

Demand for Assimilates Determines the Productivity of Intensive and Extensive Rice Crops in Primorskii Krai

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Abstract—Intensive and extensive rice crops (*Oryza sativa* L.), regionally cultivated in Primorskii krai (maritime territory), were grown under full and 50% attenuated solar radiation. Plants of different varieties were used to examine the supply of newly synthesized and reutilized ^{14}C -assimilates to caryopses and to estimate the dry weight dynamics of whole plants, vegetative organs, and grains. Cultivar-specific differences were revealed with respect to the sink capacity of caryopses, the export of photosynthates from the upper leaf and their delivery to the panicle, and the contributions of newly produced and reutilized assimilates to grain filling. In rice plants of all varieties grown under full insolation, the amount of photosynthates produced during grain filling was insufficient to satisfy the demand of caryopses; one-fourth or one-fifth of this demand was satisfied at the expense of mobilization of stored metabolites. The mobilization was accelerated by the elevated demand for assimilates and by attenuated insolation. In artificially shaded plants of intensive varieties, the pool of newly produced assimilates was lower and reutilization of previously gained assimilates started earlier than in shaded plants of extensive varieties. It is concluded that the higher grain yield of intensive rice varieties, cultivated in Primorskii krai, is determined by a higher demand for assimilates and by a higher production and accelerated supply of newly formed photosynthates to caryopses during the first half of the grain-filling stage. The potential productivity of these varieties is constrained by the deficit of assimilates during the second half of grain-filling stage. The low grain productivity of extensive varieties is caused by the insufficient number of grains in panicles and by low demand for assimilates throughout the period of grain filling.

Key words: *Oryza sativa* - shading - assimilates - reutilization - productivity

INTRODUCTION

In southern Far East Russia, with its monsoon weather type (considerable cloudiness, frequent and long rains), the amount of photosynthetically active radiation incident during the plant growth period is 15–20% lower than the rated amount for the same latitudes [1, 2]. Therefore, the study of the production and utilization of assimilates under low insolation is an important issue for the Far East region. The responses of crop plants to altered light conditions remain poorly examined and are less understood than similar responses of wild plant species [3].

Our previous works showed that a 50% reduction of solar radiation lowered the rice grain yield by 21–47%, elevated the number of seeds with imperfect plumpness, and prolonged the duration of growth period. Furthermore, the decrease in grain yield was greater for intensive varieties than for extensive varieties [4, 5]. Therefore, we proposed that the photosynthetic rate is insufficient to fully realize the potential productivity of intensive varieties and that the attenuated insolation

aggravates this insufficiency. There are grounds to believe that the intensive varieties experience a more severe deficit of newly produced photosynthates in comparison with extensive varieties. At the same time, it is known that the deficit of newly synthesized assimilates leads to reutilization of stored assimilates [6–8]. However, little is known about the combined action of an increased demand for assimilates and attenuated insolation on the production and utilization of photosynthates.

The aim of this study was to elucidate whether photosynthesis or assimilate demand determines the productivity of extensive and intensive rice varieties under low insolation typical of Primorskii krai. Therefore, we examined the delivery of newly synthesized and reutilized assimilates to the caryopses in rice plants with different source–sink relations after prolonged exposure of plants to spectrally neutral shading. The dynamics of dry matter of whole plants, vegetative organs, and seeds were also determined.

Abbreviation: DAF—days after flowering.

MATERIALS AND METHODS

The rice (*Oryza sativa*) varieties used in this study represented intensive (Primorets and Kasun), extensive (Dalnevostochnyi and Novoselskii), and semi-intensive (Dalris 11) crops regionally cultivated in Primorskii krai. Plants were grown on small plots at the experimental farm of the All-Russia Research Institute of Rice Crops (Primorskii Division). Prior to flooding the paddy fields, 330 normally developed plants were left per 1 m², which corresponds to an optimal density of rice stands in Primorskii krai [9]. The test group plants remained shaded from shoot emergence to seed ripening. A neutral material unaffacting light spectral quality was used for shading [3]. The control plants were grown unshaded. The total solar irradiance in August at midday was 0.61–0.97 kW/m² (depending on cloudiness). On sunny days, the irradiance at the upper leaf level of shaded plants was 2–2.5 times lower than for control plants. During hazy weather, the difference between the irradiances of the control and test plant groups was less pronounced. The air temperature under the screens was lower by 0.5–1°C than for control plants during daytime and was higher by the same extent during night-time. Thus, the shading was not accompanied by significant changes of daily average temperature and heat sums.

The partitioning of ¹⁴C-labeled assimilates between plant organs was studied in the Primorets intensive cultivar and Dalnevostochnyi extensive cultivar. The labeled substrate for photosynthesis was supplied simultaneously to the control and shaded plants. The flag leaves were exposed to ¹⁴CO₂, because they are the main source of assimilates in rice plants during the reproductive period [10]. The flag-leaf blade was placed for 20 min into a chamber, made of transparent polyethylene film, which contained a mixture of normal and radioactive carbon dioxide in the air. The carbon dioxide concentration in the chamber was 1%, and the radioactivity equaled 5.55 MBq. The exposure of leaves to ¹⁴CO₂ was performed at 9:00–11:00 a.m. on two dates: August 16 (the beginning of ripening) and August 28 (the stage of milky ripeness, considered provisionally as the middle of grain filling period). On August 16, we treated 12 control plants grown at full insolation (7 DAF) and 12 shaded plants (2 DAF). On August 28, we took 9 control plants (23 DAF) and 9 shaded plants (18 DAF). After certain periods, the separated organs were fixed in vapors of boiling water, dried to a constant weight at 70°C, weighed, and ground to a powder. Radioactivity was assayed according to Hein *et al.* [11] with a Delta-300 scintillation counter (Tracor Analytic, United States).

Data on the dynamics of dry matter in whole plants and organs refer to the area of 1 m² (one-third of a square meter for each of three replicates). Changes in plant dry weight were taken as a measure of photosynthesis, and changes in grain weight indicated the collective contribution of photosynthesis and assimilate reuti-

lization to the grain filling. Reutilization of assimilates was assessed from the dynamics of radioactivity in the stems and grain, as well as from the decline in the total weight of vegetative organs, without taking into account respiratory losses [12].

RESULTS

The dynamics of distribution of ¹⁴C-assimilates during the reproductive period of rice plants is shown in Fig. 1. The analysis of these data revealed different rates of photosynthate export from the source leaf and showed distinctions in assimilate storage and mobilization for grain filling in intensive and extensive rice crops at various levels of solar radiation. In the first half of the grain-filling period, under conditions of full insolation, the export of assimilates from the leaf and their delivery to the panicle started earlier and proceeded faster in intensive varieties than in extensive varieties. This view is in line with the higher level of ¹⁴C-assimilates (an approximately twofold increase) in the panicle of intensive varieties, as observed 1, 3, and 13 days after feeding the leaf with ¹⁴CO₂. We found that a considerable part of assimilates was stored in the stem during this period. The amount of assimilates stored in the stem was lower in intensive varieties than in extensive varieties, indicating the higher sink activity of panicle in intensive rice varieties. No assimilate storage in the stem was noted during the second half of grain-filling stage; i.e., almost all assimilates were directly transported to the panicle.

In plants screened from direct sunlight, the partitioning of labeled carbon in stems showed similar dynamics for both varieties. The storage of assimilates in the stem ceased earlier in shaded than in unshaded plants. The peak of assimilate partitioning to the stem and the beginning of assimilate mobilization were already detected 3 days after ¹⁴CO₂ feeding for shaded plants (13 days for unscreened plants). The earlier mobilization of reserves points to the deficit of newly formed photosynthates. Data presented in Fig. 2 and the table allowed us to estimate the contributions of newly formed and mobilized assimilates to grain filling under shading. As seen in Fig. 2, the increase in grain weight was almost always higher than in the vegetative plant organs. Although the plants retained all dead leaves until the end of the growing period, the weight of vegetative organs decreased. These observations and the data obtained with the use of ¹⁴CO₂ allow us to conclude that the biomass degradation in vegetative organs was caused by reutilization of stored photosynthates.

In full sunlight, we observed reutilization of photosynthates both in the early (7–18 DAF) and the late (19–35 DAF) halves of the grain-filling stage. However, the intensive and extensive varieties substantially differed in terms of the weight of reutilized products and reutilization dynamics. The largest early reutilization was characteristic of intensive varieties, whereas

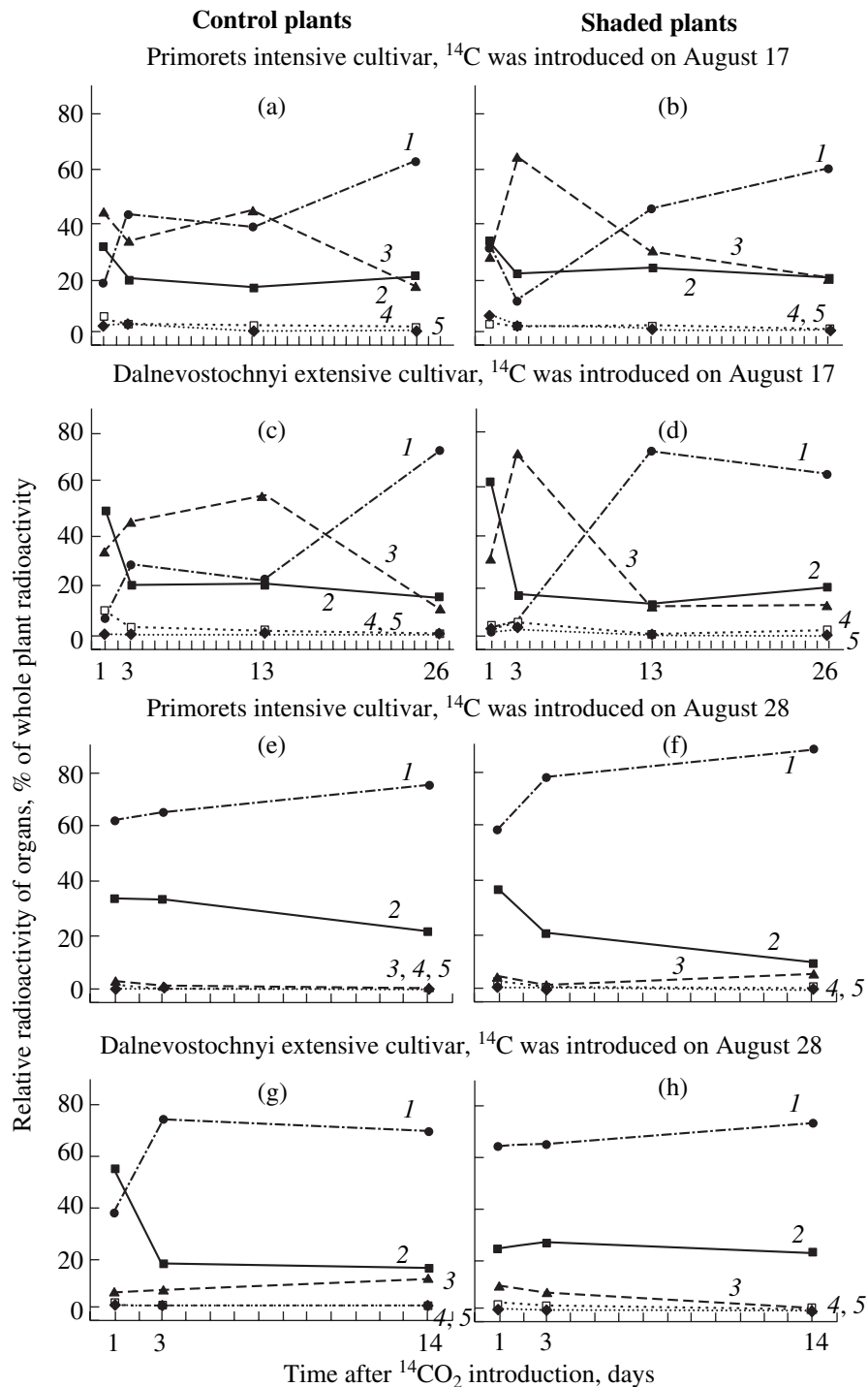


Fig. 1. Redistribution dynamics of ^{14}C -assimilates after feeding flag leaves with $^{14}\text{CO}_2$ at the onset of grain filling (August 17) and at the milky ripeness stage (August 28) in intensive and extensive rice crops grown (a, c, e, g) at full insolation and (b, d, f, h) under shading regime. The label content in organs is expressed as a percentage of whole plant radioactivity.

(1) Panicle; (2) flag-leaf blade; (3) stem; (4) flag-leaf sheath; (5) other leaves.

Data represent mean values of three replicates (individual plants), with five assays for each experiment.

the largest late reutilization was specific for extensive varieties. In shaded plants, the late reutilization stage was lacking in all varieties, and the total contribution of reutilized assimilates to grain formation during the

grain-filling stage was smaller than in plants grown at full insolation.

The calculations performed from data shown in Fig. 2 demonstrated that the relative contribution of

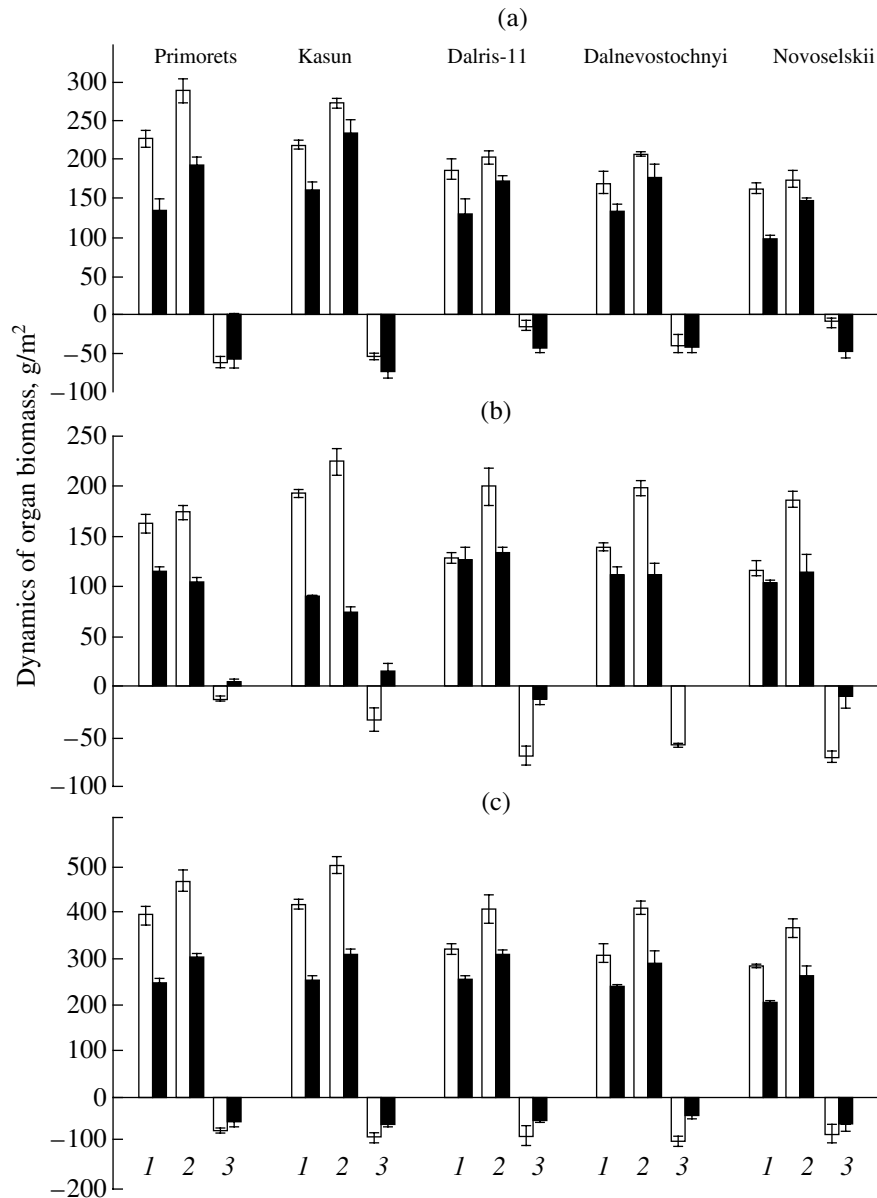


Fig. 2. Dynamics of dry weight of seeds and vegetative organs during (a) the first (7–18 DAF) and (b) second (19–35 DAF) parts of the grain-filling stage and (c) over the whole period of grain filling (17–35 DAF).

Empty columns—full insolation; solid columns—shading. (1) whole plants, (2) grain; (3) vegetative organs.

Data represent mean values and their standard errors of three replicates; each replicate was performed on 110 plants collected from the plot area of $1/3 \text{ m}^2$.

early reutilization into grain filling under full illumination in intensive genotypes and in the Dalnevostochnyi cultivar was about 20% of the final grain weight, whereas this contribution was approximately three times lower in other two varieties. The estimated contribution of reutilization for the whole period of grain filling was lower in intensive varieties (16–17%) than in extensive varieties (23–24%).

Under the influence of shading, the contribution of newly formed photosynthates and the total contribution of

metabolites to the grain yield (table) decreased in intensive varieties to a larger extent than in extensive varieties.

DISCUSSION

The results obtained in this study revealed cultivar-specific differences in terms of seed sink capacity, assimilate export from the leaf into the panicle, and the contribution of newly formed and reutilized assimilates to grain filling under different irradiances. The significance of similar differences for plant productivity at

Sources of assimilates and their contributions to grain biomass in shaded plants during the grain-filling period

Varieties	Photosynthesis		Reutilization		Total contribution	
	g/m ²	% of control plants	g/m ²	% of control plants	g/m ²	% of control plants
Primorets	146 ± 22	37	20 ± 13	27	166 ± 25	36
Kasun	163 ± 17	40	30 ± 10	34	193 ± 20	39
Dalris-11	62 ± 15	20	35 ± 22	41	97 ± 27	46
Dalnevostochnyi	63 ± 21	20	56 ± 14	58	119 ± 25	30
Novoselskii	80 ± 5	29	22 ± 22	27	102 ± 24	28

high insolation, exceeding the one in Primorskii krai, was discussed in the literature [13].

The data obtained with the use of ¹⁴C under conditions of full daylight irradiance showed that the ratio between the source capacity of the assimilatory apparatus and the sink potential of caryopses changed during the stage of grain filling. At the beginning of the grain-filling stage, the pool of newly synthesized assimilates exceeded the demand of seeds, but, in the second half of this stage, the pool became insufficient to meet the demand of seeds for assimilates. Data on partitioning of ¹⁴C do not provide an unambiguous answer to the question of whether the total pool of metabolites accumulated throughout the grain-filling stage is sufficient to meet seed demands. The results of the weighing should also be used to analyze the dynamics of stored photosynthate mobilization, plant biomass, and weights of individual organs.

Our data on reutilization of photosynthates under full irradiance are consistent with literature data [12–14]. We showed (Fig. 2) that the pool of fresh assimilates formed during the first half of the grain-filling stage was insufficient to meet the demand of caryopses for assimilates. This insufficiency is evidenced by early reutilization of assimilates. This early reutilization occurred in all cultivars, but it was particularly active in intensive cultivars. In the second half of grain-filling stage, the reutilization proceeded only in extensive cultivars due to the absence of reserve metabolites in intensive genotypes.

The enhancement of early reutilization and the lack of late reutilization in intensive cultivars is related to a large demand for assimilates. It is known that the assimilate demand affects the production of photosynthates, their export from leaves, and their partitioning between various sinks not only in rice plants [15], but also in other cultivated [14, 16] and wild [17] plants. The data obtained indicate the complexity of source–sink relationships.

The results of this study suggest that the large load imposed by sink organs on photosynthesis, which is characteristic of intensive rice cultivars, exerts both

positive and negative influences on the yield production. The positive influence of this load is due to the fact that it accelerates utilization of fresh and stored photosynthates, thereby providing conditions for export of newly synthesized products and for higher production of organic matter. The higher production of organic matter and accelerated delivery of assimilates to the caryopses promotes the increased grain productivity. The intensive cultivars accumulated a larger amount of organic matter during grain filling as compared to extensive cultivars, although the leaf indices were similar in both type cultivars [18]. This finding points to higher photosynthetic rates in intensive cultivars during the grain-filling period. This advantage of intensive cultivars, manifested only during grain filling and concealed during the vegetative development [13], can be explained by an accelerated utilization of assimilates in caryopses and by a higher frequency of chloroplasts per unit leaf area [18]. It is known that the number of plastids per unit leaf area determines the total internal surface available for CO₂ diffusion. The number of plastids is usually correlated with the photosynthetic rate [19–21]. The occurrence of well-filled ears in intensive cultivars is supposed to have a positive influence on photosynthesis during the reproductive development and on the functional longevity of upper leaves [13].

The negative influence of the excessive load on photosynthesis is caused by premature utilization of reserve metabolites. Our investigation showed that, under conditions of artificial shading, the total pool of assimilates decreased to a higher extent in the intensive cultivars than in extensive ones (table). In addition, the timing of photosynthate storage was delayed in shaded plants because of retarded plant development, but the pool of reserve metabolites was exhausted earlier than in control plants.

The results of this study clarify the mechanism of combined action on the productivity of the large demand for assimilates, which is typical of intensive cultivars, and the naturally attenuated insolation characteristic of Primorskii krai. The essence of this mechanism is that the large demand for assimilates accelerates

ates the reutilization of stored products, whereas reduced insolation lowers the amount of newly produced photosynthates and accelerates the reutilization of stored assimilates, thereby aggravating the metabolite deficit during the second half of the grain-filling stage.

This work demonstrated that the capacity of the photosynthetic apparatus in maritime rice cultivars—both intensive and extensive—is insufficient to meet the demands of developing seeds at the expense of assimilates produced during grain filling. In intensive cultivars, this demand is not completely met even at the expense of total (freshly formed and mobilized) metabolites. In the extensive cultivars, photosynthesis is not a limiting factor. The grain filling in intensive cultivars is constrained by assimilate deficiency, which is confirmed by a high frequency of fully ripened seeds with imperfect plumpness. The lack of such a limitation in extensive cultivars is evidenced by perfect seed plumpness [5].

The results obtained in this study allowed us to conclude that the higher grain yield in maritime intensive cultivars of rice is determined by a higher assimilate demand and by formation and accelerated import of newly synthesized photosynthates to the caryopses during the first half of the grain-filling stage. The potential productivity of these cultivars is constrained by the deficiency of assimilates during the second half of the grain-filling stage. In extensive cultivars, the low grain productivity is determined by insufficient potential productivity and by low demand for assimilates throughout the period of grain filling.

The discovered features of intensive and extensive cultivars are relevant to studies of source–sink relations and the production process. They can also be used by plant breeders for assessing the optimal grain number in panicles in newly bred rice cultivars.

REFERENCES

1. Efimova, N.A., Photosynthetically Active Radiation on the Territory of SSSR, *Fotosinteziruyushchie sistemy vysokoi produktivnosti* (Photosynthesizing Systems of High Productivity), Nichiporovich, A.A., Ed., Moscow: Nauka, 1966, pp. 70–77.
2. Aleshin, E.P. and Konokhova, V.P., *Kratkii spravochnik risovoda* (Concise Handbook for a Rice Grower), Moscow: Agropromizdat, 1986.
3. Tsel'niker, Yu.L., *Fiziologicheskie osnovy tenevynoslivosti drevesnykh rastenii* (Physiological Basics of the Plant Shade-Endurance), Moscow: Mosk. Gos. Univ., 1978.
4. Kholupenko, I.P., Zhemchugova, V.P., Sokirka, A.I., Chernoded, G.K., and Burundukova, O.L., The Effect of Shading on the Leaf Apparatus and Productivity of Rice Plants, *Fiziol. Biokhim. Kul't. Rast.*, 1991, vol. 23, pp. 23–29.
5. Kholupenko, I.P., Burundukova, O.L., Zhuravlev, Yu.N., Gorbach, V.M., Zhemchugova, V.P., and Voronkova, N.M., Shade-Endurance of Far-Eastern Varieties of Rice Plants, *Fiziol. Biokhim. Kul't. Rast.*, 1994, vol. 26, pp. 488–494.
6. Vorob'ev, N.V. and Skazhennik, M.A., Accumulation of Nonstructural Carbohydrates in Rice Shoots and Their Mobilization during Grain Formation, *Fiziol. Biokhim. Kul't. Rast.*, 1987, vol. 19, pp. 588–593.
7. Gladun, I.V. and Karpov, E.A., Production and Partitioning of Assimilates between the Panicle and Vegetative Organs of Rice after Flowering, *Fiziol. Rast. (Moscow)*, 1993, vol. 40, pp. 728–733 (*Russ. J. Plant Physiol.*, Engl. Transl.).
8. Kholupenko, I.P., Burundukova, O.L., Zhemchugova, V.P., Voronkova, N.M., and Chernoded, G.K., Source–Sink Relations in Far-Eastern Rice Cultivars as Related to Their Productivity, *Fiziol. Rast. (Moscow)*, 1996, vol. 43, pp.165–173 (*Russ. J. Plant Physiol.*, Engl. Transl.).
9. Krivolapov, I.E., *Ris na Dal'nevostoke* (Rice in the Far East), Vladivostok: Dal'nevost. Knizhn. Izd-vo, 1971.
10. Lizandr, A.A. and Brovtsyna, V.L., Physiological Role of the Rice Leaves in the Grain Formation and Maturation, *Fiziol. Rast. (Moscow)*, 1964, vol. 11, pp. 391–397 (*Sov. Plant Physiol.*, Engl. Transl.).
11. Hein, H.Ya., Tsel'niker, Yu.L., and Voznesenskii, V.L., Determination of the Radioactivity of Plant Material Using a Liquid Scintillation Counter, *Fiziol. Rast. (Moscow)*, 1984, vol. 31, pp. 401–408 (*Sov. Plant Physiol.*, Engl. Transl.).
12. Kumakov, V.A., Matveeva, N.F., Pavlova, S.S., Popova, V.M., Kotlyar, L.E., and Igoshin, A.P., The Role of Reutilization in the Grain Formation in Various Spring Wheat Cultivars, *Dokl. Vses. Akad. S-kh. Nauk im. V.I. Lenina*, 1979, no. 8, pp. 5–7.
13. Kumakov, V.A., *Fiziologicheskoe obosnovanie modelei sortov pshenitsy* (Physiological Basis for Wheat Cultivar Models), Moscow: Kolos, 1985.
14. Mokronosov, A.T., *Fotosinteticheskaya funktsiya i tselostnost' rastitel'nogo organizma, 42-e Timiryazevskoe chtenie* (Photosynthetic Function and Integrity of the Plant Organism, the 42nd Timiryazev Lecture), Moscow: Nauka, 1983.
15. Lafitte, H.R. and Travis, R.L., Photosynthesis and Assimilate Partitioning in Closely Related Lines of Rice Exhibiting Different Sink–Source Relationships, *Crop. Sci.*, 1984, vol. 24, pp. 447–452.
16. Kursanov, A.L., *Transport assimilyatov v rastenii*, Moscow: Nauka, 1976. Translated under the title *Assimilate Transport in Plants*, Amsterdam: Elsevier, 1984.
17. P'yankov, V.I., Yashkov, M.Yu., and Lamanov, A.A., Transport and Partitioning of Assimilates and the Structure of Source–Sink Relations in Wild Plant Species of the Middle Ural, *Fiziol. Rast. (Moscow)*, 1998, vol. 45, pp. 578–586 (*Russ. J. Plant Physiol.*, Engl. Transl.).
18. Burundukova, O.L., P'yankov, V.I., Zhuravlev, Yu.N., Kholupenko, I.P., and Gorbach, V.M., The Structure of the Assimilation Apparatus in Rice Cultivars of Extensive and Intensive Types under Primorie Conditions, *Tr. po prikladnoi botanike, genetike i seleksii Nauchn. Issl. Inst. Rastenievod.* (St. Petersburg), 1993, vol. 149, pp. 26–32.

19. Mokronosov, A.T., *Ontogeneticheskii aspekt fotosinteza* (Developmental Aspects of Photosynthesis), Moscow: Nauka, 1981.
20. Mokronosov, A.T., Mesostructure and Functional Activity of Photosynthetic Apparatus, *Mezostruktura i funktsional'naya aktivnost' fotosinteticheskogo apparata* (Mesostructure and Functional Activity of the Photosynthetic Apparatus), Mokronosov, A.T., Ed., Sverdlovsk: Ural Gos. Univ., 1978, pp. 5–30.
21. Araus, J.L., Alegre, L., Tapia, L., Calafell, R., and Serret, M.D., Relationships between Photosynthetic Capacity and Leaf Structure in Several Shade Plants, *Am. J. Bot.*, 1986, vol. 73, pp. 1760–1770.