

Peculiarities of CO₂ exchange in soybean genotypes contrasting in grain yield

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ABSTRACT

The peculiarities of leaf carbon dioxide gas exchange in soybean genotypes grown in field over a large area and contrasting in duration of vegetation, photosynthetic traits and productivity were studied. Varietal differences in the daily and ontogenetic changes in photosynthesis and photorespiration were identified. It was established that the period of the high activity of photosynthetic apparatus in high productive soybean genotypes lasts for a longer time. The photosynthetic rate and the rate of CO₂ release in light due to photorespiration are higher in high productive genotypes. A value of photorespiration in contrasting soybean genotypes constitutes about 28% - 35% of photosynthetic rate. The ratio of gross photosynthesis to photorespiration in genotypes with different productivity is constant enough during ontogenesis, indicating a direct positive correlation between gross photosynthesis and photorespiration. Therefore, contrary to conception arisen during many years on the wastefulness of photorespiration, taking into account the versatile investigations on different aspects of photorespiration, it was proved that photorespiration is one of the evolutionarily developed vital metabolic processes in plants and the attempts to reduce this process with the purpose of increasing the crop productivity are inconsistent.

Keywords: Photosynthesis; Photorespiration; Productivity; Soybean Genotypes

1. INTRODUCTION

Soybean belongs to the legume family (*Fabaceae*) originally from East Asia and one of the oldest cultivated plants. The cultivation of the soybean is referred to the Chinese literature as early as the third millennium BC. It was recognized only in the XIX century, and since then it has been widely spread worldwide. Cultural soybean is widely

grown in Asia, Southern Europe, North and South America, Central and Southern Africa, Australia, the islands in the Pacific and Indian oceans at latitudes from the equator to 55° - 60°.

The soybean is often called “the miracle plant”, such interest is determined by a high quality of its grain, which contains 35% - 55% of easily digestible proteins, 17% - 27% of fats, 30% of carbohydrates, vitamins, etc., depending on variety and growing conditions. Among all worldwide cultivated agricultural crops the soybean is one of the most high-protein ones. Due to rich and varied chemical composition it is widely used as a food, forage and industrial crop, having a great agrotechnological importance as well [1-5]. The soybean has also the ability to assimilate air nitrogen [6] and, therefore, requires minimal costs for nitrogen fertilizers, which is often considered the single major energy contribution to agriculture.

World soybean production was about 210.9 million metric tons in 2009 [7]. The consumption of soy-based products increases worldwide due to the described beneficial effects, which include reduction of cholesterol level, prevention of cancer, diabetes and obesity, protection against intestinal and kidney diseases [8].

The soybean is an annual plant with a pivotal root system. All species of the soybean has trifoliate leaves with drooping leaflets and pinnate venation, occasionally leaves with 5-, 7- and 9-leaflets are found.

The process of photosynthesis is the main part of total plant productivity. The soybean, like most agricultural crops, belongs to the so-called C₃-plants. A part of carbon dioxide assimilated during respiration in light is released from leaves simultaneously with photosynthesis [9]. This results in much less real value of CO₂ assimilation in C₃-plants than the realized photosynthesis.

Since 1970's a concept on wastefulness of photorespiration has been formulated by many researches, and attempts to decrease or suppress it with the purpose to increase the crop productivity are still made [10-16]. The conception on possibility of significant increase in productivity of C₃-plants through the selection of samples

with low rate of photorespiration was developed. It was suggested to search the ways to eliminate or reduce photorespiration by genetic or chemical means [10-13,17-20]. However, chemicals which inhibit glycolate metabolism did not reduce photorespiration and increase photosynthetic efficiency [18]. In addition, on the basis of the theory about the relationship between photosynthesis and photorespiration based on the competition between CO₂ and O₂ for ribulose-1,5-bisphosphate carboxylase, which appears at the level of carboxylase-oxygenase function of this enzyme, the existence of a positive relationship between the processes of photosynthesis and photorespiration at a constant intracellular CO₂ concentration has been demonstrated [21,22].

The results of long-term comprehensive study of components of leaf carbon dioxide gas exchange in soybean genotypes contrasting in productivity and photosynthetic traits under a natural growth conditions are presented in the paper.

2. MATERIALS AND METHODS

2.1. Plant Material

Experiments were performed on irrigated area at the Absheron Experimental Station of the Research Institute of Crop Husbandry. Research targets include different soybean (*Glycine max* (L.) Merr.) genotypes contrasting in height, architectonics, duration of vegetation, productivity and other morpho-physiological traits, Rannaya-10, Bystritsa, Volna, VNIIMK-3895, Komsomolka, Provar, VNIIMK-9, Plamya, Biyson and Visokoroslaya-3 were used (Table 1). The genotypes were short-stemmed (40 - 55 cm), medium-stemmed (60 - 70 cm), and high-stemmed (80 - 115 cm) with low productivity (2 - 2.3 t·ha⁻¹), medium productivity (2.5 - 3.0 t·ha⁻¹) and high productive (3.3 - 4.0 t·ha⁻¹). The genotypes Provar and Biyson are

introduced from the USA, the other genotypes were developed at the All-Union Research Institute of Oil and Essential Oil Crops (VNIIMK).

2.2. Growth Conditions

All genotypes were grown under identical field conditions over a large area in compliance with all requirements of cultivation agrotechnology and experimental work [23-27]. The record plot area was 54 m², field experiments were repeated 4-times, and the optimal inter-row space was 60 cm. High agricultural background (optimal conditions for mineral nutrition) was used to determine the potential photosynthetic capacity of the studied soybean varieties [26,28].

Sowing was carried out at the end of April, under soil temperature no lower than 12°C - 13°C. Soil moisture was maintained at 70% - 75% of TAW (total available water capacity). During the growing season phenological observation of plant growth and development was carried out.

2.3. Experiment Arrangement

The rate of carbon dioxide gas exchange was measured using an infrared gas analyzer URAS-2T ("Hartman and Braun", Germany) in an open air system [29,30]. The special brass made thermostatic leaf chamber with optical glass windows of 10 cm² area was made. The limits of measurements were 0.005% - 0.05% CO₂, error was ±0.5% of the upper limit of the scale [22,31]. CO₂ 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 [32]. 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.

Table 1. Characterization of soybean genotypes.

Genotype	Height	Duration of vegetation, days	Morpho-physiological traits	Productivity
Rannaya-10	short-stemmed	110 - 115	small grains, semi-compact bushes	high productive
Bystritsa	short-stemmed	80 - 90	small leaves, compact bushes	low productive
Volna				
VNIIMK-3895	medium-stemmed	115 - 126	medium-sized grain, semi-compact bushes, medium branching, high fixation of inferior beans	high productive
Komsomolka				
Provar				
VNIIMK-9	high-stemmed	120 - 138	large grains, wide bushes	medium productive
Plamya				
Biyson				
Visokoroslaya-3				

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 CO₂ 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 CO₂ concentration and air velocity passing through the leaf chamber. For the measurements a hermetically sealed clip chamber with the area of 0.1 dm², 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 close to the stem maintaining their natural location and orientation, and exposed to sunlight until the gas exchange reached the steady-state level. The CO₂ 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 [22,31] was used to prevent overheating of leaves in the chamber. Photorespiration was determined using two methods, in atmosphere without CO₂ and in atmosphere with reduced oxygen content (2%) [33,34]. In the first case, after photosynthesis had reached the steady-state level the CO₂-lacking air was passed through the leaf chamber. The increase in CO₂ 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 rate of photorespiration was determined by difference between the values of CO₂ release rate in light without CO₂ and dark respiration.

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 1**).

Leaf assimilating area was measured using an automatic area meter "AAC-400" ("Hayashi" Denkoh Co. LTD, Japan). The specific leaf density (SLD) was calculated as the ratio of its dry weight to the area. Photosynthetically active radiation (PAR) was calculated according to Tooming and Gulyaev [35]. The obtained data were statistically processed by standard analysis methods [36].

3. RESULTS AND DISCUSSION

The analysis of morpho-physiological traits of the soybean



Figure 1. Measurement of the rates of photosynthesis and photorespiration in soybean genotypes in the field.

harvest showed that main factors of the yield are conditions for the functioning of all photosynthetic systems at the crop level determined by cultivation conditions, particularly mineral nutrition and irrigation. It was shown that high agricultural background provides the increase in yield and significant improvement of grain quality [28]. Intensive genotypes with optimum architectonics possess higher photosynthetic activity and provide high yield (3 - 4 t·ha⁻¹) and high grain quality (40% protein).

The contribution of leaves to the total CO₂ assimilation largely depends on their layer location and spatial orientation [26,27]. Physiologically active leaves of middle layers (9 - 11) with higher specific leaf density (0.44 - 0.51 g·dm⁻²) assimilate CO₂ more intense than leaves of the other layers. Leaves of upper layers also have a maximal value of SLD and photosynthetic rate in comparison with that of the lower ones. Obviously, the increase in SLD of the leaves of upper and middle layers under a favorable luminosity keeps the lower layers under the luminosity insufficient for active photosynthesis.

Comparative study of the rate of photosynthesis during the day showed that, regardless of genotypes, diurnal variations in leaf photosynthetic rate are characterized by double-peak curves with sharp increase in photosynthetic rate in the morning (9-11 a.m.) and the evening (4-6 p.m.) and midday depression (**Figures 2-4**). Leaf photosynthesis in the low productive genotype Bystritsa starts at approximately 7 a.m., increases rapidly at sunrise and reaches its maximum value at 11 a.m. Then the rate of photosynthesis sharply drops at 2-3 p.m., and the lowest value during the day is being observed. After 3 p.m. the second peak is observed. It should be noted that solar radiation at 2 p.m. was the highest and amounted to 0.44 cal·cm⁻²·min⁻¹.

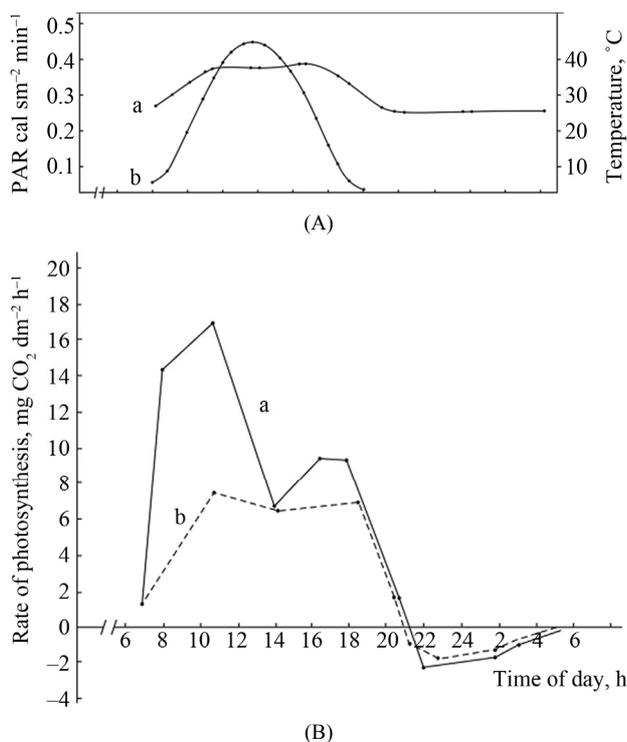
Change in ambient temperature and PAR during the day shows that their maximum value is achieved at 12 a.m.-4 p.m. (**Figure 2(A)**). Diurnal depression of photo-

synthesis occurs at this time. In the midday CO_2 assimilation drop is caused by increase in temperature of leaves, resulting in increased respiration, water regime disturbance, weakening of assimilates outflow and changes in other physiological processes.

In the evening the rate of photosynthesis decreases and carbon dioxide compensation point is being observed. At nightfall the photosynthetic gas exchange turns into the respiratory and carbon dioxide is released as a result of respiration. At night the rate of dark respiration reaches its maximum value and then begins to decrease. After 5-6 p.m. the CO_2 release rate in the dark respiration decreases sharply, and after 7 a.m., at the sunrise the respiratory gas exchange turns into the photosynthetic, which increases dramatically within a short time.

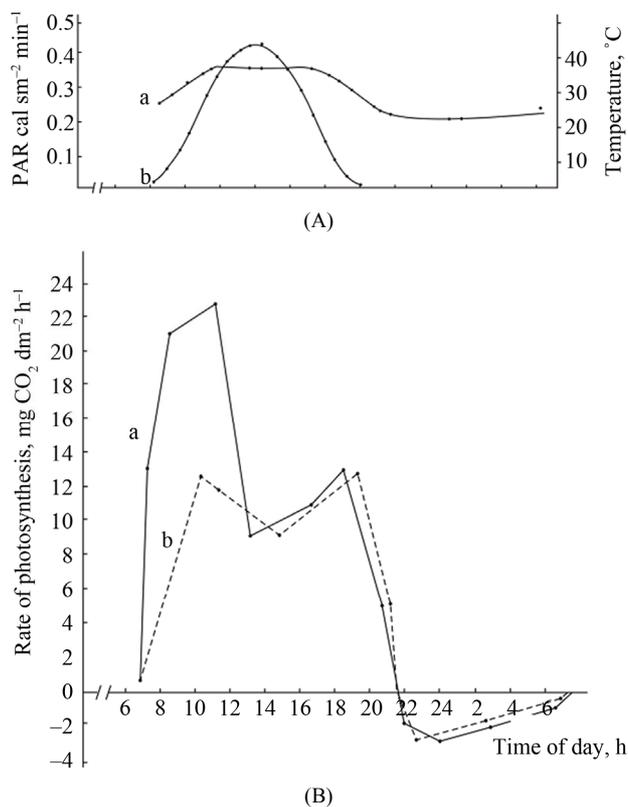
High productive genotypes have a higher photosynthetic rate than low productive ones. A similar pattern is observed in the dynamics of the respiratory gas exchange. During the night period, high productive genotypes have relatively higher respiration rate.

The leaves of lower and middle layers of high productive genotypes during the branching stage assimilate rather more CO_2 than leaves in similar layers of medium productive genotypes. Leaves of the middle layer assimilate more CO_2 during this stage in all studied genotypes (**Figure 5**).



(A) a: Ambient temperature; (A) b: PAR; (B) a: The rate of leaf gas exchange in plants grown using mineral fertilizers; (B) b: The rate of leaf gas exchange in plants grown without mineral fertilizers (control).

Figure 2. The diurnal patterns of the leaf gas exchange rate in the low productive genotype Bystritsa at the grain filling stage.

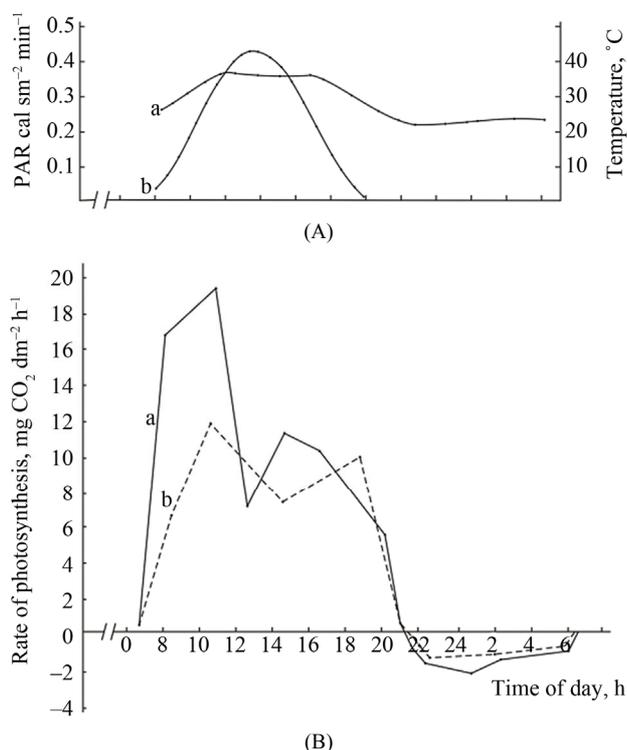


(A) a: Ambient temperature; (A) b: PAR; (B) a: The rate of leaf gas exchange in plants grown using mineral fertilizers; (B) b: The rate of leaf gas exchange in plants grown without mineral fertilizers (control).

Figure 3. The diurnal pattern of the leaf gas exchange rate in the high productive genotype Komsomolka at the grain filling stage.

During the flowering stage the rate of CO_2 assimilation increases sharply in leaves of all layers in all genotypes, but the maximum value of CO_2 assimilation is observed in leaves of the middle layer. In the period of od formation the intensity of lower layered leaves drops sharply. Throughout the growing season the leaves of the middle layer were distinguishing by the highest rate of photosynthesis. By the end of the growing season the activity of leaves of the upper layer remained high as well.

Soybean genotypes contrasting in genetic and phenotypic peculiarities differ by maximum value of photosynthetic rate and duration of their highly active period as well during ontogenesis (**Figure 6**). Photosynthetic rate in leaves of different soybean genotypes gradually increases since the branching stage and reaches the maximum at the flowering—pod formation stages, and then decreases at the end of pod formation, and reaches a maximum value in high productive genotypes (on average $24 \text{ mg CO}_2 \text{ dm}^{-2} \cdot \text{h}^{-1}$) during the periods from pod formation till grain filling. In the low productive genotypes, the greatest value of photosynthetic rate ($21 \text{ mg CO}_2 \text{ dm}^{-2} \cdot \text{h}^{-1}$) was observed at the initial stage of grain filling, and it lasted for a short period of time. Consequently, the duration of the periods from pod formation



(A) a: Ambient temperature; (A) b: PAR; (B) a: The rate of leaf gas exchange in plants grown using mineral fertilizers; (B) b: The rate of leaf gas exchange in plants grown without mineral fertilizers (control).

Figure 4. The diurnal pattern of the leaf gas exchange rate in the medium productive genotype Provar at the grain filling stage.

till grain filling has a great importance for the grain yield [30,37-39]. Improvement of the growth conditions significantly contributes to increasing of photosynthetic activity of plants in field. And rate of photosynthesis increases by 30% - 50% [30].

At the same time, leaves of the high productive genotypes (VNIIMK-3895 and Komsomolka) at all developmental stages, especially during flowering and pod formation, assimilate CO₂ more intensively and maintain high rate of photosynthesis for longer time. Pod formation stage in VNIIMK-3895 variety starts 5 - 8 days earlier and the rate of photosynthesis is maintained at a high level within 10 - 15 days. The longest flowering-pod formation period was observed in this variety (an average of 53 days over four years). Hence, the total longevity of the growing season does not play a major role in the grain yield but the duration of the period of pod formation and grain filling does [30,37-39].

In contrast to medium- and long-stemmed genotypes, the short-stemmed early maturing genotypes (Bystritsa and Volna) are characterized by a short period of high values of the photosynthesis rate. It suggests that early maturity and short stature are not always accompanied by a high value of the photosynthetic rate. The medium productive genotype Plamyra with relatively low CO₂ assimilation

(23.3 mg CO₂ dm⁻²·h⁻¹) is characterized by longer period of photosynthetic activity, and is inferior to medium-stemmed genotypes in its yield (Figure 6).

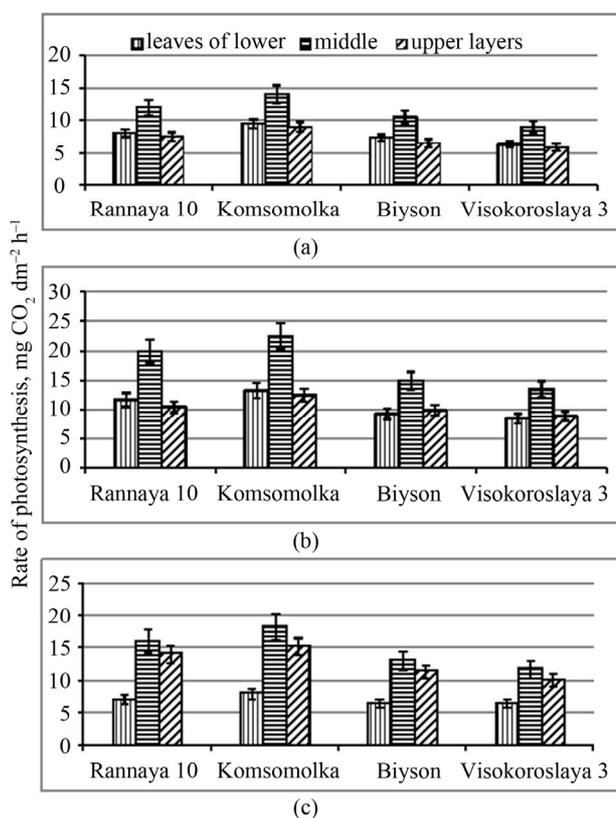


Figure 5. Seasonal dynamics of photosynthesis rate in leaves of different layers of the short-stemmed, high productive (Rannaya), medium-stemmed, high productive (Komsomolka) and long-stemmed, medium productive (Biyson, Visokoroslaya) soybean genotypes: (a) Branching; (b) Flowering; (c) Beginning of pod formation.

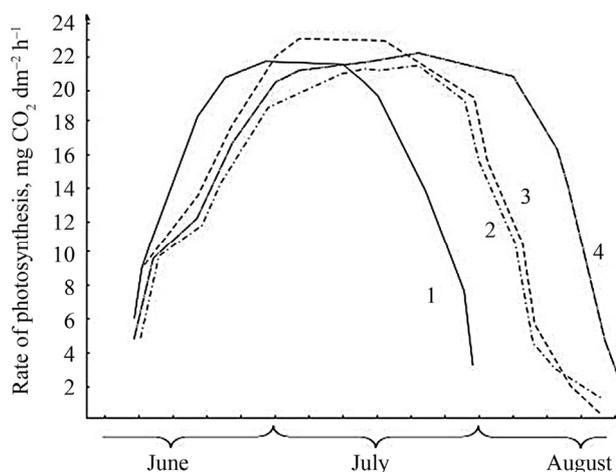


Figure 6. Ontogenetic changes in the photosynthesis rate of CO₂ assimilation in different soybean genotypes: 1: Volna; 2: VNIIMK-9; 3: VNIIMK-3895; 4: Plamyra.

Improving the growing conditions significantly contributes to enhance the photosynthetic activity of plants in the cultivated area. Herewith, the rate of photosynthesis increases by 30% - 50%.

Like most major agricultural crops related to C_3 -plants, soybean has active photorespiration that consumes the part of photosynthetic products.

Change in carbon dioxide gas exchange components, except dark respiration, occurs proportionally in all studied genotypes during ontogenesis (**Figure 7**). The maximum value of these components is observed in low productive varieties (Bistritsa, Volna) at 60th day of age, in high productive (VNIIMK-3895 and Komsomolka) and medium productive ones (Provar and VNIIMK-9) at 80th day of age, while in the Plamya—at 90th day of age.

The ratio of true photosynthesis and photorespiration in the leaf ontogenesis is considerably constant and constitutes on average 29% for low productive varieties, 35% for high and 28% for medium productive ones [27,30,37,38].

This suggests that about a third of the carbon assimilated in photosynthesis is being consumed during photorespiration.

The identical pattern of change in rates of true photosynthesis and photorespiration during the growing season

suggests the existence of a positive relationship between them.

Quantitative characteristics of carbon dioxide gas exchange components demonstrates that if we consider the true value of photosynthesis as 100%, then the average value of the net photosynthesis in low productive wheat plants will be 65%, photorespiration—29%, dark respiration—6%, in high productive—60%, 35%, 5%, and in medium productive ones—66%, 28% and 6%, respectively. The data showed that the main role in the process of CO_2 release in light belongs to photorespiration that is greater in high productive soybean genotypes in comparison with low productive ones.

On the basis of these results, we can conclude that the attempts to find or create high productive genotypes with high photosynthesis and low photorespiration rates have no future and it is appropriate in breeding programs to focus on genotypes that have higher rates of both photosynthesis and photorespiration.

The following parameters are suggested for the purposeful selection of high productive soybean genotypes: compact leaf shape, medium-sized leaves, which are located mainly in the middle layer, high rates of photosynthesis and photorespiration, high specific leaf density and longer period of pod formation-grain filling.

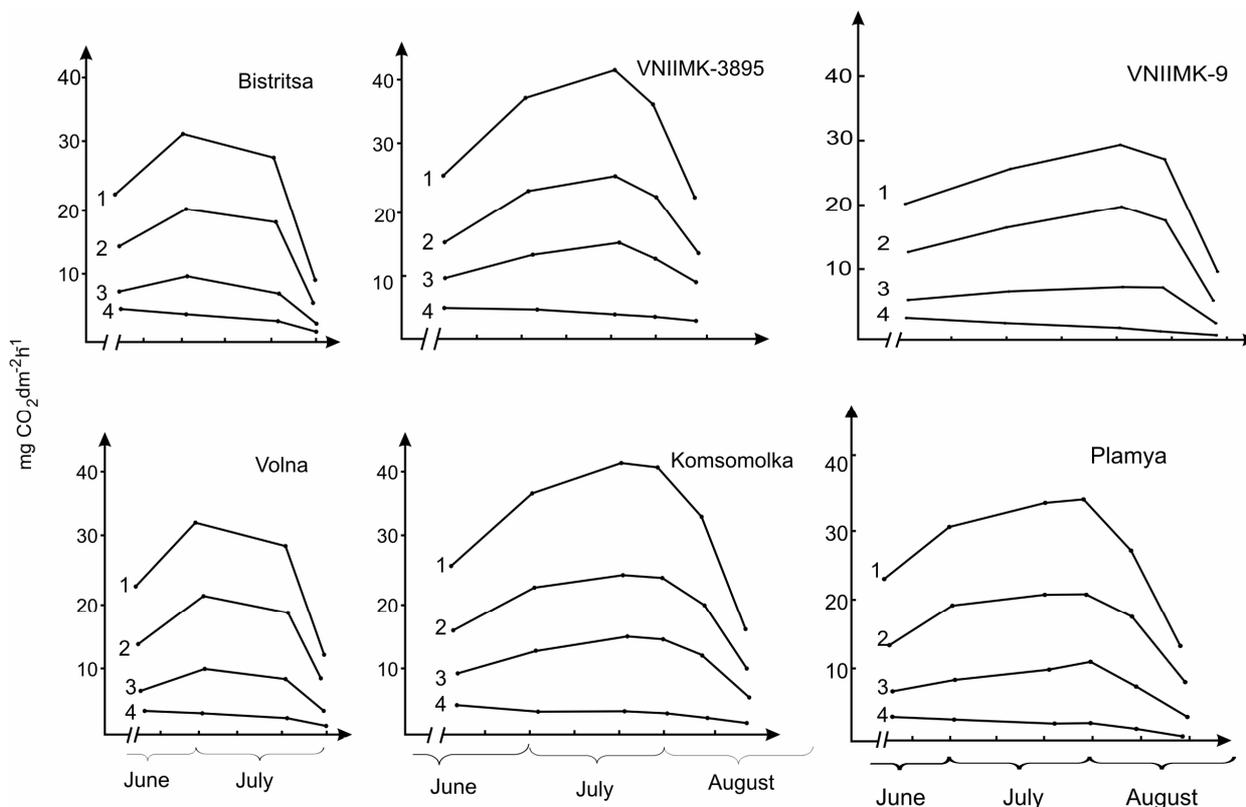


Figure 7. Components of CO_2 exchange in the leaves of the low productive (Bystritsa, Volna), high productive (VNIIMK-3895, Komsomolka) and medium productive (VNIIMK-9, Plamya) soybean genotypes: 1: Gross photosynthesis; 2: Net photosynthesis; 3: Photorespiration; 4: Dark respiration.

Thus, the high rates of photosynthesis and photorespiration in conjunction with the favorable photosynthetic traits, an optimum leaf area index and the best architectonics, define the high productivity of the soybean genotypes. Therefore, contrary to conception on the wastefulness of photorespiration, proposed in the many years by different authors, our comprehensive investigations on the different aspects of photorespiration indicate that photorespiration is one of the evolutionarily developed vital metabolic processes in plants. The attempts to reduce this process with the purpose of increasing the crop productivity are inconsistent [29,30,40-44].

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