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PHOTOSYNTHETIC CARBON METABOLISM IN COTTON PLANTS

A. Abdullaev, Z.N. Abdurakhmanova, and B.B. Djumaev
Institute of Plant Physiology and Genetics, Academy of Sciences
Republic of Tajikistan, Dushanbe

Abstract

The activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) as well as phosphoenolpyruvate (PEP) carboxylase along with photosynthetic carbon metabolism in cotton plants (Gossypium hirsutum L.) was studied in the run of greening process, of plants' and leaves' ontogenesis in different parts of cotton stem. We proved that C_3 carbon metabolism is active during all stages of cotton leaf's development and that PGA is the main primary product. At the same time the amount of C_2-, C_3-, and C_4–metabolites varied in the run of leaf's aging. The highest values of the activity of photosynthesis as well as the activity of carboxylation enzymes were observed in the middle leaves (the 3d and the 4th true leaves) at the moment of study. Specific activity of Rubisco - from 0,29 mk mol $^{14}CO_2$ /mg Rubisco min in the juvenile leaf to 3,18 mk$^{14}CO_2$/mg Rubisco min in the 3d true leaf carries evidence on the most pronounced difference between the leaves. The index of PEP carboxylase activity (total one, in particular) proved to be in positive correlation with the rate of CO_2 assimilation in photosynthesis/ However the highest PEP carboxylase activity was observed in juvenile leaves which are characterized by very weak level of photosynthetic CO_2 assimilation. So the rate of C_2-, C_3, C_4 products' synthesis varied significantly in the leaves located in different levels of the cotton stem. The index of phosphoglyceric acid's (PGA) labeling increased from the first to fifth cotton leaves in synchronous manner with its simultaneous decrease in the 6-7th leaves. The volume of ^{14}C incorporation into C_4 dicarboxylic acids was insignificant in all leaves except juvenile ones, where the labeling of malate, aspartate, citrate and glycolate pathway intermediates was much greater than that found in other leaves. However, even in this case, the bulk of ^{14}C level was incorporated into Calvin cycle metabolites. Thus, the most significant differences observed in the relationship between the early-labeling C_2-,C_3-,and C_4- products indicate a strong depends of ^{14}C distribution among the photosynthetic products in the run of leaf aging.

Introduction

Elucidation of relation between the separate photosynthetic reactions of CO_2 assimilation would be useful in solving the plant production problem and would promote a control over photosynthetic mechanism. Each plant organ, especialy each leaf contributes to the epigenetic and morphogenetic processes of the integrate plant system in accordance with its source-sink relations[1]. To develop and investigate the quantitative theory of the plant production process, it is necessary to expand studies on the physiological integrity of the whole plant organism [2].

The cotton plant, as a model system for such studies, is of special interest, fist, because it is a sun plant with a long growth season that lasts from April until November and second, because some stages of its development under the continental climate conditions in Tajikistan coincide in time with the period of the high, nearly extreme, temperatures and air drought. The absolute maximum air temperature reaches 44 C in July, the mean soil temperature rises to 56C, and relative humidity drops to 7-15% [3]. The early stages of plant development proceed under moderate weather conditions, whereas the subsequent development, i.e., budding and fruiting, need higher temperatures. Thus, the assembling of a photosynthetic apparatus in cotton plant leaves of different age proceeds under different environments: lover leaves expand under rather moderate conditions subject to high temperature while senescing; the expansion and development of upper leaves under rigorous climate conditions.

For this reason, we focused our study on the photosynthetic carbon metabolism in cotton plant leaves in greening processes, ontogenesis and with to their position on the stem.

Methods

Cotton plants (Gossypium hirsutum L.)., cv. 108-F were grown on an experimental plot until beginning of the seventh or eighth true leaf phase (early budding).

Carboxylase activities of Rubisco and PEP carboxylase were determined at 30C by the rate of acid-insoluble product labeling [4] , in the presence of the substrates RuBP and PEP, respectively. Radioactivity was measured with liquid scintillation counter Mark-II (Nucleare Chicago, USA). The reaction mixture used to determine Rubisco activity contained 50mM Tris-HCI (pH 7.8), 5mM $MgCI_2$, 0,5 mM reduced glutathionce, 25mM $NaH^{14}CO_3$, 0,5 mM RuBp and 0,2-02 mg enzyme perpetrates. The total volume of the mixture was 0,5 ml. The reaction mixture used to determine PEP carboxylase activity contained 25mM Tris-HCI (pH8.1) 50mM $MgCI_2$, 15mM NADH , and 10mM $NaH^{14}CO_3$. Malate dehydrogenase and 15mM PEP

were then added. To determine Rubisco activity, the mixture was incubate for 15 without RuBP and then for 5 min in its presence. To determine PEP carboxylase activity, the mixture was incubated for 5 min without PEP and for 2 min in its presence. Addition of 0,5ml of 6N HCI to incubation medial terminated the reaction and removed the excess $^{14}CO_2$. Th control mixture had the same composition bute did not contain the substrates.

Rubisco content was measured by the immunoelectroassay [5] with a Multifor electrophoresis system (LKB, Sweden). Photosynthetic $^{14}CO_2$ fixation was recorded as described earlier [6] under the same conditions for all the treatments : light intensity was 40klx, CO2 concentration was 0,05%, and the rate of air flow through the chamber was 40-50 l/h (chamber volume was 0,05l). The sample were exposed to $^{14}CO_2$ with a specific radioactivity of 40 mCi/mol, for 15 s. The initial radioactivity of plant material was measured with a T-25-BFL counter connected with the counter device PST-10. Labeled products were analyzed according to the of Belan and Abdurakhmanova [7], and the radioactivity of individual compound was measured with a Mark-II scintillation counter in 10 ml of scintillator solution ZhS-8.

Experiments were run in 3-5 replicate, and all assays were repeated 2-3 time. The data were statistically processed with DVK-3 computer according to a program put at our disposal by D.I. Kosov. The mean values for the response function and their standard errors are given in the text.

Results

The results of study of photosynthetic activity in the process of greening of the etiolated cotton seedlings are shown in the Fig. 1. it is proved that the total $^{14}CO_2$ fixation is significant beginning from the first hours of seedlings' e[position to light and increases slowly in the run of 25 hours of illumination. By 45th hour of the illumination the rate of photosynthesis sharply increases and reaches its maximal values. The increase of $^{14}CO_2$ fixation rate runs in two phases: 1st - slow, sluggish and the 2nd - sharp. During the first 5 hours of illumination in the chlorophyll synthesis there is lag-phase and then we observed an increase of chlorophyll content in the run of the whole illumination period (Fig.2). During the first 25 yours of illumination the rate of total $^{14}CO_2$ fixation as well as chlorophyll synthesis increases in non-synchronous manner. It may be caused by the fact that protein formation in the reaction centers of photosystem II which is necessary for the run of photosynthesis, is behind of the chlorophyll formation [8,9].

Analysis of the products of CO_2 fixation manifested that in the etiolated leaves the considerable part (30%) of ^{14}C fixed on light is incorporated into PGA and other products of Calvin cycle (Table 1). In the run of seedlings' illumination parallel to the increase of the rate of total light fixation the increase of ^{14}C volume in these products (up to 75 hours of illumination) .together with it the quota of ^{14}C in the products of PEP-carboxylation in light decreases slowly.

The intensity of dark $^{14}CO_2$ fixation increases up to 25-hour period in consideration with the first hours of illumination and then it decreases. The increase of dark $^{14}CO_2$ fixation is accompanied by more intensive synthesis of PEP-carboxylation products, malate in particular. This fact gives the ground to suppose the possibility not only RuBP-carboxylase but PEP-carboxylase leaf function in C_3-plants as well.

So the course of photosynthetic activity development in greening cotton seedlings and incorporation of ^{14}C into the products of photosynthesis confirm the supposition about the presence of RuBP-carboxylase in etioplasts which can provide partial fixation of CO_2 at primary stages of chloroplast development. It may be supposed that holoenzyme is formed in the etioplasts of new synthesized small and present large subunits which provides CO_2 photosynthetic assimilation at the primary stages of chloroplast development.

The data of the Fig.3 prove that the potential efficiency of photosynthesis depends on the leaf age and this dependence has a one-peak character. The intensity of light $^{14}CO_2$ in the juvenile leaf (3-5 days) is very weak, it increases 9-fold up to the age of 20-25 days and then it decreases slowly. Such run of the potential photosynthesis correlates with the increase of leaf area as well as with the changes in carboxylase and oxygenase activity of RuBP-carboxylase [10]. The change in the efficiency of photosynthesis may be caused either by different level of gene expression in its subunit, or by the presence of different conformational measures of the enzyme which carry functional load in dependence of the physiological state of plants.

The experiments on kinetics of ^{14}C incorporation into the products of photosynthesis made it possible to reveal the throw by aged leaves of significant part of the primary fixed ^{14}C 90 sec. after a "gulp", which carry evidence on high intensity of photorespiration in them. (Fig.4). The increase of radioactivity 30 sec. after is caused by the stability of unstable intermediate products of photosynthesis, which decompose under the fixation in boiling alcohol and can't be revealed 10 sec. after a "gulp". In 3 min. after a "gulp" the increase of specific radioactivity is observed, probably caused by re-assimilation of Co_2.

At the early and late stages of leaf development when they possess weak assimilation capacity, the loss of $^{14}CO_2$ didn't occur, more over in the course of maturation after a "gulp" the radioactivity of the powder per weight unit increased slowly. In

these leaves, in accordance with their photosynthetic efficiency, the level of photorespiration is evidently low and the discharge of CO_2 is so weak that it may be not observed in our experiment, and fluent increase of radioactivity may be caused by stabilization of unstable products or CO_2 re-assimilation.

Table 2 shows the data on ^{14}C incorporation into the products of photosynthesis in cotton leaves of different age. The table proves that the ratio and set of the products of photosynthesis which are formed during 10 sec. varied in dependence of the leaves' age. In juvenile leaf PGA and PES concentrate significant part of fixed CO_2. Significant volume of label was incorporated into glycine and serine, malate and some products of heterotrophic assimilation. The fact that PEP-carboxylation wasn't the main way of CO_2 light fixation in the juvenile cotton leaf unlike potato and other plants attracts great attention [11]. Intensive synthesis of glycine and serine is the index of significant role of glicolate carbon pathway in metabolism in juvenile cotton leaves. It is possible that the main pool of glycine is synthesized in the process of photorespiration pathway [12]. But it is not the only pathway for the synthesis of this complex and we supposed in our experiment (with high CO_2 concentration) that its significant part is formed through PGA. In the run of leaf development we observed increase of the label in the products of pentose phosphate reduction cycle, PGA in particular. Besides, in 8-9-day leaves we observed the increase of ^{14}C ratio incorporated into malate in comparison with juvenile ones. It may be caused by stimulation of PEP-carboxylation, when both carboxyles are labeled in malate because part of PEP is synthesized from ^{14}C-PGA. Label incorporation into glycine and serine in this case is comparatively high but less intensive then in juvenile leaves.

Appreciable volume of label is incorporated into citric and isocitric acids under light fixation of $^{14}CO_2$ by young 4-9-day leaves.

In the mature leaves with higher efficiency of photosynthesis, more then 80% of fixed for 10 sec. ^{14}C was concentrated in PGA and PES, considerable part of ^{14}C was incorporated into alanine and glycerate. Insignificant content of label was revealed in glycine and serine. The table carries evidence that in the course of leaves' development specific activity of RuBP-carboxylase increased and the activity of PEP-carboxylase decreased.

Thus these data demonstrate improvement of photosynthetic function in the course of leaf development which is bound with formation of structural-functional and energetic factors of pentose-phosphate cycle of carbon. Our data agree with the analysis of products of photosynthesis, content of RuBP-carboxylase [13] as well as the ratio between carboxylase and oxygenase leaf functions in ontogenesis [11]. We may suppose that conjugation between photosynthetic CO_2assimilation, photosynthetic and photorespiratory carbon metabolism, synthesis and activation of the corresponding enzymes with the requirements of cell are carried out at gene level in the plant. So the study of photosynthetic carbon metabolism in the run of leaf ontogenesis proved that in cotton in all stages of leaf development C_3-type of carbon metabolism is functioning with PGA as the main product of photosynthesis. Together with it there are changes in the ratio between separate groups of metabolites (C_2, C_3 and C_4 – products) depending on the stage of leaf development.

Study of the interconnection between separate reactions of photosynthetic CO_2 assimilation in a whole plant to some extent may promote the decision of the problem of plant productivity and management of the regulation mechanisms in photosynthesis. Since the plants are considered to be an integral system in which all physiological and biochemical processes are interconnected and interdependent, its every organ and every leaf in particular, makes its contribution into epigenetic and morphology forming processes according to the consumers' needs. With the aim to develop and study quantitative theory of production process it is necessary to expand the study of the physiologically integral plant organism [14].

It is proved that every leaf manages products of its photosynthesis mainly in proper direction to the proper consumer of assimilates or their part [15]: the lower leaves provide root with assimilates, the upper – supply the ascending flow of assimilates [16]. Any change of this flow is reflected in the photosynthetic activity of the plant [17]. It is proved that after withdrawal of the fruiting elements the intensity of CO_2 assimilation in cotton plants decreases[15,17,18].

We can say that now we insufficiently studied photosynthetic carbon metabolism, activity and content of carboxylating enzymes of photosynthesis in whole cotton plant, the development of which runs in the conditions of sharp change of environmental factors it is bound with adaptation properties of plants and needs sufficient reorganization in photosynthetic carbon metabolism.

Table 3 demonstrates some photosynthetic characteristics of cotton leaves of different age.

The analysis of the activity of the carboxylating enzymes of RuBP-carboxylase and PEP-carboxylase demonstrate that their meanings as well as the ratio between them depend on the age of leaves (Table 3). As it is clear from the table, in the run of leaf development the activity of RuBP-carboxylase increases till maximal meanings of its values in the leaves of the third and fourth levels and then in the course of leaves' aging it decreases. Minimal activity of RuBP-carboxylase is ob-

served in juvenile leaves (in this case – in the leaves of the seventh level). The above mentioned regularity is constant for any manner of calculation.

The activity of PEP-carboxylase in a whole is significantly lower then that od RuBP-carboxylase but it is adequately high and in the formed leaf it is more than 15% of the sum of carboxylase activity of both enzymes and more then 20% of the RuBP-carboxylase activity.

The activity of PEP-carboxylase in the leaves, which are located in different levels of the plant, varies within more narrow bounds then that for RuBP-carboxylase (from 1.88 till 3.98). The leaves of the first level have the lowest both specific and total activity of PEP-carboxylase. It increases upstem, then decreases somehow and maximal but the same meaning as in the activity of the fourth leaf is the meaning for juvenile leaf.

So our results carry evidence of significant varieties in the activity of carboxylating enzymes advantage in the activity of RuBP-carboxylase in all leaves but juvenile one.

It was interesting to compare the activity of the enzymes under study with the intensity of photosynthesis.

Table 4 shows that the developing juvenile leaf possess very low assimilating capacity which means insufficient part of the mature leaf's photosynthesis. In the run of leaf's development the activity of photosynthesis increases and reaches maximal values in the leaves of 4-5th levels and than it decreases .

Some differences in the changes of the RuBP-carboxylase activity and the efficiency of $^{14}CO_2$, in particular more sharp changes of RuBP-carboxylase activity can be explained by the peculiarities of the measurement of these parameters: photosynthesis is determined in vivo, and the enzyme's activity in vitro. In a whole the run of changes in the efficiency of photosynthesis is equal to those in the activity of RuBP-carboxylase as well as in PEP-carboxylase except juvenile leaf. We may suppose that in CO_2 photosynthetic assimialation in leaves under study both with RuBP-carboxylase, which determines the rate of this process, the contribution of PEP-carboxylase is significant too. It might be bound with ecological conditions of plants' development.

The analysis of products which are formed in the run of photosynthesis made it possible to reveal noticeable distinguishes in their ratio (Table 4). The efficiency of photosynthesis in the first true leaf in this period is of about 50-dais age and possess the efficiency of photosynthesis 2 fold lower then its maximal value in this plant. More than 70% of the assimilated carbon is incorporated into Calvin cycle products and 30% of them – into PGA. The largest part of the label is found in glycine with serine (about 8%) as well as in glycolate (about 6%) which carry evidence on the increase of the reaction of carbon glycolic metabolism. We must note that in C_4-units we can observe incorporation of insignificant part of the assimilated carbon, malate and aspartate are formed in trace values.

The second true leaf is 5-6 younger then the first one. The efficiency of photosynthesis in this leaf are some lower then in the first one. In early products the quota of Calvin cycle metabolites increases mainly at the expense of phosphoric ester of sugars. The quota of ^{14}C in glycine, serine and glycolate somehow decreases. The increase of the efficiency of photosynthesis in other following leaves - 3d, 4th, 5th is accompanied by the increase of net and relative label content in PGA and phosphoric esters of sugars with its slow decrease in glycine, serine and glycolate. In the 5th leaf in PGA we observe maximal content of $^{14}CO_2$ (53%). The 6th leaf in this period of plant's development achieved 14-15-day age, its efficiency of photosynthesis was 2-fold lower then that one in the 5th leaf, but was close the photosynthesis in the first leaf. $^{14}CO_2$ incorporation into PGA in comparison with the previous leaf is significantly slow, but the intensity of incorporation into phosphoric ester sugars, including di- and monophosphates of sugars and glycine with serine.

In the 7th juvenile leaf as it was noticed the quota of ^{14}C incorporated into C_4- and C_2-units increases, though the quota of C_3-products is significant their too, PGA in particular. The analysis convinced us that leaves' efficiency of photosynthesis as well as the ratio of its products are in dependence with the demand for assimilates.

It is supposed that photorespiration can be considered to be the regulatory factor in the management of photosynthesis because this process depends on the balance between source-sink.

At the decrease of epigenetic demand on photosynthesis the process of photorespiration increases so this is the way to remove the abundance of the products, but at that time there appear additional source of energy [19]. It is true equally for the leaves of the first levels as well as juvenile one in which at this stage of development the metabolites are spent for formation of the leaf itself and it is the main consumer of assimilates. The data we obtained may to some extent confirm this supposition. It's worth to be emphasized that stimulation of PEP-carboxylase activity doesn't cause correresponding synthesis of C_4 acids. Evidently the activity of PEP-carboxylase, which doesn't take part in the photosynthetic carbon as-

similation, changes and this fact proves that the enzyme plays significant role in the developing leaf and its adaptation to the changing environment.

Thus in cotton plant the maximal efficiency of photosynthesis is in the leaves with maximal leaf area. The increase of photosynthetic CO_2 assimilation is accompanied by the corresponding increase in the activity of carboxylating enzymes of RuBP-carboxylase and PEP-carboxylase as well, by change of the ratio between photoassimilates which is caused by ontogenetic peculiarities of leaves, their donor-acceptor interaction with the whole plant and the conditions in which runs the development of every leaf.

It is interesting that the increase of the efficiency of photosynthesis is accompanied not only by corresponding increase in the activity of RuBP-carboxylase and to some extent the activity of PEP-carboxylase, which equals the level of enzyme's activity at heterotrophic assimilation (in the juvenile leaf) under the condition of maximal values of the efficiency of photosynthesis. The response of the plant on unfavorable factors of the environment, in particular high temperatures and soil draught is stimulation of the activity of PEP-carboxylase and primary synthesis of the products of metabolism [20]. Formation of late cotton leaves is bound with the action of severe ecological conditions (high temperatures, atmosphere draught) and the increase of the activity of PEP-carboxylase and so primary photosynthesis at the proper stages of leaf development in C_4-metabolites. It is possible that it reveals as adaptogenic trait under the influence of unfavorable factors of environment.

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Table 1. Incorporation of 14C into the products of photosynthesis in the process of greening of etiolated cotyledon cotton leaves, % from alcohol-water extract (exposition in $^{14}CO_2$-10sec, concentration of CO_2-0,5%).

	Variant of assay						
	etiolated	5 h of illumination		25 h of illumination		75 h of illumination	
Compounds	**cotyledon**	**light**	**dark**	**light**	**dark**	**light**	**dark**
Phosphorylated	30,6	50,2	16,4	57,4	7,4	83,5	2,6
Including PGA	17,4	46,9	10,3	41,9	2,3	45,3	2,0
PEP carboxylation products,	60,7	41,8	75,7	30,5	89,8	8,1	83,5
Malate	37,9	25,9	40,9	14,7	68,2	2,5	49,0
Aspartate	11,5	7,9	21,2	7,6	4,0	2,0	14,2
Others	8,7	8,0	7,9	12,1	2,8	8,4	13,9
Common fixation 14CO2, imps / mines on 1 g dry substance	129,5	242,5	111,9	615,3	221,2	1,215	88,3

Table 2. Incorporation of ^{14}C in the products of photosynthesis (in % from total radioactivity) and activity carboxylating enzymes (mkMol CO_2/mg.of protein·min).

	Age of leaves, days			
Metabolites, enzymes	**4-5**	**8-9**	**15-16**	**22-23**
Residial; fraction	10,0±1,0	5,2±0,5	2,0±0,01	2,5±0,2
Sugar diphosphate	12,8±0,1	4,8±0,4	3,6±0,2	4,4±0,4
Glycosemonophosphate	-	-	4,2±0,3	9,7±0,9
Fructozomonophosphate	10,5±0,1	10,1±1,0	28,4±3,0	5,8±0,5
PGA	14,5±0,1	30,2±2,5	36,4±3,1	63,6±6,0
Aspartate	9,6±0,9	9,3±0,1	5,9±0,5	1,1±0,1
Glycin, serin	11,2±1,0	5,0±0,5	1,0±0,1	0,8±0,1
Alanine, glycerateглицерат	11,7±1,1	4,8±0,5	1,8±0,1	7,1±0,6
Malate	7,6±0,8	14,1±1,1	9,2±0,1	2,8±0,2
Citrate and isocitrate	8,5±0,7	5,6±0,4	-	-
Rubisco activity	0,11±0,01	0,16±0,016	0,29±0,01	0,31±0,03
PEP -carboxylase activity	0,2±0,02	0,10±0,01	0,06±0,01	0,05±0,01

Table 3. Functional properties of photosynthesis in cotton plant leaves located at various levels the stem.

	Rubisco activity				PEP carboxylase activity		
Leaf No (from the botton)	**MkMol $^{14}CO_2$/mg soluble protein**	**MkMol $^{14}CO_2$/mg Rubisco· min**	**MkMol $^{14}CO_2$/g fr. wt·min**	**Rubisco content, mg/g. fr.wt**	**Mk Mol $^{14}CO_2$/mg Solube protein.min**	**MkMol $^{14}CO_2$/g. fr. Wt. min**	**Rate of Photosynthesis, mg CO_2/g dry wt.min**
1	0,45±0,02	0,97±0,02	6,21±0,06	3,36±0,26	0,09±0,01	1,19±0,01	0,42±0,08
2	0,54±0,01	2,27±0,01	8,68±0,02	3,05±0,04	0,11±0,01	1,70±0,01	0,52±0,07
3	0,74±0,09	3,18±0,33	18,33±2,33	5,10±0,06	0,11±0,02	2,84±0,40	0,73±0,07
4	0,73±0,01	2,84±0,05	18,33±1,33	4,84±0,25	0,15±0,03	3,88±0,70	0,89±0,04
5	0,46±0,03	2,29±0,12	12,34±1,31	4,14±0,08	0,11±0,01	3,11±0,27	0,91±0,09
6	0,14±0,02	1,36±0,14	2,11±0,22	3,26±0,05	0,15±0,03	2,16±0,44	0,48±0,08
7	0,06±0,02	0,29±0,03	0,84±0,07	3,90±0,12	0,24±0,02	3,98±0,26	0,02±0,00

Table 4. ^{14}C distribution among photosynthetic products of cotton plant leaves, % of ethanol-water fraction. Exposed to 1 $^{14}CO_2$ for15 c.

^{14}C labeled ol compound	**Leaf 1**	**Leaf 2**	**Leaf 3**	**Leaf 4**	**Leaf 5**	**Leaf 6**	**Leaf 7**
Sugar diphosphates	8,5±1,7	5,7±0,6	4,4±0,5	4,1±0,3	4,7±0,5	7,5±0,7	8,8±1,0
Sugar monophosphates	22,0±1,6	31,3±3,0	24,0±0,3	26,8±0,8	20,6±2,2	33,8±0,8	20,2±1,4
PGA	38,1±3,4	41,7±5,1	47,3±4,3	48,2±5,4	53,0±4,7	37,4±2,6	14,3±1,3
Triose phoshphate	4,0±0,4	2,8±0,4	5,6±0,6	4,0±0,3	3,9±0,5	5,0±0,8	-
Glycin. Serin	7,8±0,1	6,2±0,8	4,5±0,6	4,1±0,8	3,5±0,2	5,2±0,5	11,2±1,2
Sucrose	4,4±0,5	1,6±0,1	1,8±0,1	2,0±0,1	2,3±0,2	1,9±0,2	-
Monosaccharides	-	1,4±0,1	1,7±0,1	1,5±0,1	1,9±0,3	1,8±0,3	-
Ala	3,5±0,5	2,2±0,4	3,2±0,4	2,1±0,3	2,8±0,3	-	16,2±2,4
Glicerate			2,2±0,4	1,9±0,1	2,6±0,2	-	
Glycolate	5,7±0,7	3,6±0,6	2,1±0,3	1,5±0,2	2,0±0,1	2,5±0,4	-
Malae	-	-	-	0,7±0,1	-	-	6,7±1,1
Aspartate	-	-	-	-	-	-	9,6±0,8
Citrate, Isocitrate изоцитрат	-	-	-	-	-	-	8,0±1,5
Residial; fraction	5,9±0,7	3,0±0,1	3,1±0,2	2,5±0,2	2,6±0,2	4,7±0,2	8,4±0,9

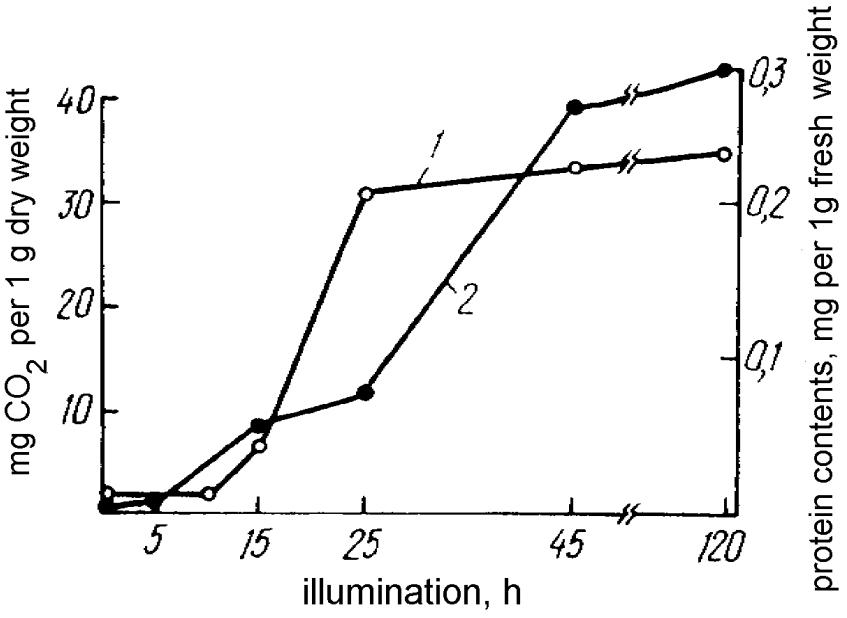

Figure 1. Dynamics of protein fraction (1) assimilation and the intensity of $^{14}CO_2$ fixation (2) in the run of greening of the etiolated cotton leaves (exposure with $^{14}CO_2$ 3 min.).

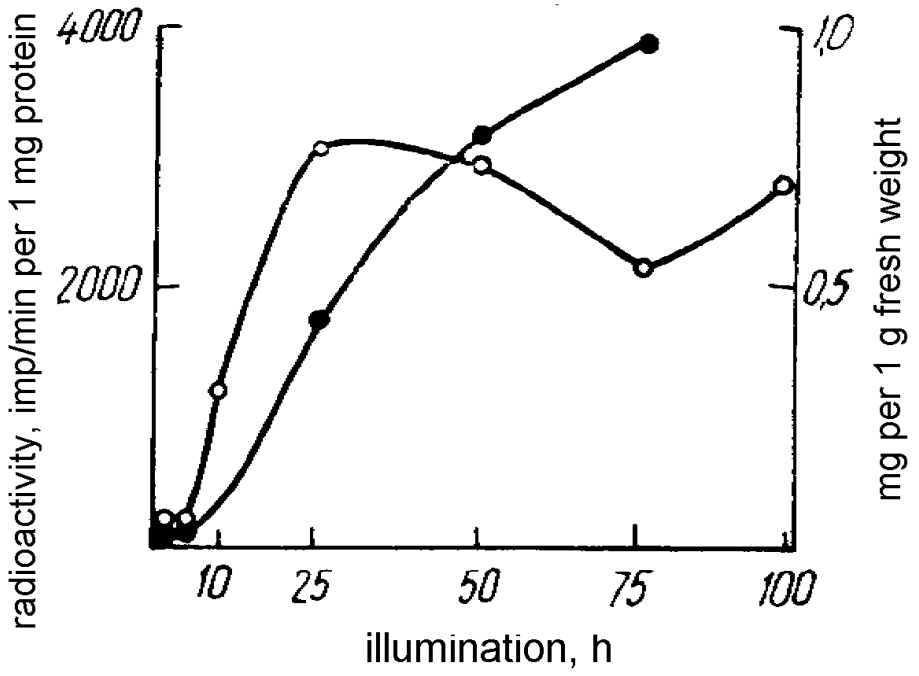

Figure 2. Chlorophyll content (the curve with black circles) and $^{14}CO_2$ incorporation into polypeptides of RUBP-carboxylase under immunoprecipitation (the curve with light circles) in the process of cotton biogenesis.

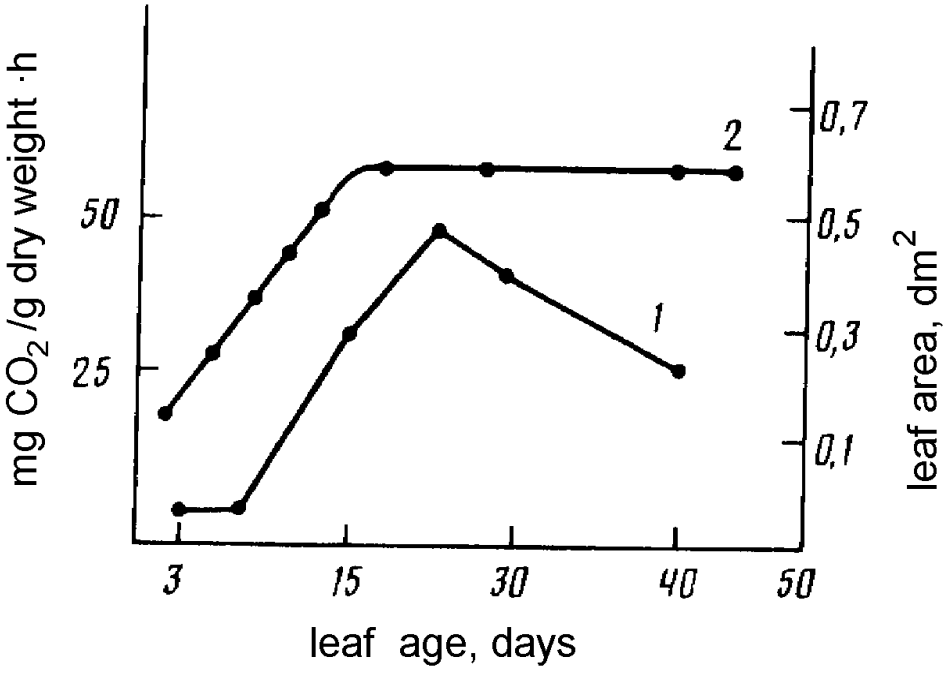

Figure 3. Potential efficiency of photosynthesis (1) and leaf area (2) in the cotton leaves of different age.

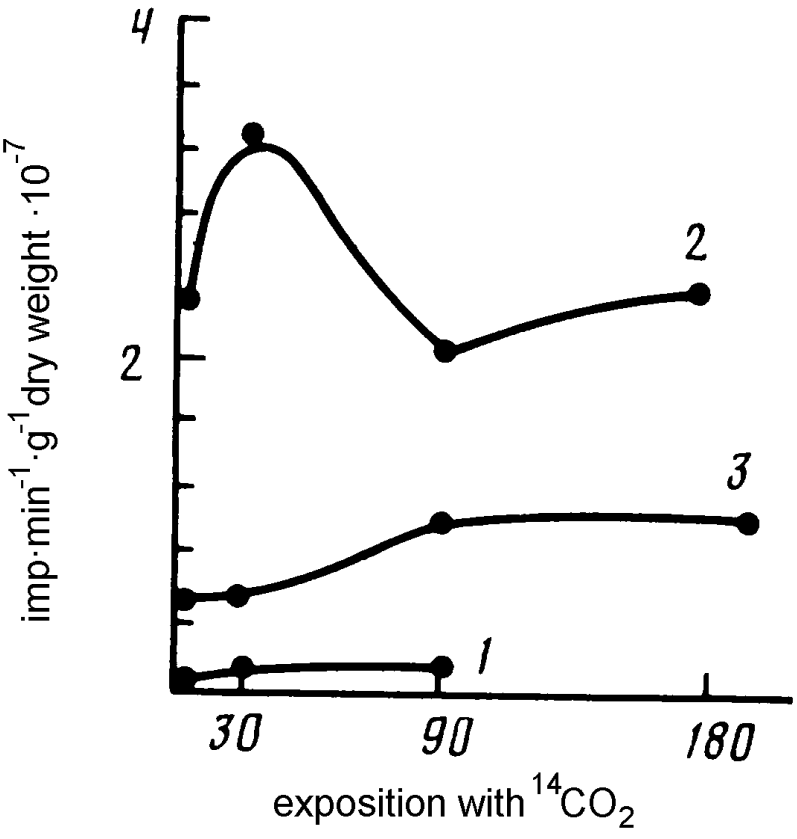

Figure 4. Kinetics of ^{14}C incorporation into the stable products of photosynthesis in cotton leaves of different age: 1 – juvenile leaf; 2 - mature leaf; 3 - aged leaf.