resulting non-carbohydrate compounds activate the growth processes in the leaf. At the same time, an excess of phosphates of sugars metabolizes through the shikimate pathway with the formation of hormonal substances.

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