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Photosynthesis, Photorespiration and Productivity of Wheat and Soybean Genotypes

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The results of the numerous measurements obtained during the last 40 years on gas exchange rate using an infrared gas analyzer URAS-2T (Germany), photosynthetic carbon metabolism by exposition in $^{14}CO_2$ and activities of enzyme of primary carbon fixation, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPC/O), in various wheat genotypes grown over a wide area in the field and contrasting in photosynthetic traits and productivity are presented in this paper. It was established that high productive wheat genotypes with the optimal architectonics (7-9 t ha^{-1}) possess higher rate of CO_2 assimilation during leaf ontogenesis. Along with the high rate of photosynthesis, high values of photorespiration are characteristic for high productive genotypes. There is a parallel increase in the rates of true photosynthesis and photorespiration in ontogenesis. Genotypes with moderate (4-5 t ha^{-1}) and low (3 t ha^{-1}) grain yield are characterized by relatively low rates of both CO_2 assimilation and photorespiration. The ratio of true photosynthesis to photorespiration in genotypes with different productivity is equal on average to 3:1. A value of photorespiration constitutes 28-35% of photosynthetic rate in contrasting wheat genotypes. The activities of RuBP carboxylase and RuBP oxygenase were changing in a similar way in the course of the flag leaf and ear elements development. RuBP oxygenase activity was higher in high productive wheat genotypes than in low productive ones. The rates of sucrose (the main transport metabolite in plants) biosynthesis and products of glycolate metabolism also correlate with the CO_2 assimilation rate and the activity of RuBP oxygenase. High productive genotypes are also characterized by a higher rate of biosynthesis and total value of glycine-serine and a higher photosynthetic rate. Pattern of changes in biosynthesis rate and total value of glycine-serine as well as ratio of RuBP carboxylase to oxygenase activities and CO_2 assimilation rate predisposes to parallel change in the rates of photosynthesis and photorespiration during leaf ontogenesis. High rates of photosynthesis and photorespiration in conjunction with favourable photosynthetic traits, an optimum leaf area index and the best architectonics define high productivity of wheat genotypes. Therefore, contrary to conception arisen during many years on wastefulness of photorespiration, taking into account the versatile investigations on different aspects of photorespiration it was proved that photorespiration is one of the evolutionary developed vital metabolic processes in plants and the attempts to reduce this process with the purpose of increasing the crop productivity are inconsistent. Phosphoglycolate phosphatase, a key enzyme of photorespiration was first homogeneously purified from eukaryotic green algae *Chlamydomonas reinhardtii* with subsequent determination of complete nucleotide and deduced amino acid sequences (NCBI Nucleotide 1:AB052169). Since metabolic processes of photorespiration in the leaf occur in the light simultaneously with photosynthesis, it is evident that released energy is used in certain reactions of photosynthesis.

Keywords: *photosynthesis, photorespiration, productivity, architectonics, gas exchange, carbon metabolism, RuBPC/O, Triticum L. genotypes, soybean genotypes*

INTRODUCTION

Among the processes ensuring a high plant productivity leading role belongs to photosynthesis (Aliyev, 1974). Photosynthesis is unique process, in course of which light energy is utilized for carbon dioxide conversion into sugars. About 92% of all vascular plants that use only Calvin-Benson cycle belong to C_3-plants because their first product of CO_2 fixation is three-carbon compound termed

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3-phosphoglycerate (PGA). In plants with C_3-metabolism photosynthesis takes place simultaneously with the opposite process, which relates both to the oxygen and carbon dioxide gas exchange. This process occurs only in the light and is associated with photosynthetic metabolism, and therefore was named photorespiration. Photorespiration was discovered in 1955 by I. Decker (1955). Photosynthesis and photorespiration are closely linked processes catalysed by the key photosynthetic enzyme, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39) with the dual catalytic activity. The process of photorespiration is associated with oxygenase activity of RuBP, the function of which is to fix carbon dioxide (Lorimer and Andrews, 1973). The adhesion of CO_2 to this enzyme substrate results in formation of two molecules of 3-phosphoglycerate. Rubisco has affinity not only for CO_2, but also for molecular oxygen, that results in formation of one molecule of 3-phosphoglycerate (integrated into the Calvin cycle) and one molecule of 2-phosphoglycolate (starting molecule of photorespiratory glycolate cycle) instead of two molecules of 3-phosphoglycerate (Ogren and Bowes, 1971). During photorespiratory metabolism oxygen is fixed and carbon dioxide is released. Photorespiratory carbon metabolism requires the integration of biochemical pathways in three separate leaf cell organelles: chloroplasts, peroxisomes and mitochondria (Figure 1). In mesophyll cells peroxisomes, chloroplasts and mitochondria are often located nearby, supporting an intensive metabolism between these organelles. Currently biochemical mechanism of photorespiratory pathway is sufficiently enough studied. The initial stage of photorespiration takes place in chloroplast stroma. According to the most researchers, the initial substrate for the photorespiration is glycolate. Reactions associated with photooxidative transformation of RuBP and formation of phosphoglycolate are considered to be key processes of photorespiration (Somerville and Ogren, 1979; Andersson, 2008). Under the influence of a key photorespiratory enzyme, phosphoglycolate phosphatase (PGPase, EC 3.1.3.18), phosphoglycolate is converted into glycolate which then leaves the chloroplast and enters the peroxisome. Carbon metabolism in photorespiration describes the sequence of reaction series of so-called "glycolate pathway", most of which take place in peroxisomes and mitochondria.

Photosynthesis and photorespiration are high-flux pathways that involve redox exchange between intracellular compartments. In particular, the photorespiratory pathway interacts directly with the redox signaling cascades that control plant growth and defence responses as well.

Photorespiration has been studied for more than 50 years. For a long period of time the rate of photorespiration was considered as a negative factor in determining the dependence of plant productivity on photosynthesis. While evaluating photorespiration magnitude many researchers supposed that carbon losses in photorespiration occur through the use of newly formed products, and therefore this process was considered to be wasteful. Hence, it was proposed to search the ways for elimination or decreasing photorespiration by biochemical or genetic means with the purpose of increasing the crop productivity (Zelitch, 1966, 1971, 1973, 1975; Zelitch and Day, 1973; Hough, 1974; Chollet and Ogren, 1975; Kelly and Latzko, 1976; Ogren, 1976; Servaites and Ogren, 1977; Holaday and Chollet, 1984; Somerville, 2001; Ogren, 2003; Igarashi et al., 2006; Long et al., 2006; Kebeish et al., 2007; Khan, 2007; Mueller-Cajar and Whitney, 2008; Maurino and Peterhansel, 2010; Peterhansel et al., 2010; Peterhansel and Maurino, 2010). However, screening for species with low level of photorespiration and high productivity was not successful. Any intervention in the plant functions led to decrease in plant growth and productivity. But few researchers believed that photorespiration is essential for normal plant functioning (Barber, 1998; Evans, 1998; Eckardt, 2005). Taking into account very high rates of photorespiration comparable only to the rates of photosynthesis, it remained unclear why such a wasteful process of energy dissipation has not disappeared during the evolution. On the contrary, there is a complex enzyme apparatus for recycling of phosphoglycolate, inevitable product of RuBP oxygenase reactions (Tolbert, 1997).

The fact that photorespiration has not been completely eliminated even in evolutionary more advanced C_4-plants (Dever et al., 1995; Zelitch et al., 2008) along with the discovery that C_4-plants have photorespiratory enzymes (Popov et al., 2003; Majeran et al., 2005) may reflect the functional relevance of the pathway.

The study of photorespiration also occupies a central position in the history of modern plant biology (Eckardt, 2005; Maurino and Peterhansel, 2010; Peterhansel et al., 2010; Peterhansel and Maurino, 2010). A lot of plant scientists attempt to resolve this dilemma. The pathways of biochemical reactions, the genes of key photorespiratory en zymes, energetics, redox signaling, and transporters of photorespiratory intermediates were discovered (Leegood et al., 1995; Booker et al., 1997; Wingler et al., 1999; Mamedov et al., 2001, 2002; Mamedov and Suzuki, 2002; Eisenhut et al., 2006; Schwarte and Bauwe, 2007; Foyer et al., 2009; Peterhansel et al., 2010).

But, there is still no unanimous opinion about the role of this process in photosynthesis and plant

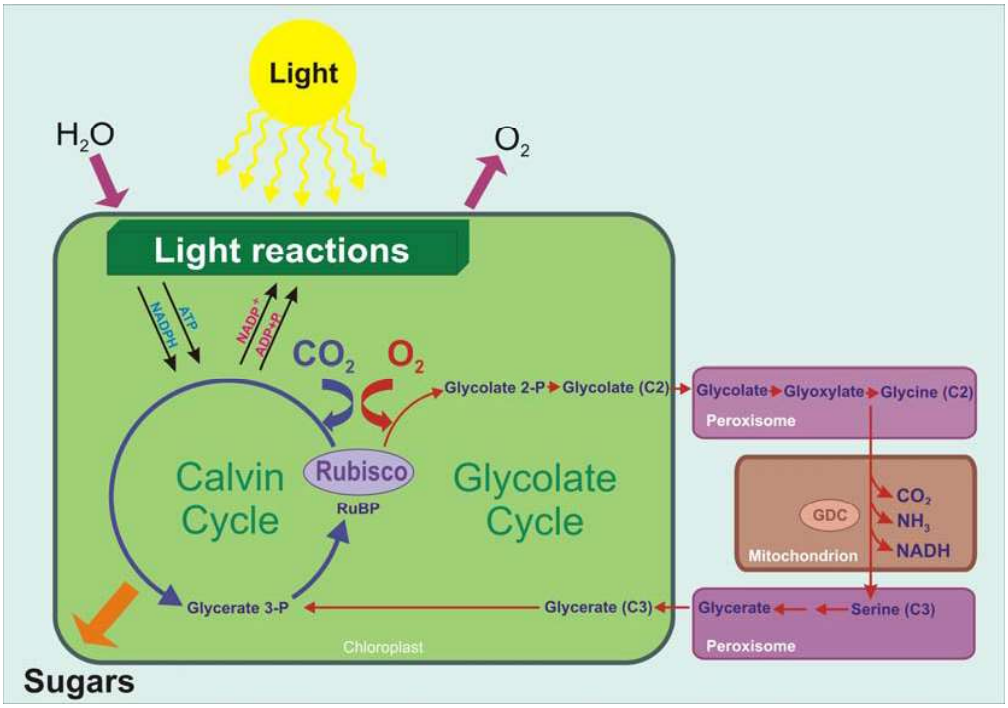

Figure 1. Schematic overview of photosynthesis and photorespiration.

productivity. It is particularly important to note that most of the previous studies on photorespiration were performed mainly in controlled environment experiments. The results of such studies cannot fully reveal real environmental conditions.

In the present paper the results of long-term experiments on the relationship between the rates of photosynthesis, photorespiration and productivity of wheat genotypes grown in the field are presented.

MATERIALS AND METHODS

The rich genefund, comprising several thousand wheat genotypes, selected from both the ancient, aboriginal varieties of national selection and introduced from the world genefund, particularly, from *CIMMYT, ICARDA* and other International Centres, with contrasting photosynthetic traits, productivity and tolerance to water stress was created (Figure 2). All these genotypes were grown in field conditions in a wide area at the Absheron Experimental Station of the Research Institute of Crop Husbandry at the optimal regime of mineral nutrition and water supply (Figure 3).

Genotypes were also grown with normal water supply and at severe water deficit under the guidelines established by the Department of Plant Physiology and Biotechnology of the Research Institute of Crop Husbandry on the base of long-term studies of morpho-physiological traits of the varieties. The experimental plot area was 54 m^2; all experiments were replicated at least four times. Numerous winter wheat genotypes were the main targets of the researches, and most typical of them are presented in this paper. The main parameters for selection of these genotypes were grain yield, plant phenotypic features (stem height, area and architectonics of the leaf surface, etc.), duration of the vegetation and other morpho-physilogical traits, as well as drought resistance (Figure 4, 5, 6, 7, 8, 9, 10) (Aliyev and Kazibekova, 1977; Aliyev et al., 1982 b; Aliyev, 1983, 2002). Due to leaves oriented under different inclination angles, plants create canopies with drooping (the angle is 30-40º from the vertical), semi-vertical (20-27º) and erect (10-18º) leaves. Varieties of intensive type are short-stemmed, leaves of vertical orientation, high productive, and varieties of extensive type are long-stemmed with drooping leaves of horizontal orientation, low productive. Bread wheat (*Triticum aestivum* L.) varieties contrast in architectonics, Gyrmyzy gul and Azamatli-95, are short-stemmed (with the stem height of 85-90 and 60-75 cm, respectively), intensive type, with vertically oriented small leaves, high productive (7-9 t ha^{-1}); Giymatli-2/17 is short-stemmed (85-95 cm), intensive type, with broad drooping leaves, high productive (7 t ha^{-1}), and Kansas-63323 is medium-stemmed (90 cm), with a small ear and small leaves, and grain yield of 3 t ha^{-1}. Durum wheat (*Triticum durum* L.) varieties,

Shiraslan-23 and Garagylchyg-2, are short-stemmed (78 and 82-85 cm, respectively), intensive type, with the vertical orientated leaves and potential grain yield of 6-8 t ha^{-1}; Shark and Caucasus are medium-stemmed (110-120 cm), semi-intensive, with semi-vertical leaf arrangement and medium grain yield (4-5 t ha^{-1}); Oviachik-65 (***CIMMYT***) is short-stemmed (60-70 cm), with erect leaves and average grain yield of 6 t ha^{-1}; Gyrmyzy bugda and Sary bugda are long-stemmed (150-180 and 125-150 cm), extensive type, with drooping horizontal leaves and grain yield of 3 t ha^{-1} were used. Except Kansas-63323, Oviachik-65 (***CIMMYT***) and Caucasus (***Krasnodar Agricultural Research Institute***) all other varieties are of local selection (Figure 11) (Catalogue, 2000; Aliyev, 2006).

At the same time, various soybean (*Glycine max* (L.) Merr.) genotypes differing in height (40-110 cm), duration of vegetation, grain yield (2-4 t ha^{-1}) and other morpho-physiological traits were also research targets (Figure 12). All genotypes were grown in field conditions over a large area following guidelines of the experimental procedure (Figure 13). The experiments were performed in irrigated area at the Absheron Experimental Station of the Research Institute of Crop Husbandry.

The basic parameters of photosynthetic activity: leaf, stem and ear area, the rates of photosynthesis and photorespiration were determined during the ontogenesis.

In order to measure the rate of gas exchange in leaves of various layers and other assimilating organs, an infrared gas analyzer URAS-2T ("Hartman and Braun", Germany) with a short exposure of the whole plant in sowings in $^{14}CO_2$ atmosphere (Figure 14) was used. The limits of measurements were 0.005-0.05% CO_2, error was ± 0.5% of the upper limit of the scale (Voznesensky, 1977; Aliev et al., 1996 b). CO_2 concentration in the analyzed air was recorded using automatic recorder. The measurements were performed in an open air flow system connected in the differential mode (Karpushkin, 1971). The initial air flow was divided into two parts. One part passed through the air dehumidifier, filled with calcium chloride, through the filter, and then through the control cuvette of the gas analyzer. The other part passed through the leaf chamber, dehumidifier, filter, and then through the measuring cuvette. The air flow velocity through the entire system was adjusted using needle valves and rotometer. The gas analyzer recorded the difference in CO_2 concentration at the inlet and outlet of the leaf chamber. The rate of gas exchange in leaves placed in the leaf chamber was determined by the difference in CO_2 concentration and air velocity passing through the leaf chamber. For the measurements a hermetically sealed clip chamber with the area of 0.1 dm^2, which has two inlets and outlets for air flow, separately surrounding the upper and lower leaf surface, was used.

During the measurements chamber was attached to leaves of different layers close to the stem maintaining their natural location and orientation, and exposed to sunlight until the gas exchange reached the steady-state level. The CO_2 concentration in air was determined close to the leaf chamber before each gas exchange measurement. Night respiration was determined using the above mentioned equipment without use of thermostat, in a steady night temperature. In the heat of the day a light filter SZS-24 (Voznesensky, 1977; Aliev et al., 1996 b) was used to prevent overheating of leaves in the chamber. Photorespiration was determined using two methods, in atmosphere without CO_2 and in atmosphere with reduced oxygen content (2%) (Šesták et al., 1971; Akhmedov, 1986). In the first case, after photosynthesis had reached the steady-state level the CO_2-lacking air was passed through the leaf chamber. The increase in CO_2 concentration at the chamber outlet is an indicator for the estimation of photorespiration. In the second case, after photosynthesis had reached the steady-state level the air with a reduced content of oxygen was blown into the chamber, and the obtained values of photosynthesis were measured. The value of photorespiration was determined as the difference between the photosynthetic values in low and normal oxygen content of the air.

The gas analyzer which was placed in a mobile laboratory allowed multiple measurements in the sowings of different genotypes to be performed in a short time while keeping the high sensitivity of the facility in the field and maintaining the natural course of physiological processes in entire plants (Figure 14).

Photosynthetic carbon metabolism and utilization of main photosynthetic products were studied radiometrically under ambient CO_2 (0.03%) and O_2 (21%) (Aliev et al., 1996 b, c). In the experiments an open gas system was used for the $^{14}CO_2$ incorporation into various organs of plants. The required air reserve with radiolabelled carbon dioxide was prepared and kept under high pressure in 10-liter steel cylinder with a needle valve. The 50 cm^3 thermostated leaf chamber made of organic glass was used.

Transparent plastic bags were used for the $^{14}CO_2$ incorporation into the entire plants. The experiments were carried out under direct sunlight illumination. Initially, photosynthesis reached the steady-state level in an atmospheric air flow, then the radiolabelled air from the cylinder was blown through the leaf chamber with velocity of 1 l/min and CO_2 specific radioactivity of 1.000MBq/l. After 10 minutes of exposure, plants were removed from

Figure 2. Wheat genefund at the Research Institute of Crop Husbandry.

Figure 3. Experimental crop fields of the Department of Plant Physiology and Biotechnology of the Research Institute of Crop Husbandry.

Figure 4. Wheat genotypes with contrast architectonics.

Figure 5. *Triticum aestivum* L. wheat variety Gyrmyzy gul with ideal architectonics.

Figure 6. *Triticum aestivum* L. wheat variety Giymatli-2/17.

Figure 7. *Triticum durum* L. wheat variety Barakatli-95.

Figure 8. Drought resistant *Triticum* L. wheat variety developed at the Department of Plant Physiology and Biotechnology of the Research Institute of Crop Husbandry.

Figure 9. Professor Jalal Aliyev at his experimental wheat field of the Research Institute of Crop Husbandry.

Figure 10. Winter wheat genotype.

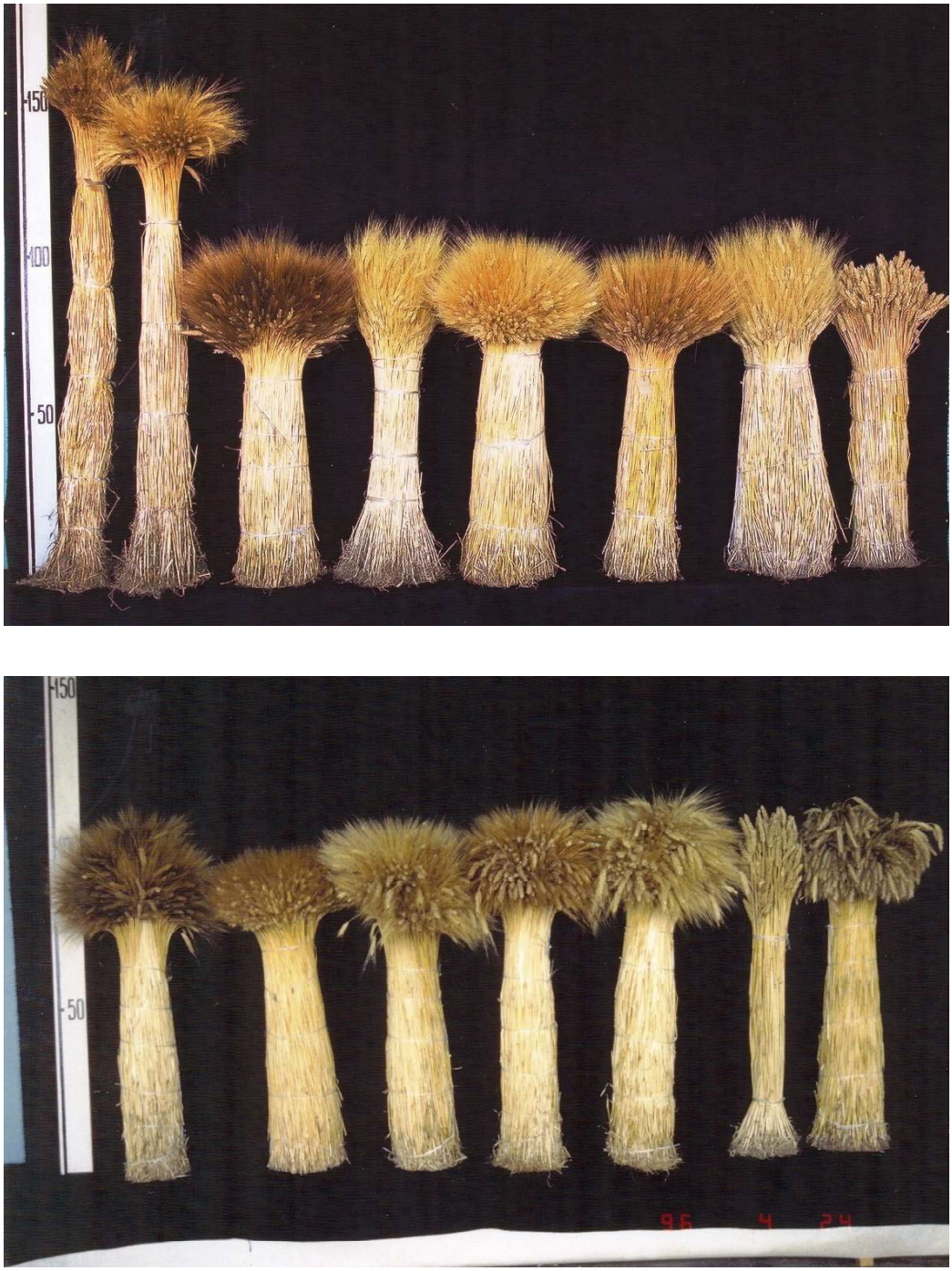

Figure 11. *Triticum durum* L. and *Triticum aestivum* L. wheat varieties developed at the Department of Plant Physiology and Biotechnology of the Research Institute of Crop Husbandry.

Figure 12. Different soybean genotypes (*Glycine max* (L.) Merr.): low productive (Volna) and high productive (Komsomolka and Visokoroslaya-3) (left to right).

Figure 13. Sowings of different soybean genotypes at the period of intensive growth.

the leaf chamber and quickly fixed with boiling ethyl alcohol. Experiments were repeated 4-5 times. Radiochemical analysis of fixed plant material was carried out using the standard technique (Voznesensky et al., 1965; Keerberg et al., 1970). Water- and alcohol-soluble products were separated by two-dimensional paper chromatography. Measurement of the radioactivity of fractions and separate compounds was carried out using a scintillation counter SL-30 in dioxane-based standard scintillator. Radioactivity of fractions and separate compounds was calculated taking into account the self-absorption coefficient.

Figure 14. Various devices used to carry out studies on photosynthesis and photorespiration in the field.

To investigate the transport and distribution of photosynthetic products under field conditions, $^{14}CO_2$ of ambient concentration and specific activity of 200 MBq/l was incorporated during photosynthesis into leaves of certain layers for 15-20 min, and then samples preparation to determine their radioactivity were made. After a 20 min exposure, the chamber was removed from the plant; then after 24 h or at the end of plant growth the plants were withdrawn from the soil, fixed with dry heat, dissected into individual organs and dried. The plant organs were weighed and then grounded for sample preparation (Aliev et al., 1996 a), and the radioactivity calculated per units of weight and per organ was measured. The radioactivity of the samples was measured using the end-window counter of SBT-13 in a layer of complete absorption.

The rate of true photosynthesis was determined in the short exposures (15-30 sec) in $^{14}CO_2$. The rates of the net photosynthesis and dark respiration

in the light were measured using infrared gas analyzer INFRALYT-4. The magnitude of photorespiration was estimated on the basis of the values of true and net photosynthesis and dark respiration as well (Jahangirov, 1987).

In order to determine the enzymes activities, the leaves were washed, after both ends were cut off they were homogenized by mechanical MPW-302 type disintegrator for 3 min in 0.05 M Tris-HCl buffer, pH 8.5, containing 1 mM dithiothreitol (DTT), 5 mM $MgCl_2$, 1 mM EDTA and 1% polyvinylpyrrolidone K-25 ("FERAK"). Homogenization of wheat ear elements was performed in a mortar after the ear had been divided into separate elements, i.e. awns, glume and grains. Homogenate was squeezed through the 4-layered gauze and centrifuged first for 10 min at 1000×g, then for 30 min at 5000×g at 4°C. The precipitate was removed, and the supernatant was decanted and immediately used for enzymes assays.

The activity of Rubisco was determined spectrophotometrically ("ULTRASPEC", LKB, Sweden) at the 340 nm of optical density and 30°C based on the quantitative determination of 3-phosphoglycerate (3-PGA) in the presence of phosphoglycerate kinase and glyceraldehyde phosphate dehydrogenase (Aliev et al., 1988, 1996 b, c). The reaction mixture contained 0.05 M Tris-HCl buffer, pH 7.8, 0.05 M $NaHCO_3$, 0.01 M $MgCl_2$, 0.005 M DTT, 0.01 M ATP, 0.25 mM NADH, 0.3 mM RuBP, 10 U of glyceraldehyde phosphate dehydrogenase, 10 U of phosphoglycerate kinase and 0.2-0.4 mg of the studied preparation. Control contained all components excepting NADH.

The activity of RuBPO was assayed by amperometric method (Romanova, 1980; Aliev et al., 1988, 1996 b, c). The reaction mix contained 50 mM Tris-HCl buffer, pH 8.6, 5 M $MgCl_2$, 0.5 mM RuBP, 1-3 mg of protein of preliminarily activated enzyme preparation. The enzyme was activated by incubation at room temperature for 5-10 min in the presence of 10 mM $NaHCO_3$ and 5 mM $MgCl_2$ at pH 8.6.

The rate of light-saturated electron transport was measured spectrophotometrically.

Leaf assimilating area was measured using an automatic area meter "AAC-400" ("Kayashi" Delkon Co LTD, Japan). The specific leaf density was calculated as the ratio of its dry weight to the area.

Parameters of water regime were determined according to the procedure (Methodological guidelines, 1987; Boyer, 1995). Determination of relative water content and water deficit was repeated ten times.

Protein concentration was determined according to the Lowry et al. (1951).

The arithmetic mean and standard errors presented in the figures and tables were calculated based on the data from at least 4 biological replicates. The obtained data was statistically processed by standard analysis methods (Kaplan, 1970; Dospekhov, 1985).

RESULTS AND DISCUSSION

During 50 years of comprehensive investigations of photosynthesis and productivity of various wheat genotypes in natural conditions of cultivation, characteristics and parameters of photosynthetic activity of these genotypes in crop fields most closely correlating with plant productivity, have been established. The main emphasis was put on: 1) architectonics; 2) CO_2 assimilation; 3) leaf activity within the day and vegetation, and others. One of the aspects of the study was photorespiration.

According to our previous concept (Aliyev, 1974; Aliev and Kazibekova, 1979; Aliyev and Kazibekova, 1988), the optimum plant height and favourable leaf orientation in compact sowings contribute to the effective absorption of solar radiation and development of vegetative and economically valuable organs, i.e. activate those key links of productivity, which ultimately determine the high productivity of wheat variety of "ideal" type (Aliyev, 1983).

Analysis of various wheat genotypes with different values of photosynthetic traits and productivity in conjunction with a range of environmental factors, including mineral nutrition, water, light, etc. showed the wide range of CO_2 assimilation variability in ontogenesis, depending on the morpho-physiological peculiarities of genotypes and their sink-source relations (Aliev and Kazibekova, 1995).

The photosynthetic rate has increased steadily during flag leaf development and reached its maximum value in the earing stage (Figure 15). Two peaks of CO_2 exchange in the most active leaves were observed during ontogenesis: the first peak at the beginning of stalk emergence and the second one at the beginning of flowering. It is important to search genotypes with no or less evident decrease of the photosynthetic rate in this period. High productive genotypes posses a higher rate of CO_2 assimilation throughout the whole lifespan of their flag leaves up to the end of the grain filling stage. This pattern of carbon dioxide exchange at the end of growth period in different genotypes may be due to early death of the lower leaves of extensive varieties. However, in the intensive genotypes, in comparison with extensive ones, the decrease in CO_2 assimilation in the flag leaf was counterbalanced by the ac-

tive CO_2 assimilation in the lower leaves. High productive varieties significantly exceeded (up to 1.5 times) low productive ones by the mean of the photosynthetic rate of upper leaves (flag leaf and the second leaf from the top).

In intensive varieties with the best architectonics, the rate of photosynthesis is higher in the morning, and especially in the evening hours, and afternoon depression of photosynthesis occurs later and is much weaker than that of semi-intensive and extensive varieties. The total photosynthesis during the daytime is higher in high productive varieties than in low productive ones.

The study of the dynamics of photosynthetic rate in ontogenesis showed the availability of multiple peaks specific for genotypes depending on the crop architectonics at the period, when rate of photosynthesis was determined.

It was found out that the rate of photorespiration is higher in intensive varieties than in extensive types. The rate of photorespiration reaches its maximum in the earing stage, and then decreases (Figure 16). In high productive varieties photorespiration remains at a high level during the periods from stalk emergence up to the grain formation and filling than in the low productive ones. Along with increase of photosynthetic rate, the rate of photorespiration increases too. Photorespiration follows the course of photosynthesis, the more intense is photosynthesis, and the more intense is photorespiration. Daily course of photorespiration, in general, coincides with the daily course of leaf photosynthesis at various stages of plant development. However, photorespiration begins at the later hours than photosynthesis, and ends earlier; the curve of its course is unimodal.

The rate of CO_2 assimilation in leaves and other photosynthesizing organs is determined by the size and structure of these organs, plant architectonics both at the individual cultivation and in crop fields, by the sink-source relations genetically stipulated in each genotype, taking into account all affecting factors (Aliyev, 2001 a). The average results from multiple measurements are presented in the Table 1.

Wheat genotypes are characterized by following parameters: leaf length, width, surface area, specific leaf density, leaf inclination angle and orientation, that create an optimal architectonics more favourable for turbulence and high rate of CO_2 assimilation, and possibly for long-term photosynthetic activity of all leaves, ear and other non-leaf organs during grain formation.

The genotypes with two or three times less leaf areas than that with broad leaves produce similar or even greater grain yield. Genotype Gyrmyzy bugda with flag leaf area of 28 cm^2 yields up to 3 t ha^{-1}, and those of 18-19 cm^2 – 7-9 t ha^{-1}. In highly productive genotypes with grain yield ~ 7-9 t ha^{-1}, the flag leaf areas differ almost three times. The studied varieties of winter wheat exhibited significant differences in the rate of flag leaf CO_2 assimilation. The highest values were detected in high productive genotypes Gyrmyzy gul and Azamatli-95, whereas the lowest CO_2 assimilation was characteristic for genotype Gyrmyzy bugda. Vertically oriented small leaves creating an optimal architectonics, probably, promote a relatively high CO_2 assimilation of photosynthesizing leaves of all layers during grain filling.

A comparative study of photosynthetic rate of wheat genotypes with contrast architectonics during the day showed that the diurnal changes in the photosynthetic rate of leaves of all layers and genotypes are characterized by a double-peaked pattern indicating a drastic increase in the photosynthetic

Table 1. Rates of CO_2 assimilation and photorespiration, flag leaf area and grain yield of wheat genotypes

	Genotype	Potential grain yield, t ha^{-1}	Mean flag leaf area, cm^2	Rate [mg CO_2 dm^{-2} h^{-1}]	
				Photosynthesis	Photorespiration
Triticum aestivum L.	Azamatli-95	9	19	34.0±1.7	12.4±0.5
	Giymatli-2/17	7	47	25.2±1.4	8.1±0.4
	Gyrmyzy gul	7	18	36.5±2.1	10.9±0.6
Triticum durum L.	Gyrmyzy bugda	3	28	21.3±1.1	6.2±0.3

*Measurements were carried out at the earing stage, when the rate of photosynthesis reached its maximum, and at the end of leaf growth.

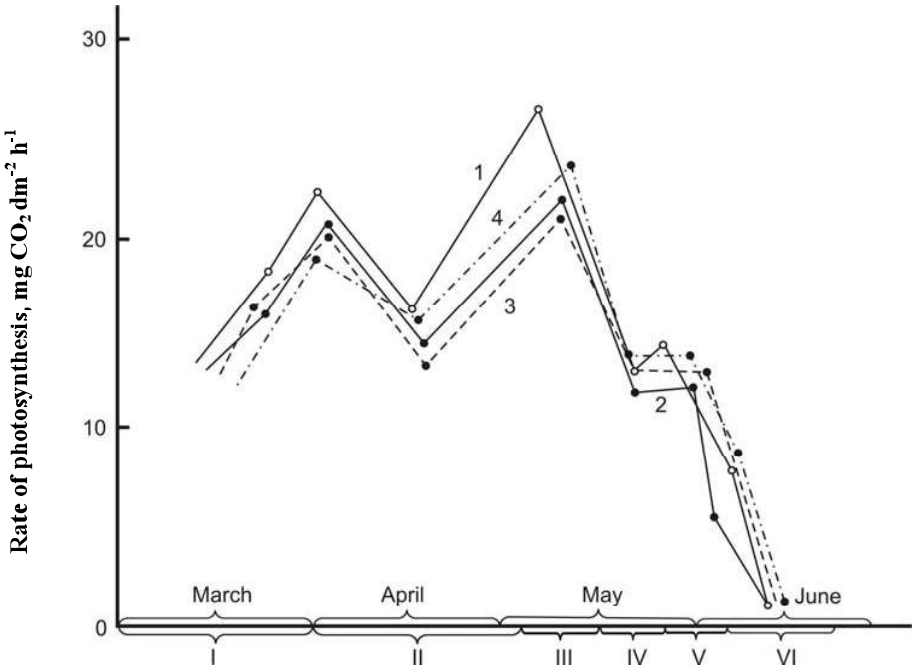

Figure 15. Ontogenetic changes in the rate of CO_2 assimilation in different wheat genotypes:
1 – Oviachik-65, 2 – Shark, 3 – Gyrmyzy bugda, 4 – Caucasus
I – stalk emergence, II – earing, III – flowering, IV – grain formation and filling.

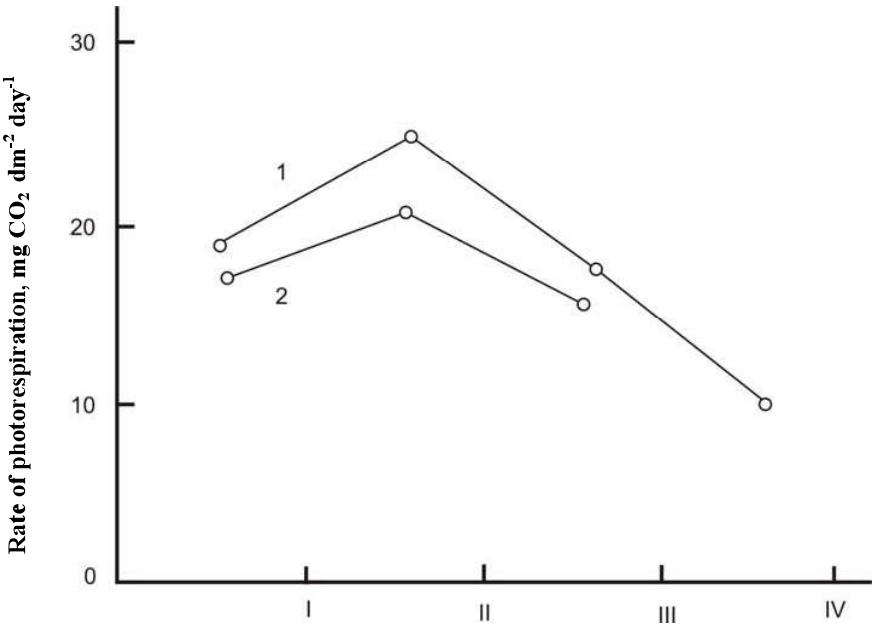

Figure 16. Ontogenetic course of total photorespiration in high productive (Oviachik-65 – (1)) and low productive (Gyrmyzy bugda – (2)) genotypes:
I – stalk emergence, II – earing, III – flowering, IV – grain formation and filling.

rate in the morning and decrease in the evening (Figure 17). Photosynthesis in the flag leaves began early in the morning (at 6 a.m.), increased during sunrise, reaching its maximum level at 11 a.m. Then photosynthetic rate declined to its lowest at midday. After midday depression of photosynthesis, the second peak was observed at 5 p.m. that correlates with increased photosynthesis.

Not all genotypes with small leaves are high productive and not all genotypes with broad leaves are high or low productive. Genotypes with broad leaves and high yield require sufficient water supply.

In order to better understand the correlation between rates of CO_2 assimilation, photorespiration and productivity, the consideration of basic parameters of plant architectonics is also essential (Figure 18). Obtained data indicates that genotypes with vertically oriented short and narrow leaves (20-30 cm^2), high specific leaf density (SLD) – 600 mg/100 cm^2, with stable and long-term intensive CO_2 assimilation (30-40 mg dm^{-2} h^{-1}) and a high tolerance to water stress yield up to 10 t ha^{-1}.

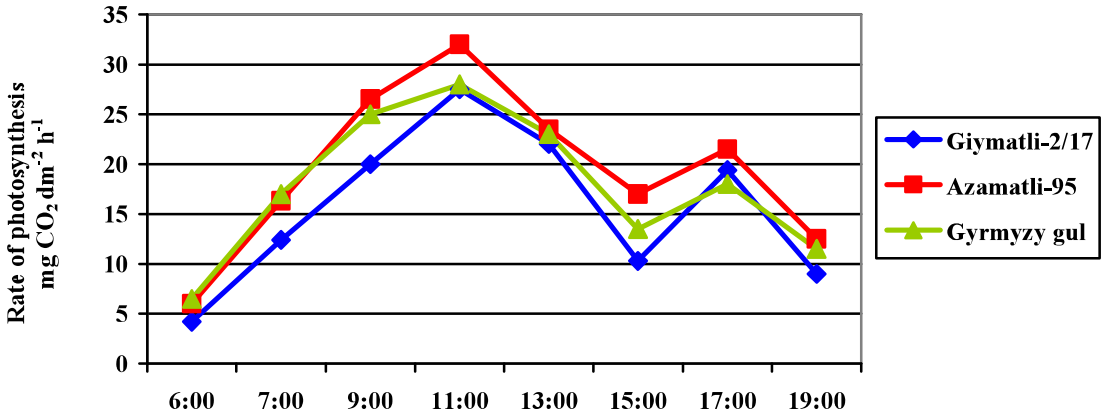

Figure 17. Diurnal course of CO_2 gas exchange of flag leaves of wheat genotypes with different architectonics at the milk ripeness stage.

The high rate of CO_2 assimilation is not accompanied by low rate of photorespiration. For high productive genotypes, the high values of photorespiration are common. Genotypes with grain yield of 7-9 t ha^{-1} possess high rates both of CO_2 assimilation and photorespiration at corresponding architectonics. Genotypes with moderate (4-5 t ha^{-1}) and low (3 t ha^{-1}) grain yield have relatively low rates of CO_2 assimilation and photorespiration.

Gas exchange data closely agree with the measured enzymes activities directly involved in CO_2 fixation.

Throughout the entire period of flag leaf development high productive intensive genotypes in comparison with extensive ones were distinguished by higher activities of RuBP carboxylase and carbonic anhydrase (Aliev et al., 1988, 1996 b). RuBP carboxylase activity as well as CO_2 assimilation rate, increased monotonously since the beginning of the flag leaf formation, reaching its maximum at the earing stage, and then decreased up to the end of the leaf growth (Figure 19). On the contrary, activity of this enzyme in high-stemmed wheat varieties of extensive type decreases rapidly after it has achieved its maximum.

The fact that activities of RuBP carboxylase and carbonic anhydrase changed in parallel during the flag leaf development is evident, indicating that there is a coordinated operation of these enzymes in wheat genotypes (Aliev et al., 1988, 1996 b, c; Aliev and Kazibekova, 1995). Such correlation was found between the rate of CO_2 assimilation and the activity of these enzymes in high productive varieties. Thus, our data show that high activities of RuBP carboxylase and carbonic anhydrase play an important role in maintaining a high CO_2 assimilation rate in the high productive wheat varieties (Aliev et al., 1988, 1996 b).

The activities of the RuBP carboxylase and RuBP oxygenase were higher in the high productive wheat genotypes than in the lower ones (Figure 19, 20). The variation of RuBPO activity in the course of the flag leaf development was similar to that of RuBP carboxylase. As known, RuBPC/O catalyzes a unique reaction of carboxylation and oxidation of RuBP with the subsequent formation of 3-PGA, the primary product of photosynthesis, and phosphoglycolic acid, which is a substrate for photorespiration (Zelitch, 1975). On the other hand, photorespiration is a process, in which part

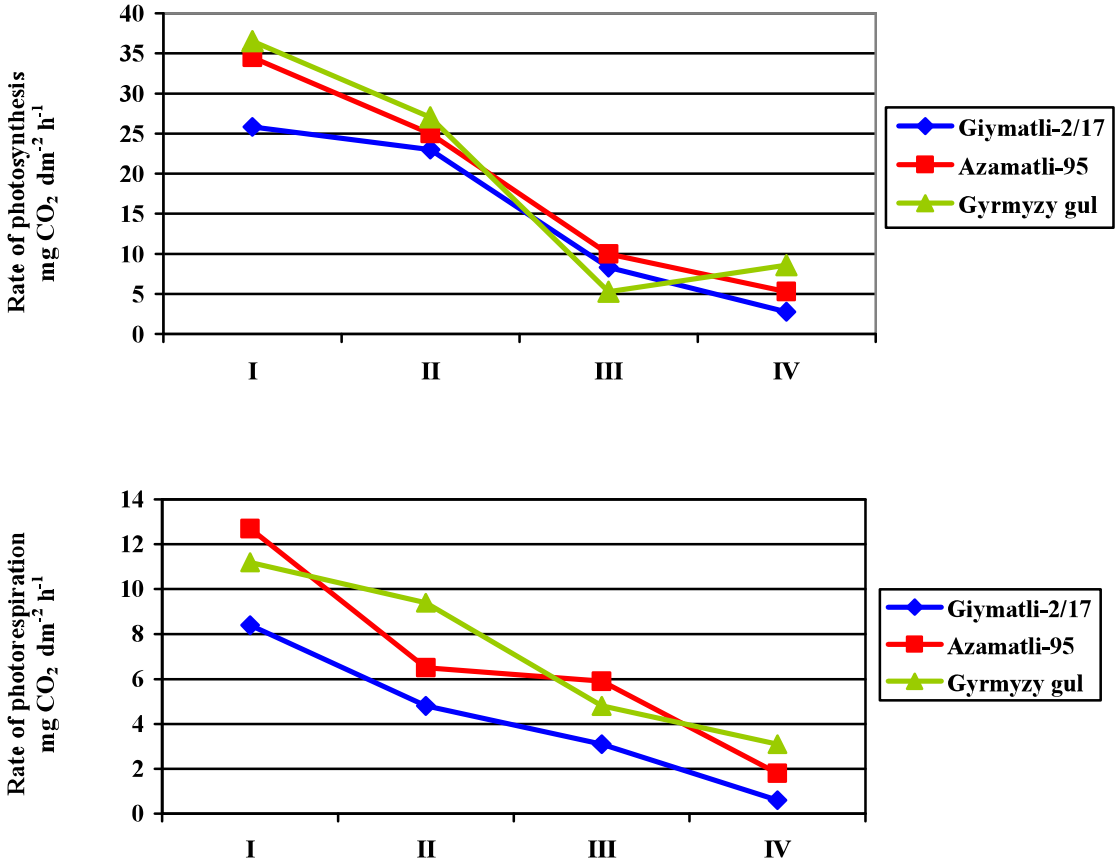

Figure 18. Ontogenetic changes of the rates of photosynthesis and photorespiration in wheat genotypes with different architectonics:
I – earing-flowering, II – milk ripeness, III – end of the milk ripeness, IV – wax ripeness.

of assimilated CO_2 is lost. However, we also observed that short-stemmed wheat varieties with high RuBP oxygenase activity had high grain yield.

During flag leaf ontogenesis of the studied genotypes the ratio of RuBPC/RuBPO activities was maintained approximately at the same level, tending to have a high ratio in intensive types (Garagylchyg-2 – 19.0 ± 1.4; Shiraslan-23 – 18.7 ± 0.9; Gyrmyzy bugda – 16.0 ± 2.0; Sary bugda – 16.2 ± 1.1) (Figure 21) (Aliev et al., 1988, 1996 b; Aliev and Kazibekova, 1995; Aliyev and Kazibekova, 2002). Nevertheless, the variation in the ratio of RuBPC/RuBPO activities during the flag leaf formation is associated with a certain genotypic difference. Hence, studied genotypes differed in the rates of photosynthesis and photorespiration.

Large changes in the RuBPC activity of different ear elements depend on its development and peculiarities of the plant genotype (Figure 22). In comparison with other ear elements, the glume of both intensive and extensive genotypes is characterized by higher RuBP carboxylase activity. At the beginning of the grain formation, the RuBPC activity in the ear glume of the intensive genotype was also higher than in the extensive one. However, later this activity, calculated per mg of protein, decreased in the intensive genotypes, but remained the same in the extensive ones. Later, during grain filling, a significant increase of RuBPC activity in the glume occurred both in the intensive and extensive genotypes.

During all periods of measurements, the ear awns of the intensive genotype had a higher activity of RuBP carboxylase than those of the extensive genotype at the earing and grain filling stages.

The RuBPC activity in grain of the low productive genotype was higher than that of the high productive one only at the beginning of grain filling. A gradual decrease in the enzyme activity during grain formation was observed in both genotypes.

The measurement of RuBP oxygenase activity in the different ear elements indicated that

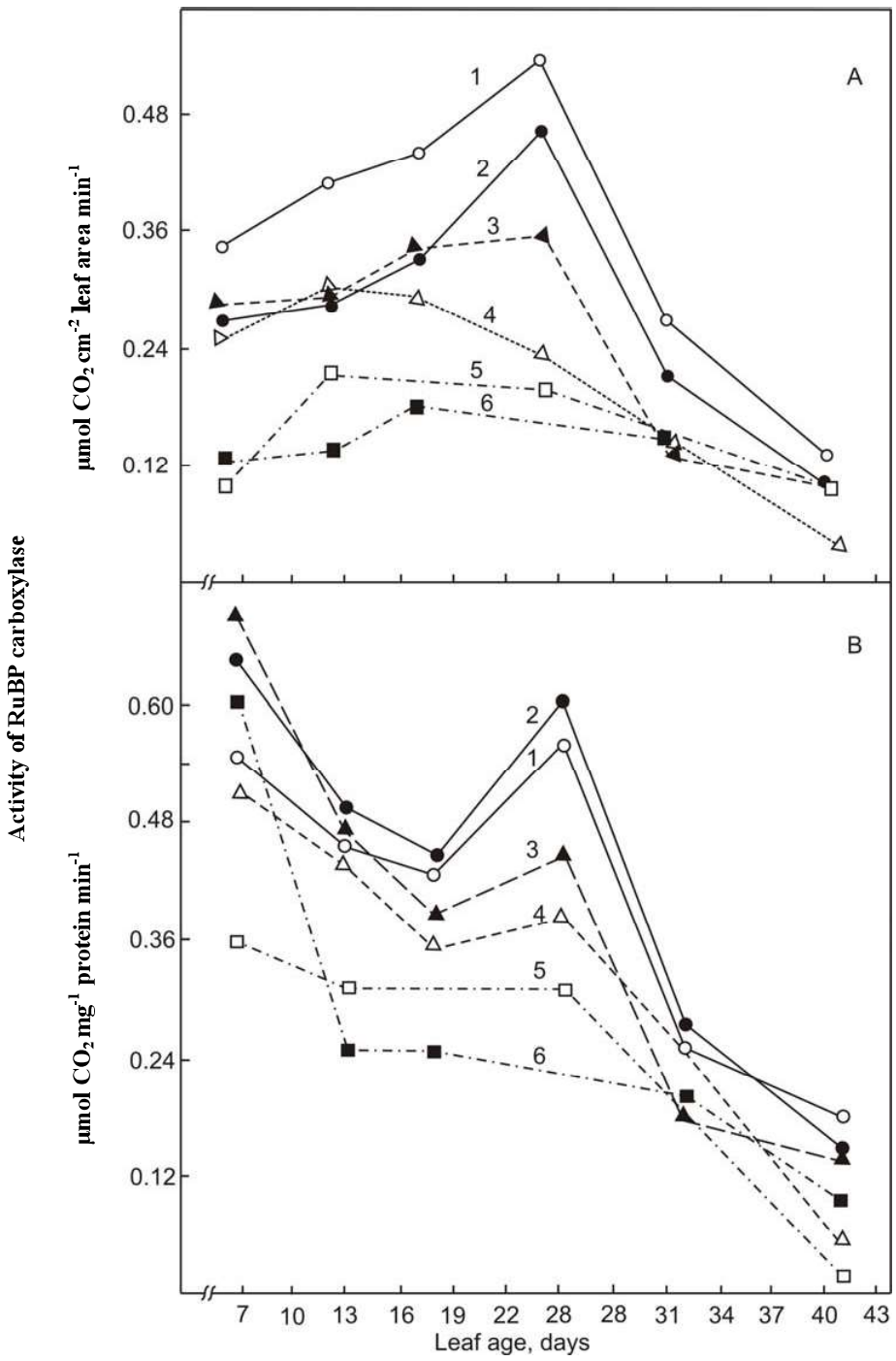

Figure 19. Ontogenetic changes in RuBP carboxylase activity (A - µmol cm^{-2} (leaf area) min^{-1}; B - µmol mg^{-1} (protein) min^{-1}) in flag leaves of wheat genotypes:
1, 2 – short-stemmed, high productive; 3, 4 – small leaves, medium productive; 5, 6 – long-stemmed, low productive wheat varieties.

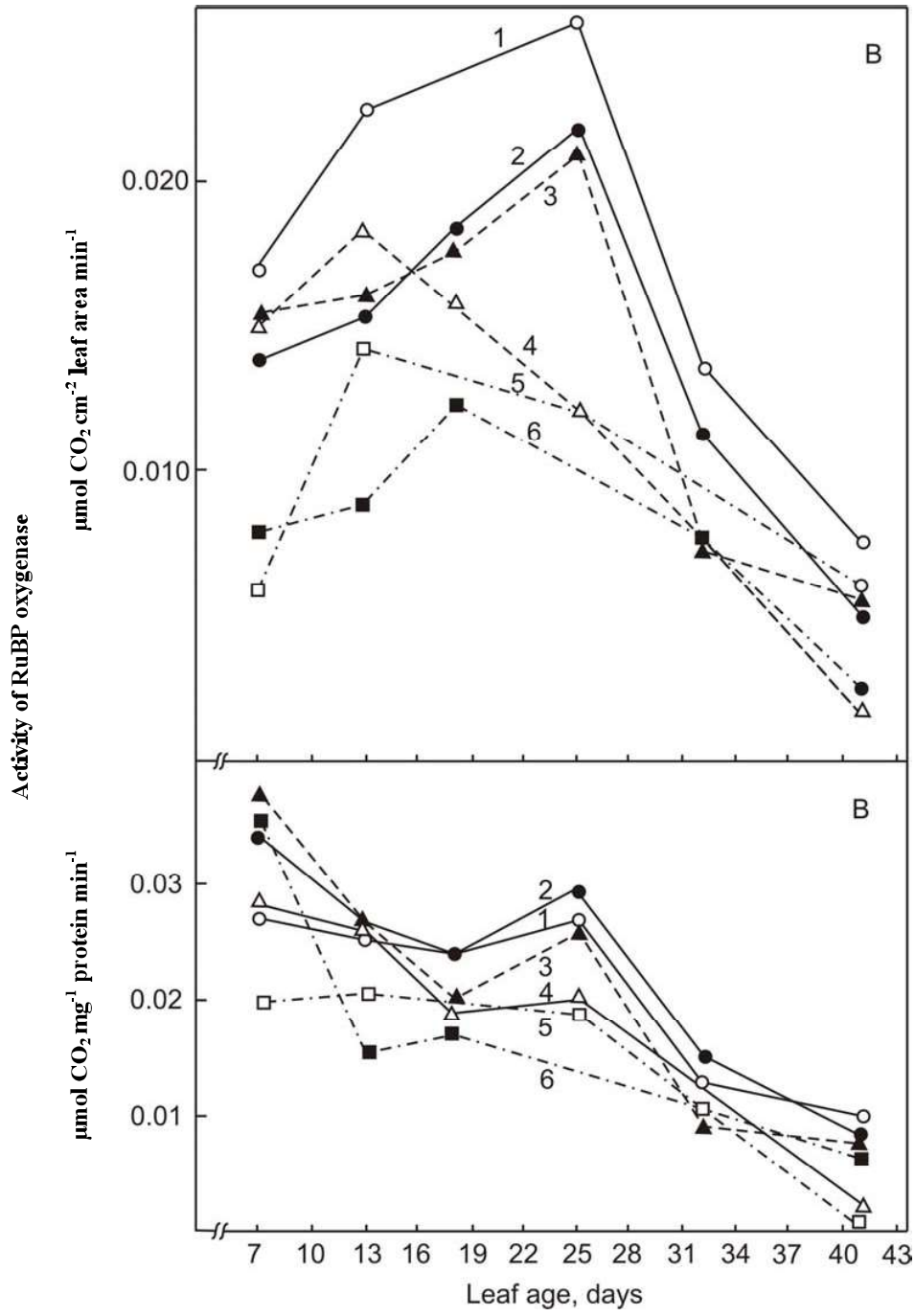

Figure 20. Ontogenetic changes in RuBP oxygenase activity (A - μmol cm^{-2} (leaf area) min^{-1}; B - μmol mg^{-1} (protein) min^{-1}) in flag leaves of wheat genotypes:
1, 2 – short-stemmed, high productive; 3, 4 – small leaves, medium productive; 5, 6 – long-stemmed, low productive wheat varieties.

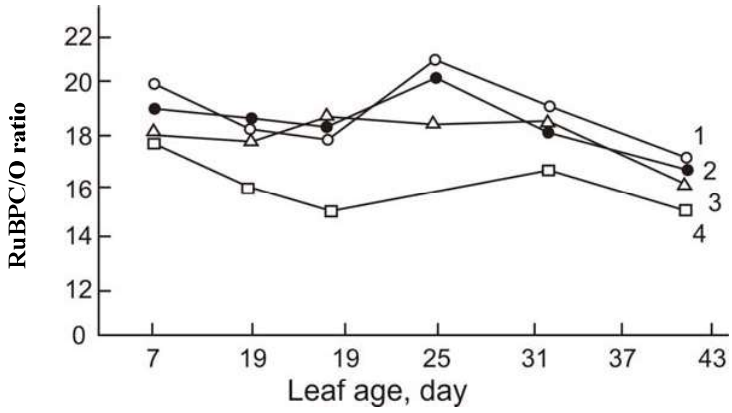

Figure 21. Changes in the ratio of RuBP carboxylase to oxygenase activities in flag leaf ontogenesis of different wheat genotypes:
1 – Garagylchyg-2, 2 – Shiraslan-23, 3 – Gyrmyzy bugda, 4 – Sary bugda.

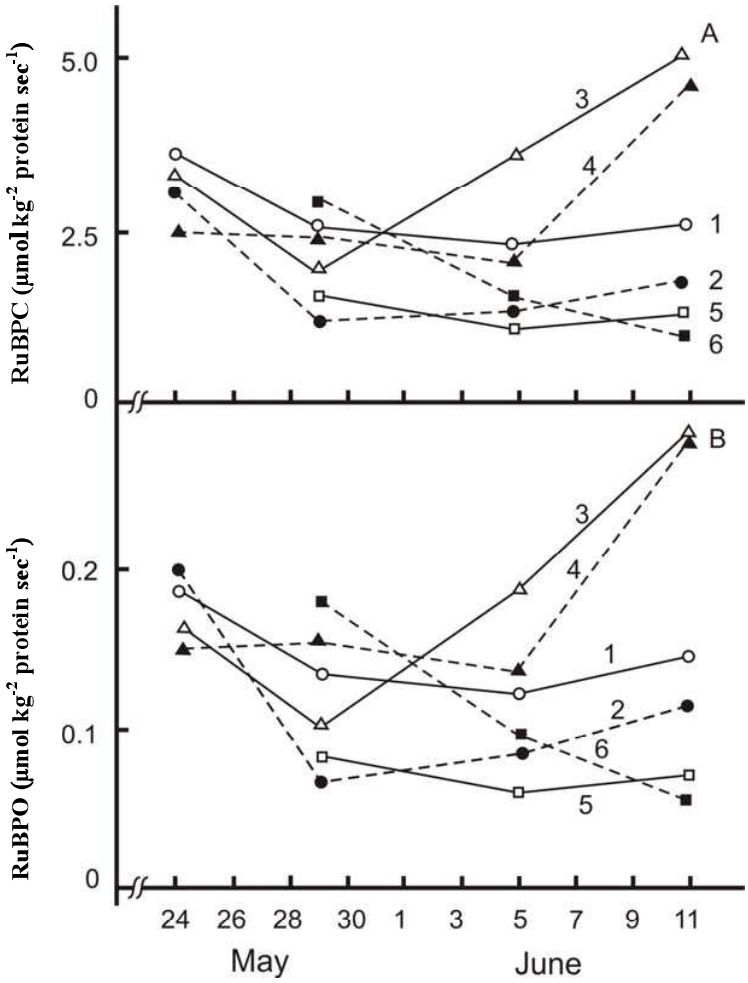

Figure 22. Variations in activities of RuBP carboxylase (A) and RuBP oxygenase (B) in ear elements of wheat genotypes during grain filling:
1 – awn, 3 – glume, 5 – grain of short-stemmed high productive genotype Shiraslan-23;
2 – awn, 4 – glume, 6 – grain of long-stemmed low productive genotype Gyrmyzy bugda.

during grain formation the activities of RuBPC and RuBPO changed in parallel similarly as it is observed for the flag leaf (Figure 20).

Activities of RuBP carboxylase and RuBP oxygenase in high and low productive genotypes increased in awns, and especially in the glume, during grain filling. Notably, the sharp increase in the activity of both enzymes in the glume coincides temporally with a decrease in their activity in flag leaf. Therefore, during the period of grain filling, the ear elements and the glume actively participated in the process of CO_2 assimilation (Aliyev, 2002).

Thus, the results obtained using various methods on different plant genotypes showed that RuBP carboxylase and oxygenase activities change in parallel in the course of plant breeding process. Each wheat genotype was characterized by a definite value of RuBPC/O ratio and its variation under different influences (in particular, under artificial violation of the sink-source relations) was temporary.

Photorespiration requires the integration of biochemical pathways in three separate leaf cell organelles: chloroplasts, peroxisomes and mitochondria (Figure 23). Peroxisomes as glyoxysomes refer to microbodies. In mesophyll cells peroxisomes, chloroplasts and mitochondria are often located nearby, supporting an intensive metabolism between these organelles. Currently the biochemical mechanism of photorespiratory pathway is sufficiently well studied. The initial stage of photorespiration takes place in chloroplast stroma. According to most researchers, the initial substrate for the photorespiration is glycolate. Reactions associated with photooxidative transformation of RuBP and formation of phosphoglycolate are considered to be key processes of photorespiration. As a result of oxygenase activity, one molecule of 3-phosphoglycerate (integrated into the Calvin cycle) and one molecule of 2-phosphoglycolate (first molecule of photorespiratory glycolate cycle) instead of two molecules of 3-phosphoglycerate are formed. Under the influence of a key photorespiratory enzyme, phosphoglycolate phosphatase (PGPase), the phosphoglycolate is converted into glycolate, which then leaves the chloroplast and enters the peroxisome.

$$RuBP + O_2 \rightarrow \text{phosphoglycolate} + PGA$$
$$\text{Phosphoglycolate} \rightarrow \text{glycolate} + P_i$$

Phosphoglycolate phosphatase catalyzes the hydrolysis of phosphoglycolate, which is produced under the ribulose-1,5-bisphosphate oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase. PGPase-deficient mutants cannot grow in the ambient air (0.04% CO_2 and 21% O_2) and require elevated levels of CO_2 (Randall, 1976; Husic and Tolbert, 1984; Hall et al., 1987; Suzuki et al., 1990; Norman and Colman, 1991). This is most likely because phosphoglycolate accumulated during photosynthesis in the ambient air strongly inhibits an enzyme triose phosphate isomerase (Wolfendon, 1970; Anderson, 1971; Suzuki et al., 1999).

Richardson and Tolbert (1961) were the first to find a phosphatase activity specific for phosphoglycolate in tobacco leaves. Later it was shown that all plants and algae possess such activity (Randall and Tolbert, 1971; Randall et al., 1971). The occurrence of phosphoglycolate in mammalian cells was first shown by Rose and Salon (1979) and has been confirmed by Spear and Vora (1986). Data obtained with pyruvate kinase-deficient red blood cells suggest that phosphoglycolate is synthesized by pyruvate kinase *in vivo* (Rose, 1976). The remarkable similarity in the kinetic characteristics of animal PGPases to plant PGPases has been described previously (Seal and Rose, 1987). Although PGPase requires a divalent cation such as Mg^{2+} and a monovalent anion such as Cl^- for its activity in presence of phosphoglycolate as a substrate.

PGPase has also been partially purified from human red blood cells and other tissues (Turner and Hopkinson, 1981). The one autosomal gene locus for PGPase has been assigned to human chromosome 16 (Povey et al., 1980), and enzyme exhibits genetic polymorphism in some ethnic groups.

It is known that phosphoglycolate as a specific substrate for the PGPase initiates a 2,3-bisphosphoglycerate phosphatase activity of the bifunctional enzyme 1,3-phosphoglycerate mutase (BPGM, EC 5.4.2.1). In the presence of phosphoglycolate phosphatase BPGM activity is stimulated more than 100 times (Rose, 1976). Phosphoglycolate inhibits rabbit (Wolfendon, 1970) muscle triose phosphate isomerase (EC 5.3.1.1) and it activates the breakdown of 2,3-bisphosphoglycerate (Rose and Liebowitz, 1970), which is a regulator of the oxygen affinity of hemoglobin (Rose et al., 1986). PGPase also seems to have an important role in animals by affecting the phosphoglycolate level.

Thus, the PGPase is essential for all autotrophic organisms and is also important for the function of human red blood cells (Rose et al., 1986; Mamedov et al., 2001). Another reaction catalyzed by bisphosphoglycerate mutase, which transforms 1,3-bisphosphoglycerate into 2,3-bisphosphoglycerate (2,3-BPG), which may be then converted into 3-phosphoglycerate, a glycolysis metabolite by 2,3-bisphosphoglycerate phosphatase activity (EC 3.1.3.28), can occur in glycolytic pathway. In the erythrocytes 2,3-BPG is produced in significant quantities and serves as the allosteric regulator of hemoglobin. 2,3-BPG binding to hemoglobin de-

creases its affinity for oxygen, promotes the dissociation of oxygen and its transition into tissues. Hemoglobin, oligomeric protein, is able to bind 4 different ligands: O_2, H^+, CO_2 and BPG to its specific sites. All these ligands are bound to spatially separated sites, but the conformational changes of the protein in the one ligand binding site are transmitted to the whole oligomeric protein and alter the affinity of the other ligands to this protein (Severin, 2006, 2009). So, the O_2 amount that enters the tissue depends not only on the partial pressure of O_2, but also on the concentration of allosteric ligands that increases possibilities of hemoglobin functions regulation.

Further conversion of glycolate takes place in the peroxisomes. Carbon metabolism in photorespiration describes the sequence of reactions series of so-called "glycolate pathway", most of which are localized in peroxisomes and mitochondria (Beevers, 1969; Zelitch, 1972; Tolbert, 1973, 1981, 1997). Surrounded by single membranes peroxisomes are small, ubiquitous eukaryotic organelles mediating a wide range of oxidative metabolic activities that vary by the species, cell type, and environmental conditions, in which organism lives (Beevers, 1979; Van den Bosch et al., 1992). Plant peroxisomes are essential to physiological processes such as lipid metabolism, photorespiration, and plant hormone biosynthesis and metabolism (Olsen and Harada, 1995; Reumann and Weber, 2006; Reumann et al., 2009). Peroxisomes are characterized by high activity of catalase and flavin oxidases and contain most of the enzymes of the glycolate pathway.

In peroxisomes glycolate is oxidized to glyoxylate by glycolate oxidase (EC 1.1.3.1.), a flavin-containing enzyme. The second product of the reaction, hydrogen peroxide, is decomposed to H_2O and O_2 by catalase (EC 1.11.1.6) due to high content of latter in peroxisomes (Grodzinski, 1978; Walton and Butt, 1981; Wingler et al., 1999). The next reaction step in the photorespiratory pathway is the transamination of glyoxylate to glycine (Igarashi et al., 2006) by glutamate:glyoxylate aminotransferase (GGAT, EC 2.6.1.4.), which transfer the amino group from glutamate to glyoxylate with production of 2-oxyglutamic acid.

Further photorespiratory reactions occur in mitochondria. Glycine produced in peroxisomes moves to mitochondria, where conversion to L-serine occurs via condensation reaction of two molecules of glycine with release of one molecule of ammonia (NH_3) and carbon dioxide (CO_2) (Walker and Oliver, 1986; Oliver, 1994; Bauwe and Kolukisaoglu, 2003; Voll et al., 2006). NADH is generated during glycine decarboxylation, which oxidation in the mitochondria requires additional O_2 fixation. NH_4^+ synthesized in the reaction of decarboxylation is effectively refixed to produce glutamate. The oxidation of glycine to serine is accompanied by the synthesis of three ATP molecules. This amount of ATP is more than enough to reassimilation of ammonia and its utilization in glutamine synthesis, so the plant does not lose its nitrogen. Nitrogen assimilation in the process of photosynthetic carbon assimilation consumes ~ 13% of recovery force. Proteins synthesis from amino acids and synthesis of carbohydrates such as sucrose and starch require additional energy consumption. In another way the recovered energy from glycine oxidation can be transferred to peroxisomes and used in recovery of hydroxypiruvate to glyceric acid.

The synthesized serine returns to peroxisomes. Serine is converted to hydroxypiruvate by serine:glyoxylate aminotransferase (EC 2.6.1.45), which is then reduced by hydroxypiruvate reductase (EC 1.1.1.29) to form the glycerol. Further metabolism of serine may also be related to its inclusion into proteins. Glycerate returns from peroxisomes to the chloroplasts. Glycerol kinase (EC 2.7.1.31) localized in chloroplasts (Boldt et al., 2005) catalyzes glycerol conversion to 3-phosphoglycerate, which then enters the Calvin cycle.

Translocators in the inner membrane of chloroplasts and mitochondria perform the exchange of metabolites between compartments involved in photorespiration. Metabolism occurs through porin-like channels localized in the membrane of leaf peroxisomes, which are integral pore membrane proteins performing direct non-selective transport of low-molecular-mass compounds (Yu et al., 1983; Weber and Flügge, 2002; Reumann and Weber, 2006; Kaur et al., 2009).

Hence, the reactions associated with the conversion of glycolate to phosphoglycerate and accompanied by oxygen fixation (in the chloroplasts and peroxisomes) and CO_2 release occur during photorespiration. Accordingly, the total balance of gas exchange in leaves in the light consists of two processes - photosynthesis and photorespiration.

The rate of integral photosynthetic process and also its enzymatic and metabolic activity changes during the leaf life cycle. Obtained results showed that studied genotypes also differed significantly in the level of photosynthetic carbon metabolism (Jahangirov, 1987, Aliev et al., 1996 b).

During flag leaf formation the rate of CO_2 assimilation increases, but reaches the maximum at the earing stage (Figure 24, A). Flag leaf grows to its largest area in this stage (Figure 24, B). At flowering stage rate of CO_2 assimilation decreases and then remains almost constant until milk ripeness. As far as leaf grows and active photosynthetic ap-

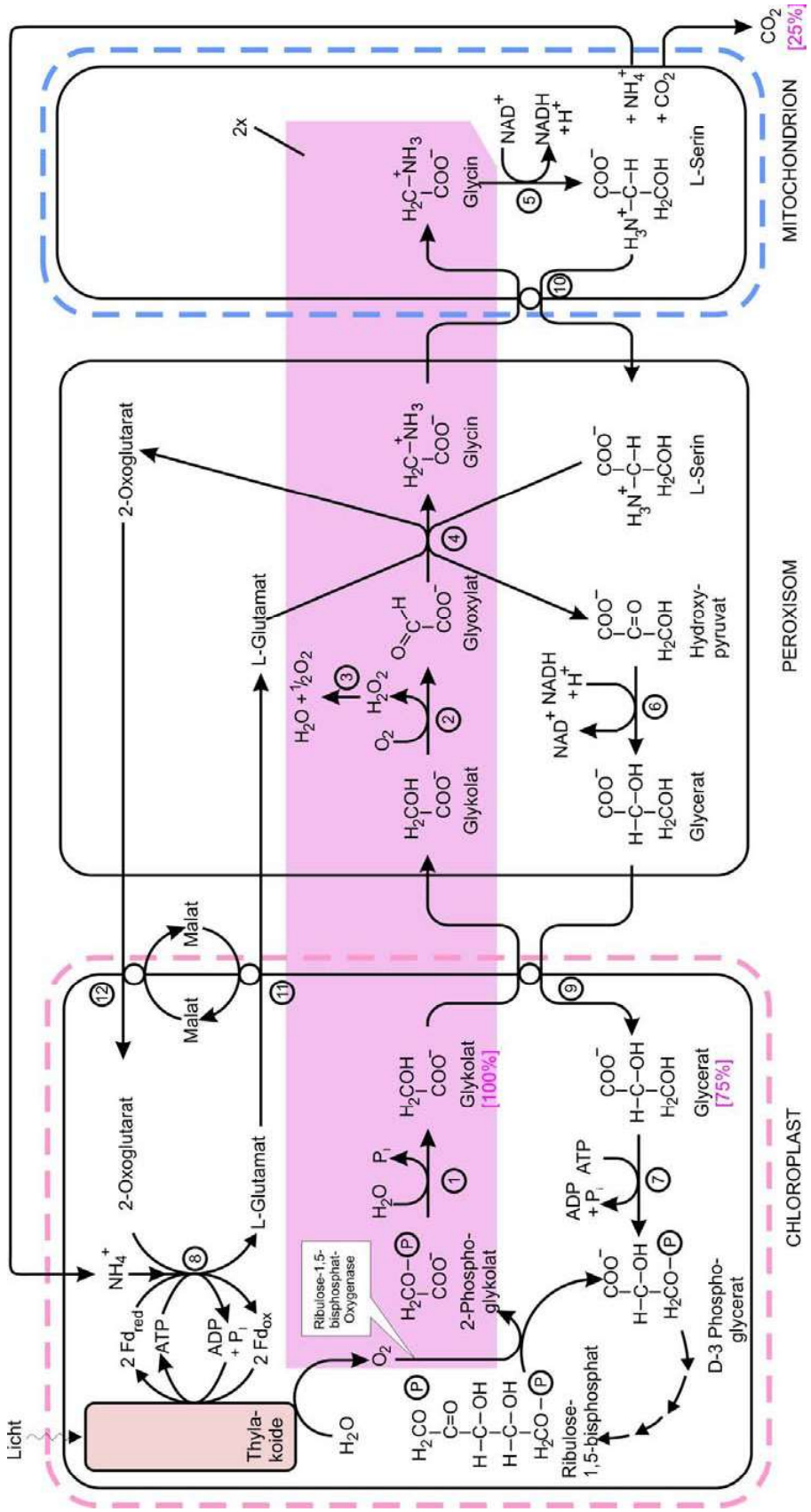

Figure 23. Reaction pathways and compartmentation of photorespiration (Grafic: E. Weiler) (Bresinsky et al., 2008).

paratus develops, it completely changes from acceptor of assimilates into it source. In the flag leaf ontogenesis, the biosynthesis of non-sugar compounds such as alanine, malate and aspartate decreased in absolute and relative units (Figure 24, C, D), and the biosynthesis of sucrose, the main transport form, increased (Figure 25, A). The rate of sucrose biosynthesis was about 80% of the total rate of CO_2 assimilation (Jahangirov, 1987). The pattern of sucrose biosynthesis changes in the same way as the total CO_2 assimilation during ontogenesis. Unlike the abovementioned compounds, the starch biosynthesis was more constant (Figure 25, A, B). Value of sucrose/starch ratio was maintained at a very high level (Figure 25, B).

Studies showed that the biosynthesis rate and the total value of glycine-serine increased during transition from the stalk emergence to earing, then decreased at the flowering stage, and then its level remained virtually constant (Figure 25, C, D).

These characteristics directly depend on the rate of CO_2 assimilation. It is known that under the ambient CO_2 and O_2, the biosinthesis of glycine and serine is linked to photorespiratory carbon pathway during photosynthesis. **Therefore, correlation between biosynthesis rate as well as the total value of glycine-serine and photosynthesis is due to the fact that photosynthesis and photorespiration change proportionally to one another during the wheat leaf ontogenesis.**

Kinetic characteristics of photosynthetic carbon assimilation calculated from the kinetics of $^{14}CO_2$ incorporation into photosynthetic products are listed in the Table 2. The data show that radiocarbon was allotted to sugars (mainly, sucrose), glycolate metabolites (glycine-serine) and, to a small extent, amino and organic acids such as malate, aspartate and alanine. Flag leaves were fully expanded at the time of labeling and served as active assimilate sources and, perhaps, the rates of amino and organic acid labeling were similar in both groups of wheat varieties, measured as 3-6% of the total rate of $^{14}CO_2$ assimilation (Aliev et al., 1996 b, c).

The studied varieties hardly differed in ^{14}C incorporation into starch. Unlike sugars, starch incorporated not more than 5-8% of the label.

Comparative studies of the photosynthetic carbon metabolism showed that at the milk ripeness stage the rates of sucrose and glycine-serine synthesis averaged 5.7 and 1.1 μmol CO_2 $dm^{-2}min^{-1}$, respectively, and these rates were similar both in extensive and intensive varieties. It should be noted that value of the sucrose biosynthesis and the rate of the total value and biosynthesis of glycine-serine at the stage of earing was higher in the short-stemmed intensive genotypes compared with the extensive ones. The rate of sucrose synthesis for high productive genotypes averaged 10.8 and 8.0 μmol CO_2 dm^{-2} min^{-1} for low productive ones; and rates of glycine-serine synthesis for high and low productive genotypes were approximately 2.7 and 1.64 CO_2 $dm^{-2}min^{-1}$, respectively. At earing stage, these genotypes had higher rate of CO_2 assimilation. Photorespiration rate could be evaluated by the rate of synthesis and total value of glycine-serine. Experimental data suggest that photorespiration rate at this stage was also higher in high productive genotypes.

Thus, the rates of $^{14}CO_2$ incorporation into starch and also alanine, malate and aspartate in high and low productive genotypes were similar. However, the rate of ^{14}C incorporation into glycolate metabolites and sucrose, as well as CO_2 assimilation rates, were higher in high productive genotypes.

Wheat along with other C_3-plants is characterized by relatively high value of CO_2 release in the light, which consists of photorespiration and dark respiration in the light. A similar conclusion can be drawn on the basis of measurements of the components of carbon dioxide exchange in different wheat varieties. Accordingly, the rates of net and true photosynthesis were highest in Garagylchyg-2. The rate of CO_2 release in the light was 11.4 and 8.7 mg CO_2 dm^{-2} h^{-1} in Garagylchyg-2 and Gyrmyzy bugda, respectively (Figure 26).

The rate of CO_2 release in the light due to dark respiration was similar in all studied genotypes. However, the rate of CO_2 release due to photorespiration was higher in genotype Garagylchyg-2 and reached 8.7 and 6.2 mg CO_2 dm^{-2} h^{-1} in Garagylchyg-2 and Gyrmyzy bugda, respectively. The ratio of CO_2 release rate in the light due to photorespiration to the net CO_2 assimilation rate was similar in both varieties and averaged about 22.0 and 21.2%, respectively, that indicates a positive correlation between the rates of photosynthesis and photorespiration (Jahangirov, 1987; Aliev et al., 1996 b). These results demonstrate that, despite increased photorespiration in high productive genotypes, they showed high rates of net photosynthesis due to increased true photosynthesis. This statement is also confirmed by higher rates of true photosynthesis and the amount of CO_2 released in the light by photorespiration. Thus, there is a parallel increase in the rates of true photosynthesis and photorespiration in leaf ontogenesis. The ratio of true photosynthesis to photorespiration in genotypes with different productivity is equal on average to 3:1 and a slight increase in intensive genotypes. A value of photorespiration constitutes 28-35% of photosynthetic rate in contrasting wheat genotypes.

Based on these results we can conclude that attempts to find or create high productive genotypes

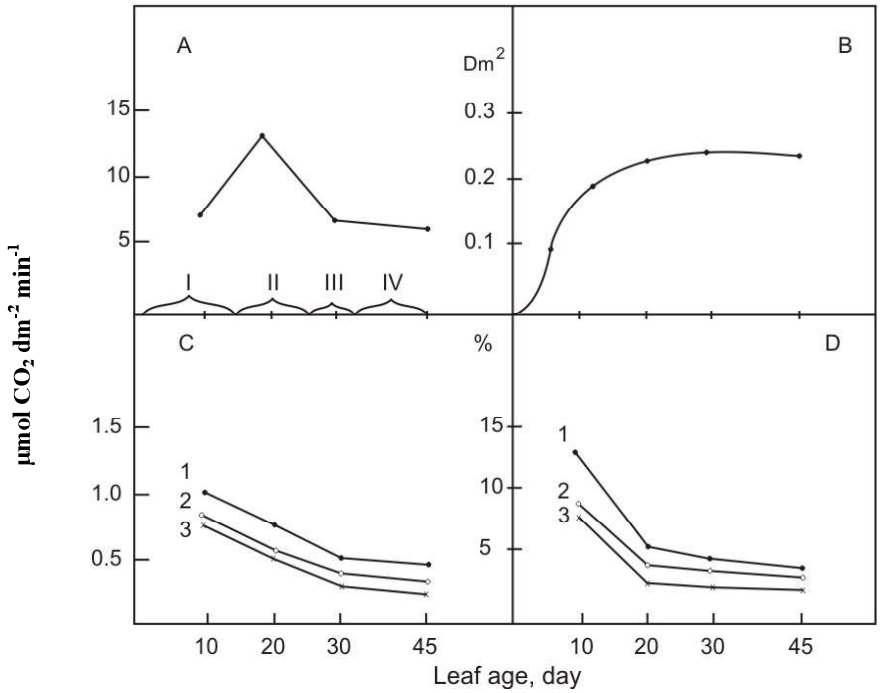

Figure 24. Biosynthesis of malate, aspartate and alanine in flag leaf ontogenesis of wheat variety Garagylchyg-2:

I – stalk emergence, II – earing, III – flowering, IV – grain filling
A – rate of CO_2 fixation; B – leaf area; C – malate (1), aspartate (2), alanine (3); D – the same as C (% of the total CO_2 fixation rate).

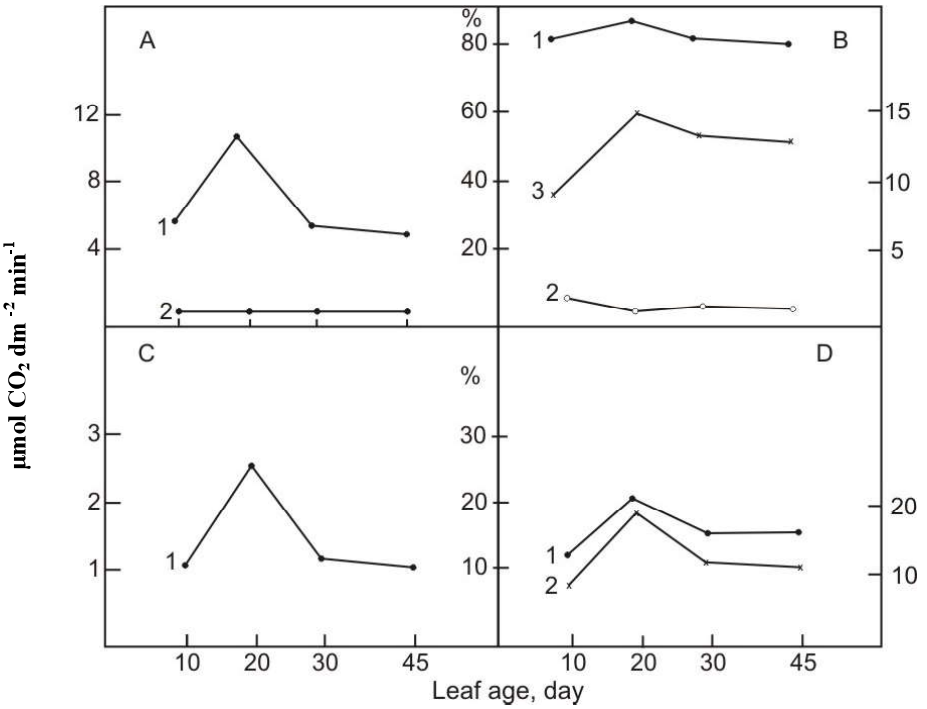

Figure 25. Biosynthesis of sucrose, starch and total glycine-serine in flag leaf ontogenesis of wheat variety Garagylchyg-2:
A – sucrose (1), starch (2); B - the same as A (% of the total CO_2 fixation rate) (1, 2), rate of sucrose to starch (3); C – glycine-serine; D – the same as C (% of the total CO_2 fixation rate) (1), total value of glycine-serine (2).

Table 2. Kinetic characteristics of photosynthetic carbon metabolism in different varieties of winter wheat at the earing and milk ripeness stages

Metabolite		Garagylchyg-2		Azamatli-95		Gyrmyzy bugda		Sary bugda	
		earing	milk ripeness	earing	milk ripeness	earing	milk ripeness	earing	milk ripeness
Total assimilation, [μmol CO_2 dm^{-2} min^{-1}]		12.3	7.0	13.0	7.3	9.6	7.1	9.8	6.8
Alanine	1	0.41	0.21	0.40	0.25	0.36	0.23	0.32	0.20
	2	3.30	3.00	3.20	2.40	3.90	3.20	3.30	2.90
Malate	1	0.70	0.29	0.68	0.30	0.59	0.32	0.56	0.31
	2	5.70	4.10	5.20	4.20	6.10	4.50	5.70	4.60
Aspartate	1	0.49	0.23	0.51	0.24	0.47	0.20	0.50	0.22
	2	4.00	3.30	3.90	3.30	4.90	2.80	5.10	3.20
Glycine-serine	1	2.50	1.10	2.80	1.20	1.57	1.0	1.70	1.10
	2	20.7	15.7	21.5	16.0	16.4	14.7	17.0	15.7
Sucrose	1	10.6	5.50	10.9	5.80	7.80	5.50	8.20	5.80
	2	86.0	78.0	84.0	79.0	81.0	77.0	82.0	81.0
Starch	1	0.70	0.45	0.72	0.48	0.70	0.50	0.65	0.53
	2	5.70	6.40	5.50	6.60	7.30	7.00	6.60	7.80

Note: 1 – rate of synthesis [μmol CO_2 dm^{-2} min^{-1}]; 2 – rate of synthesis (% of the total CO_2 fixation rate). The kinetic characteristics were calculated from the pattern of $^{14}CO_2$ incorporation into photosynthetic products.

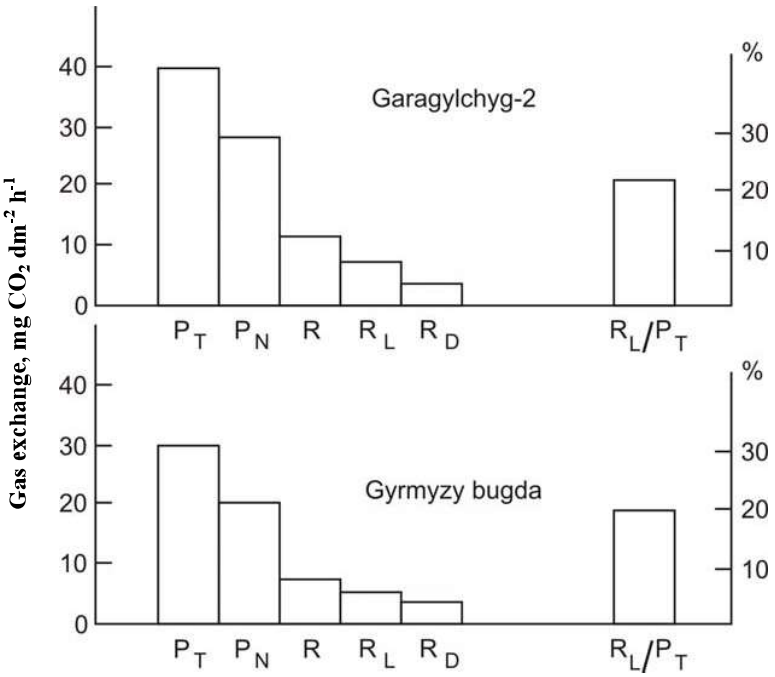

Figure 26. Components of CO_2 exchange in the wheat varieties Garagylchyg-2 and Gyrmyzy bugda (mg CO_2 dm^{-2} h^{-1}):
P_T – true photosynthesis; P_N – net photosynthesis; R – CO_2 release in the light; R_D – CO_2 release in the light due to dark respiration; R_L – CO_2 release in the light due to photorespiration; R_L/R_T – rate of photorespiratory CO_2 release to true photosynthesis (%).

with high photosynthesis and low photorespiration (or low RuBP oxygenase activity) have no future and it is advisable for plant breeders to focus on genotypes that have higher activities of carbonic anhydrase and RuBP carboxylase and high photorespiration.

As mentioned above, high productive wheat genotypes are characterized by higher value of RuBP oxygenase activity and rate of CO_2 release during photorespiration. Obtained data shows that short-stemmed varieties developed by plant breeders with optimal architectonics for the effective use of solar energy, despite high rate of photorespiration have a high rate of net photosynthesis due to enhanced true photosynthesis provided by high activities of RuBP carboxylase and carbonic anhydrase, and the latter contributes to the efficient functioning of the former at carboxylation sites of chloroplasts. On the other hand, it should be noted that the products of glycolate metabolism can also be used in sucrose synthesis or may be transported from the leaves. Therefore, under certain conditions the products of glycolate metabolism can contribute to the active transport of assimilates, thereby creating conditions for the maintenance of photosynthesis at a high level.

Investigation of the transport and distribution of assimilates showed that the higher a leaf layer, the greater an amount of assimilates exported to the ears (Aliev et al., 1996 a). At the same time because of a shorter distance between the leaf and the ear and high attractive force of the ear in high productive genotypes, more assimilates exported from the leaves than in other genotypes. Particularly, the lower leaves of high productive genotypes in all growth stages more actively involved in grain filling than lower leaves of low productive ones, and they gain assimilates from the flag leaf. In the short-stemmed genotype synthesized assimilates are more effectively used in grain formation and less are spent on vegetative mass growth.

Intensive varieties distinguish by higher rate of photosynthetic rate of ear (Figure 27) (Aliyev et al., 1987). Under similar conditions the rate of flag leaf photosynthesis is higher than that of the ear, and ear exports more assimilates into the grain than the flag leaf. Apparently, assimilating ear mass is higher than that of the flag leaf and ear assimilates directly exported to the grain.

Contribution of ear in formation of grain yield is higher in high productive genotypes than in low productive ones (Table 3). After leaf death, the role of the ear gain a particular importance, since at this time ear become, in fact, the only source of assimilates required for the completion of grain filling.

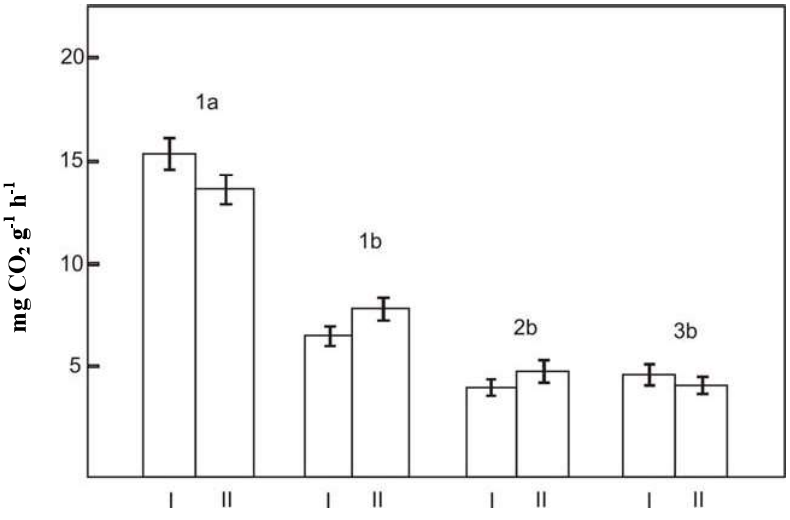

Figure 27. The rate of ear photosynthesis in different wheat genotypes:
I – flowering, II – milk ripeness; a – flag leaf, b – ear;
1 – Garagylchyg-2, 2 – Gyrmyzy bugda, 3 – Kansas-63323.

Table 3. The radioactivity of ear under $^{14}CO_2$ incorporation into ear and flag leaf ($\times 10^3$ impulse per min)

Genotype		Garagylchyg-2		Gyrmyzy bugda		Kansas-63323	
Phase of $^{14}CO_2$ incorporation		flowering	milk ripeness	flowering	milk ripeness	flowering	milk ripeness
Donor of ^{14}C	Ear	75.0±3.8	118.3±5,8	63.1±2.5	86.6±3.5	32.3±1.2	30.4±1.9
	Flag leaf	54.0±2.7	53.1±1.9	41.1±1.8	59.0±2.0	20.6±2.0	21.1±2.6

Changed sink-source relationships with the removal of leaves ^{14}C incorporation into carbohydrates increased and into glycolate metabolites decreased in low productive genotypes due to increase in source capacity of flag leaf. In high productive genotypes it is less expressed. The removal of a part of the ear resulted in a reduction of its acceptor force; and the rate of ^{14}C incorporation into the glycine-serine decreased and into sucrose slightly increased in extensive genotypes. At the same time the activity of all studied enzymes, including RuBP oxygenase, decreased. In intensive genotype removal of the ear part is accompanied by a slight increase in the rate of ^{14}C incorporation into the glycine-serine, and labeling into sucrose decreased notably. In high productive genotype removal of the ear part resulted in reduced RuBP carboxylase activity in the flag leaf. However, the activities of the RuBP oxygenase and carbonic anhydrase slightly increased (Khudiyev, 1998).

Similar results were obtained in the study of photosynthesis, photorespiration and key indexes of photosynthetic activity of the other wide spread C_3-plant, the representative of leguminous family, the soybean (Glycine max (L.) Merr.). The soybean is one of the oldest cultivated plants. The seeds of soybean are widespread food known in China as early as the third millennium BC. In 62 countries the total area under the soybean grown as a universal food, forage and industrial legume, is more than 60 million ha and the gross grain production exceeds 100 million tons. Soybean is distinguished by not typical for plants right balance of proteins, fats and carbohydrates and other valuable substances: vitamins (A, B, C, D, E), easily digestible mineral salts (Ca, K, M, P), enzymes and phosphatides. The soybean seeds contain up to 50% of proteins, 27% of fats, and about 30% of carbohydrates. About 400 kinds of different products are made from soybean (Aliyev and Akperov, 1995, 1998).

As a result of long-term researches on photosynthetic activity of highly contrasting soybean genotypes under different growth conditions the optimal morpho-physiological traits, parameters which determine the formation of the optimal structure of crop were revealed, and a model that meets the time, place and environmental requirements was created (Aliyev et al., 1981, 1982 a; Aliyev and Akperov, 1985, 1986, 1995, 1998). "Ideal" soybean genotypes under the optimal growth conditions should maximize the use of environmental factors (light, water, mineral and organic elements sources, etc.), should be characterized by a high level of homeostasis, high photosynthetic productivity, increased synthesis of high-quality proteins, compact shape of bunch, medium-sized leaves with minor inclination angles between petioles from stem and branches, multibean tassels, and well filled pods and medium-sized seeds.

Analysis of morpho-physiological traits of the soybean genotypes showed that the main yield factors are the conditions of all photosynthetic systems functioning at the crop level determined by the cultivation conditions, especially, mineral nutrition and irrigation. It was shown that high agricultural background provides not only the increase in productivity, but also a significant improvement in grain quality (Aliyev and Akperov, 1986). Intensive genotypes with the optimal architectonics have high photosynthetic activity and provide high yield (3.5-4 t ha^{-1}) and high grain quality (40% of proteins).

The dynamics of diurnal variations in CO_2 gas exchange is similar in various soybean genotypes in many respects and possess some common trends (Figure 28). It was established that regardless of growth conditions the observed photosynthetic activity is characterized by double-picked curves, sharply increasing photosynthetic value in the morning and the midday depression. At sunset the photosynthetic gas exchange turns into the respiratory one. The high productive genotypes are distinguished by a higher rate of photosynthesis. Application of mineral fertilizers significantly improves the photosynthetic activity of plants in field and influence on the course of diurnal variations in gas exchange. This, generally, manifests as maximum values of photosynthesis and respiration over the day (Mirzoyev, 1990; Aliyev et al., 1992).

The rate of photosynthesis in leaves of various soybean genotypes gradually increases from branching stage, and reaches a maximum value in high productive genotypes (on average 24 mg CO_2 dm^{-2} h^{-1}) during the periods from pod formation till grain filling. In the low productive genotypes, the greatest value of photosynthetic rate (21 mg CO_2 dm^{-2} h^{-1}) was observed at the initial stage of grain filling, and it lasted for a short period of time (Figure 29). Consequently, the duration of the periods from pod formation till grain filling has a great importance for the grain yield (Mirzoyev, 1988 a, b; Akperov and Mirzoyev, 1990; Aliyev et al., 1992). Improvement of the growth conditions significantly contributes to increasing of photosynthetic activity of plants in field. And rate of photosynthesis increases by 30-50% (Aliyev et al., 1992).

The change in carbon dioxide gas exchange components, excepting dark respiration, in all studied genotypes occurs proportionally during ontogenesis (Figure 30). The maximum value of these components in the low productive genotypes is observed at 60 days of age, in the high and medium productive ones - at 80-90 days of age. The ratio of true photosynthesis to photorespiration in leaves is quite constant and averages 29% in the low productive varieties and 35%

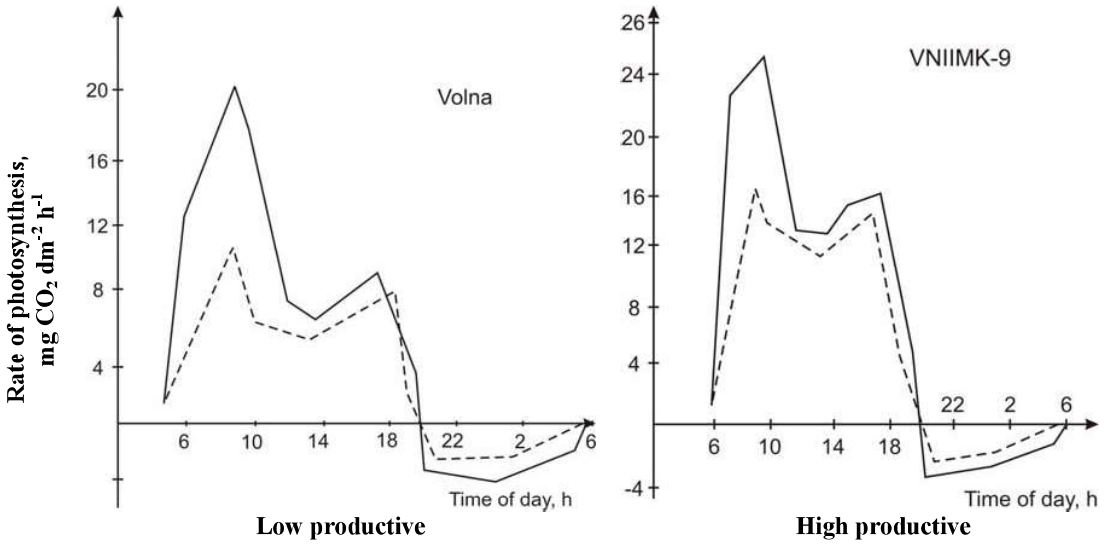

Figure 28. The diurnal pattern of the gas exchange rate in leaves of various soybean genotypes at the grain filling stage. Solid lines - the gas exchange rate in the leaves of plants grown using mineral fertilizers, dotted lines - the gas exchange rate in leaves of plants grown without mineral fertilizers (control).

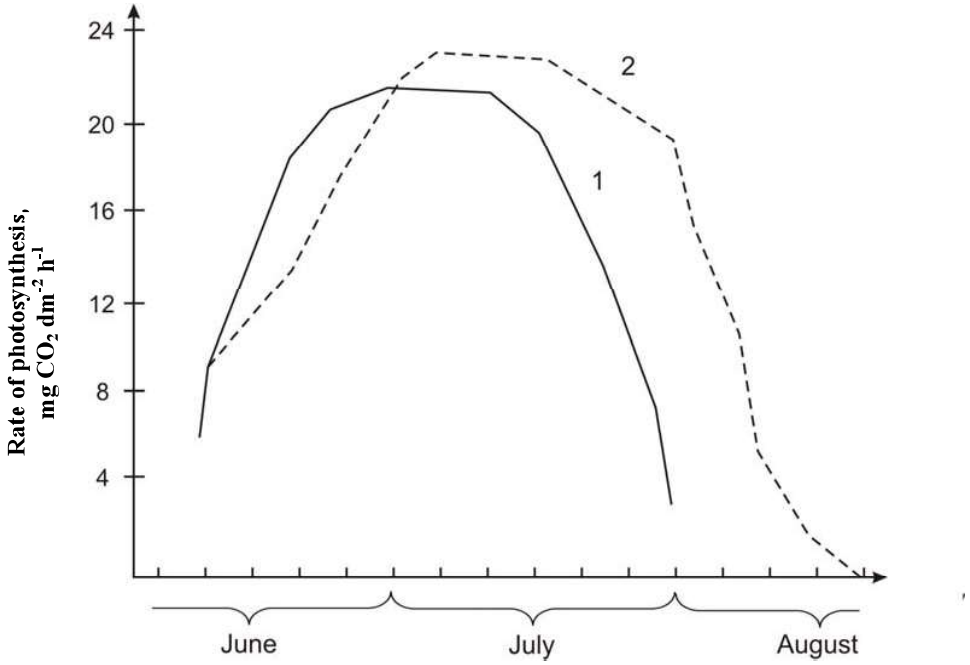

Figure 29. Ontogenetic changes in the rate of photosynthesis in low (1) and high productive (2) soybean genotypes.

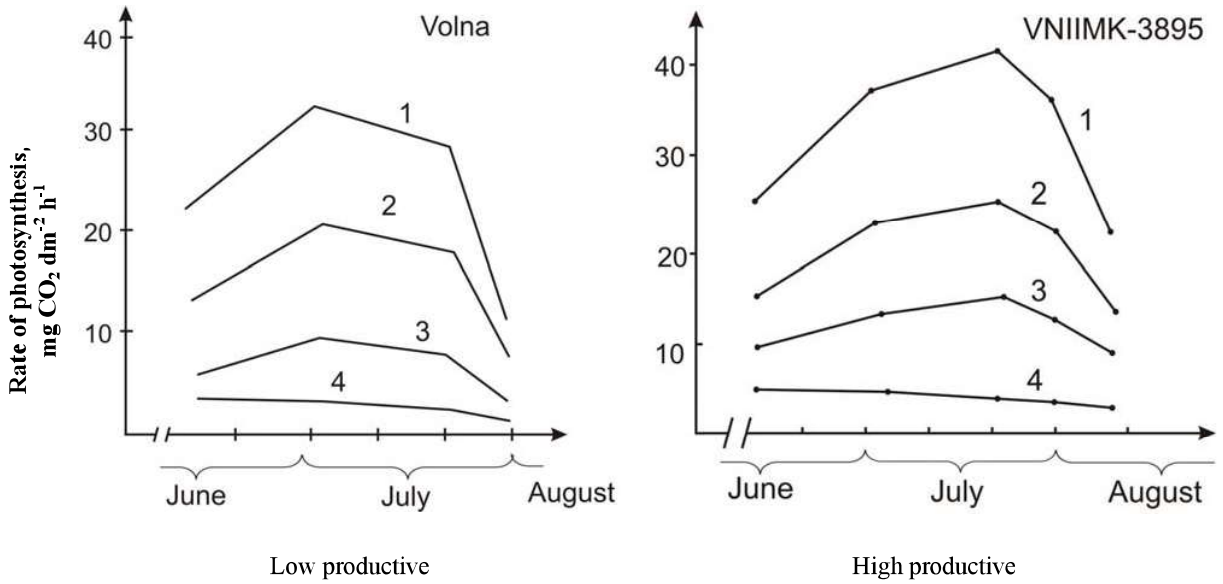

Figure 30. Components of carbon dioxide gas exchange in soybean leaves:
1 - true photosynthesis; 2 - net photosynthesis; 3 - photorespiration; 4 - dark respiration.

in the high productive ones (Mirzoyev, 1988 a, b, 1990; Aliyev et al., 1992).

The similarity in the pattern of change in the rates of true photosynthesis and photorespiration during ontogenesis exhibits a positive relationship between them. The absolute value of dark respiration in the studied soybean genotypes differ slightly. Our research findings showed that the value of photorespiration in the high productive soybean genotypes compared to the same of the low productive ones is higher. Hence, during the execution of purposeful breeding program with the aim of developing high productive soybean varieties, genotypes with higher photorespiration value should be used as a starting material.

Under the water stress active photosynthetic function of different assimilating organs, mainly of an ear, plays a crucial role in yield formation. Drought as a negative environmental factor adversely affects the photosynthetic gas exchange in wheat, reducing its rate by 30-40% in the short-stemmed varieties and by 35-45% in long-stemmed ones. Lower leaves are more affected by drought than the upper leaves. The greatest decrease in the photosynthetic rate during ontogenesis in short-stemmed varieties occurs at the flowering and grain formation, and in the long-stemmed varieties - at the flowering and milk ripeness (Figure 31). Hence, in intensive genotypes the critical period of water deficit is the end of flowering and grain formation, in extensive ones it starts from beginning of flowering and covers the whole following period of ontogenesis (Maharramov, 1995).

Leaf area begins to decrease starting from the earing and flowering stages, and at the end of ontogenesis its area shortens by more than half. The ear surface area at the end of ontogenesis decreases in short-stemmed varieties by 32% and in long-stemmed ones by 23%.

Alterations in the correlation between assimilating and consuming organs in different wheat genotypes under drought led to a change in photosynthetic rate. Variation of the source potential with the removal of 7-layered leaves increased the rate of the 8-layered leaves in the short-stemmed varieties under normal irrigation and water deficit on average by 19 and 21%, in long-stemmed ones by 36 and 28%. After removal of 8-layered leaves, these parameters changed to 22 and 28% in short-stemmed and 37 and 23% in long-stemmed genotypes. The decrease of the ear acceptor force leads to a decrease of the rate of photosynthesis of leaves in the control and stressed variants on average to 15 and 9.5% in intensive types, and 18 and 12.5% in extensive ones, respectively (Ahmadova, 1996).

In drought tolerant intensive wheat variety in sowing more than 60% of grain yield and protein synthesis occurs due to ear photosynthesis. Such benefits of intensive and tolerant to water stress genotypes as great assimilating ability of the ear in current photosynthesis and the best acceptor activity in the utilization and reutilization of reserve products of photosynthesis are crucial in developing of both high productive and drought tolerant genotypes. When leaves lose their photosynthetic functions under drought an ear does the main contribution to the photosynthesis at the earing and grain filling (Aliyev, 1998). In compact sowings of

these genotypes with optimal assimilating surface and sufficient donor ability the value of photosynthetic rate is always high. Together with high photosynthetic activity and attractive force of the ear it constitutes the basis of high yield. For this reason in high productive genotypes with high photosynthetic function of the car grain yield is considerable under extreme water supply.

The rate of photorespiration is to some extent in inverse correlation with the water supply. With increasing tolerance of genotypes to water stress or with strengthening of the drought, the photorespiration rate decreases to a large degree in the ear elements.

The regular alterations of carboxylase, oxygenase and glycolate oxygenase contribute to direct correlation between the rates of photosynthesis and photorespiration. Study of plant gas exchange fully confirms the close relationship and direct correlation between these processes (Somerville and Ogren, 1980; Bidwell, 1983; Chanh et al., 1985). When the rate of photosynthesis is high, photorespiration is active too. The increase of temperature

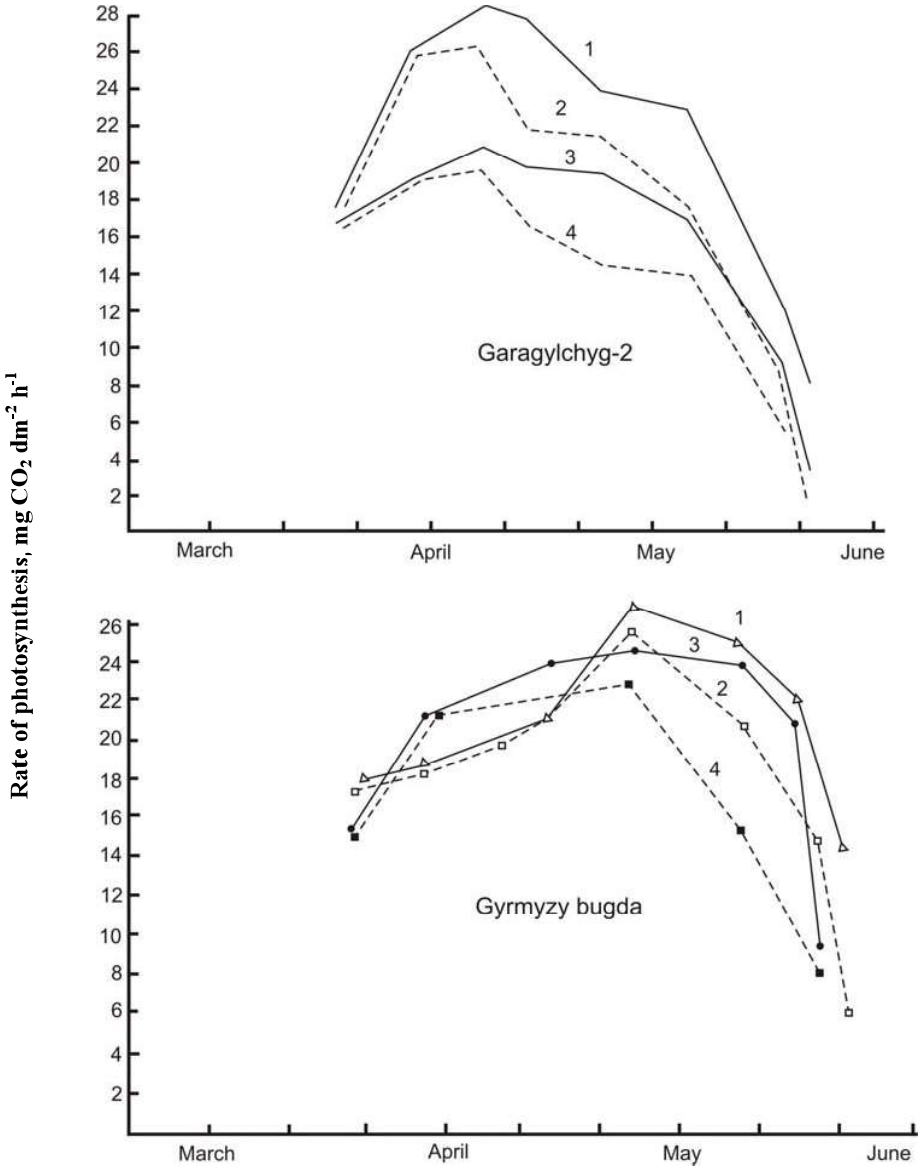

Figure 31. Ontogenetic changes of photosynthetic rate in wheat leaves under normal water supply and water deficit:

1, 2 – leaves of eighth layer, 3, 4 – leaves of seventh layer;

Control - solid curves, Stress - dashed curves.

enhances photorespiration relative to photosynthesis. Yield of glycolate metabolism may vary depending on the photosynthesis conditions. It increases when the outflow of assimilates from the leaves is inhibited and when nitrate levels in the environment is getting high (Lenz, 1979).

Decrease of photorespiration rate as a result of genetic abnormality of the individual reactions is accompanied with decreased rate of photosynthesis. In *Arabidopsis* mutants deficient in the serine glyoxylate aminotransferase, enzyme responsible for the completion of glycolate pathway, photosynthesis decreased by 79% over 30 min and quantity of ^{14}C in glycine and serine increased 2-2.5 times in ambient air (21% O_2) in comparison with the wild type. Reduced photorespiration could be the reason for abnormalities of nitrogen conversions associated with inhibition of growth processes and reducing overall productivity.

Investigations of primary processes of photosynthesis allowed to specify that chloroplasts from high productive genotypes were characterized by high rates of electron transport and photophosphorylation, and also to approve the availability of relationship between photosynthetic electron transport, CO_2 assimilation and productivity (Kazibekova et al., 1985).

High rates of photosynthesis and photorespiration in conjunction with favorable photosynthetic traits, an optimum leaf area index and the best architectonics define the high productivity of wheat genotypes. Therefore, contrary to conception on wastefulness of photorespiration, proposed in the many years by different authors (Zelitch, 1966, 1971, 1973, 1975; Zelitch and Day, 1973; Chollet and Ogren, 1975; Kelly and Latzko, 1976; Ogren, 1976; Servaites and Ogren, 1977; Ogren and Chollet, 1982; Holaday and Chollet, 1984; Leegood et al., 1995; Somerville, 2001; Ogren, 2003; Igarashi et al., 2006; Long et al., 2006; Kebeish et al., 2007; Khan, 2007; Mueller-Cajar and Whitney, 2008; Maurino and Peterhansel, 2010; Peterhansel et al., 2010; Peterhansel and Maurino, 2010), our comprehensive investigations on different aspects of photorespiration indicate that photorespiration is one of the evolutionary developed vital metabolic processes in plants. The attempts to reduce this process with the purpose of increasing the crop productivity are inconsistent (Aliev et al., 1988, 1996 b, c; Aliyev et al., 1992; Aliev and Kazibekova, 1995; Aliyev, 1995, 1998, 2001 a, b, 2002, 2004, 2007, 2010; Aliyev and Kazibekova, 2002). Phosphoglycolate phosphatase, a key enzyme of photorespiration was first homogeneously purified from eukaryotic green algae *Chlamydomonas reinhardtii* with subsequent determination of complete nucleotide and deduced amino acid sequences (Mamedov et al., 2001, 2002; Mamedov and Suzuki, 2002) (NCBI Nucleotide 1:AB052169). Later the same gene was identified in *Arabidopsis* (Schwarte and Bauwe, 2007). Since metabolic processes of photorespiration in the leaf in the light take place simultaneously with photosynthesis, it is possible that released energy is used in certain reactions of photosynthesis.

Although long time generations of plant scientists have pondered the incongruous nature of the photorespiratory pathway's complexity and its apparent disadvantages, we are perhaps only now gaining sufficient knowledge to address the potential benefits of photorespiratory metabolism.

So, there are high productive genotypes among plants with C_3-photosynthesis and low productive among plants with C_4-photosynthesis. Despite the low value of photorespiration in C_4-plants (such as maize, sorghum, amaranth, etc.), many plants of C_3-type with high photorespiration, including major crops (wheat, rice, peas, etc.) compete successfully with C_4-plants and have high potential productivity and biological yield.

Along with establishing the key indicators of "ideal" wheat it is necessary to study the genetic basis of valuable qualities, i.e., the degree of inheritance of these valuable traits. In modern breeding one of the important steps is to identify genes responsible for the necessary morphological parameters, to transfer them into the genomes of developing variety and fixing there. Presence of the genetic potential in grain crops is expressed by physiological realization in the field. Therefore, selecting practical specimens for direct breeding and establishing an effective framework for decoding the molecular mechanisms of drought resistance in wheat it is necessary to use fully physiological potential of various genotypes under water limited conditions. Tolerance to water stress is not determined by one gene, i.e. it is a trait controlled by many genes. Many genotypes created by us, especially Barakatli-95, possess a number of core genes of the tolerance (Huseynova et al., 2006, 2007, 2009, 2010 a, b).

Photorespiration, in which part of organic compounds produced in photosynthesis is used, has gained a certain physiological value in the integrated system of plant organism. Goldsworthy (1969) opined that glycolate formation appeared in photosynthesizing plants during evolution as a result of reducing the carbon dioxide concentration in the atmosphere. Higher plants oxidize glycolate and metabolize it to more useful compounds. RuBPC/O is one of the most ancient enzymes. Appeared later in evolution PEP carboxylase does not have oxygenase function. Photorespiration prevents the accumulation of toxic intermediates (phosphoglycolate, glyoxylate) (Peterhansel et al., 2010). On the

other hand, photorespiration is a source of a number of significant metabolites (glutamate, γ-glutaric acid, glycine, serine) required for various biosyntheses (synthesis of proteins and phytohormones) (Novitskaya et al., 2002). Recently photorespiration gained a special importance as a producer of H_2O_2, the reactive oxygen species, which plays a role in cell signaling (Queval et al., 2007). Since hydrogen peroxide production significantly increases in peroxisomes under stress and is associated with activation of photorespiration, it is supposed that this process protects reaction cascade in the cell on purpose to provide adaptation of C_3-plants to unfavorable conditions (Noctor et al., 2002). Photorespiration utilizes excess energy that arises due to photochemical processes and is not used in photosynthesis and, thus, prevents photoinhibition of CO_2 fixation, which may be due to photooxidation and destruction of the photosynthetic apparatus (Heber et al., 1996; Kozaki and Takeba, 1996; Wingler et al., 2000). In addition, it was stated that under field conditions there is no doubt that photorespiration plays a significant protective role in preventing chronic photoinhibition (Osmond and Grace, 1995). It regulates the redox balance in the cell during decrease of CO_2 assimilation, when the power of the Calvin cycle is not enough to use the entire amount of NADPH and ATP produced in the light phase of photosynthesis. Energy dissipation during photorespiration prevents chloroplast over-reduction leading to photoinhibition of photosynthesis, thus supporting the functional activity of photosynthetic apparatus (Takahashi et al., 2007).

Photorespiration contributes to the maintenance of CO_2 level inside the leaf. It is known that at extreme conditions of water supply stomata are being closed and photorespiration increases sharply. ATP produced at intermediate stages of photorespiration is metabolized within mitochondria, where its concentration sharply drops due to limitations of triose phosphate outflow from the chloroplast and CO_2 entering to the tissue. Photorespiration is closely associated with general metabolism in the green cell; it often increases with decreasing of plant requirements in photosynthesis products and, in principle, aimed at maintenance of the enzyme system activity and chloroplasts and mitochondria functions. The role of photorespiration is sometimes associated with the nitrogenous compounds metabolism. The nitrogen conversion in glycolate pathway is closely linked to the carbon reactions (Oliver, 1994; Husic et al., 1987) and, thus, undoubtedly represents photorespiration, a substantial part of the photosynthetic oxidative cycle. Keys et al. (1978) suggested the inseparable link between photorespiration and nitrogen metabolism. It was established that the conversion of nitrogenous compounds during photorespiration is a cyclical process, called photorespiration nitrogen cycle (Keys et al., 1978; Walker et al., 1984; Schneidereit et al., 2006).

It is assumed that organic acids and their oxidation products, which are formed during photorespiration, via interaction with oxygen can act as antioxidants (Foyer and Noctor, 2005; Foyer et al., 2009), ensuring persistent operation of non-cyclic electron transport chain.

Phosphorylation in C_3-plants is balanced with chloroplast carbon metabolism and therefore, chloroplast is not able to export the ATP and provide energy to the entire cell. At the same time respiration (glycolysis - Krebs cycle) can not occur simultaneously with photosynthesis. Therefore, there is a change of respiratory substrate in the light, and acid oxidation in the Krebs cycle is replaced by glycine oxidation. Respiratory chain and phosphorylation remain active, that is, changes affect only the carbon metabolism. Thus, in the light respiratory chain accomplish the same reactions as that of dark respiration, then respiratory substrate is glycine produced in the photorespiratory pathway (Husic et al., 1987; Gardeström and Wigge, 1988; Oliver, 1994). Moreover, the photo-oxidative processes, in particular the glycolate oxidation, are energetically useful.

All these data indicate that photorespiration, which is, virtually, an integral part of the production process cannot be considered as wasteful, useless or even harmful process.

Recently new information about possible alternative pathways in phosphoglycolate metabolism was revealed, showing the metabolic flexibility of photorespiration (Maurino and Flügge, 2009; Peterhansel et al., 2010). The point is to change the course of photorespiration instead of its decrease.

However, photorespiration is not always linked to photosynthesis. For example, chlorophyll-deficient *Chlorella* mutants are able to synthesize only carotenoids. Photorespiration occurs in such mutants under strong illumination, and compose 50% of the dark respiration. When disabling photosynthesis by respiratory poison, O_2 absorption and CO_2 release also occurs in green photosynthetic cells.

In conclusion, we emphasize the close relationship between photosynthesis and photorespiration; the optimal correlation of these two essential processes is one of the most important conditions that secure the highest plant productivity. High rate of true photosynthesis and photorespiration, high activity of the primary photochemical processes in conjunction with favourable phenotypic traits, the optimum leaf area index and architectonics are crucial to the high productivity of wheat genotypes.

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