

UDC 633.12:631.52:631.524.85:581.132

doi: 10.15389/agrobiol.2016.1.79rus

doi: 10.15389/agrobiol.2016.1.79eng

ADAPTIVENESS OF PRODUCTIVITY AND PHOTOSYNTHESIS IN BUCKWHEAT (*Fagopyrum esculentum* Moench) LANDRACES AND VARIETIES PRODUCED AT DIFFERENT PERIODS

A.V. AMELIN¹, A.N. FESENKO², E.I. CHEKALIN¹, V.V. ZAIKIN¹

¹Orel State Agrarian University, 69, ul. Generala Rodina, Orel, 302019 Russia, e-mail amelin_100@mail.ru, hmet83@rambler.ru, valeriy.zaikin@mail.ru;

²All-Russian Research Institute of Legumes and Groat Crops, Federal Agency of Scientific Organizations, 10, ul. Molodezhnaya, pos. Streletskii, Orel Region, Orel Province, 302502 Russia, e-mail: fesenko.a.n@rambler.ru

Acknowledgements:

The equipment of Center for Plant Genetic Resources and Usage of Orel State Agrarian University was used

Received October 1, 2015

doi: 10.15389/agrobiol.2016.1.79eng

Abstract

Crop breeding if aimed mainly at the highest productivity results in a significant loss of defense system activity thus causing a decreased plant resistance to adverse environment factors. Reasonably, more attention is now being paid to evolution base in breeding. With this, we studied the norm of reaction to environment changes in buckwheat (*Fagopyrum esculentum* Moench) cultivars and landraces as reflecting plant adaptation potential for photosynthesis and yield production to be further involved in breeding. A total of 11 buckwheat cultivars of which Kalininskaya, Bogatyr' and Shatilovskaya 5 have been derived in 1930–1970, and Chatyr-Tay, Batyr, Devyatka, Dizain, Demetra, Dikul' and Bashkirskeya krasnostebel'naya are the modern cultivars, together with landraces k-406 and k-1709 (VIR collection, St. Petersburg) were investigated. For the first time it was shown that in the course of buckwheat breeding no improvements in photosynthesis and production sustainability, as well as in homeostasis of grain formation have been achieved. Modern buckwheat cultivars possess high photosynthesis and productivity under favorable weather conditions, whereas at stresses do not have any significant advantage over their predecessors. In dry 2010 the seed production in modern cultivars was not reliably different from that in landraces and old cultivars, while in 2011–2013 at more favorable water supply and temperature it was on average 67.5 % higher, mostly due to the response of photosynthetic system to growing conditions. When drought occurred during the seed filling phase the photosynthetic activity in leaves decreased on average by 32.1 %, dry mass of the aboveground parts and seeds was lower by 46.7 % and 67.5 %, respectively, compared to those under favorable conditions in 2011–2013. With increasing water deficit the situation becomes worse. At soil moisture of 30 % of full capacity the activity of photosynthesis in buckwheat plant leaves was on average 4.4 times less, and seed production was 41.8 % less compared to the optimal moistening. At that, the losses were significantly higher in modern cultivars, e.g. in the k-1709 plants a 66.1 % decrease was found compared to 78.8 % in Dikul' and Dozhdik plants. Thus the obtained data suggests a low adaptive potential of modern buckwheat varieties. So we propose to improve the seed formation homeostasis in buckwheat plants. In this regard, the selection of autogamous form and the creation of self-pollinating varieties can be used as more effective approaches. The hybridization with *F. homotropicum* can significantly improve the viability of self-pollinated inbred lines of buckwheat, which can be successfully used in breeding programs to create autogamous varieties. Moreover, the adaptiveness of the of yield formation processes which are not sustainable enough to guarantee the high and sustainable crop production must be improved. An increased activity and effectiveness of photosynthesis and initial growth seem to be of interest. It is shown that the leaf photosynthetic rate in buckwheat varies plants varies widely from 4.65 to 17.8 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which allows to select forms both by hybridizing and using selection within a population.

Keywords: crop, buckwheat, selection, adaptation of variety, dry mass, photosynthesis, transpiration.

Over the past 50 years, the productivity of winter wheat, barley, buckwheat, soybeans, peas, broad beans and other crops has grown twice and more [1]. Undoubtedly, this is determined by the breeding process, since cultivar contributions in crop yields make over 50 % in many countries [2–5]. At the same time, the resistance to biotic and abiotic factors has been deteriorated considera-

bly [6-9]. According to the researchers, the latter is due to the fact that agriculture in general and breeding in particular aimed primarily at achieving maximum productivity weaken protective plant systems substantially and reduce their resistance to adverse conditions, consequently [10-13]. The effects of artificial and natural selection differs more and more distinctly, because the cultivar productivity and high yields (production efficiency) have been basic in crop breeding for a long time while the ability to survive (adaptability) is the determining feature of evolving species.

Therefore, the change of crop breeding priorities, in particular an objective to develop adaptive varieties based on evolutionary principles, is becoming increasingly urgent in recent years [10, 12, 14]. In Russia adaptive cultivars are needed due to contrasting local conditions exacerbated by global climate change and the increasing weather unpredictability [15-17].

This problem is relevant for buckwheat, the productivity of which remains low in Russia averaging 0.75 t/ha primarily due to lack of modern cultivar sustainable under extreme weather [18]. According to G.E. Martynenko et al. [19], average buckwheat cultivar productivity correlates negatively with their ecological plasticity ($r = -0.737$). Therefore, the further increase in the crop yield is planned to be achieved through the adaptive reconstruction of its genome [12] which requires a comprehensive research.

In connection with the problem of preserving and enhancing adaptive crop capacity, we for the first time studied the seed production process and the photosynthesis response under the extreme environment changes in pot and field experiments with buckwheat cultivars derived in various breeding periods.

The purpose of this study was to determine the adaptive potential of photosynthesis and seed yield in buckwheat plants with regard to breeding.

Technique. The research was performed in 2010-2013 (Orel region) in the following 13 buckwheat (*Fagopyrum esculentum* Moench) cultivars divided provisionally into three groups depending on the peculiarities and time of breeding: local cultivars (k-406, k-1709, VIR collection, Saint Petersburg) derived by breeders in the 1930-1970s (Kalininskaya, Bogatyr', and Shatilovskaya 5) and modern cultivars (Chatyr-Tay, Batyr, Devyatka, Dizain, Dozhdik, Demetra, Diku', and Bashkirskaya krasnostebel'naya).

Plants were grown in breeding crop rotation (All-Russia Research Institute of Legumes and Groat Crops). At the experimental plot the medium loamy gray forest soil predominated. For sowing in rows with a seeding rate of 3 million seeds/ha the SKS-6-10 seeding machine (Russia) was used. The plot area was 10 m² with a randomized seeding in 4 replicates. Sowing and harvesting were performed according to the regional guidelines. Pot experiments to study cultivar drought resistance were carried out in 6 replicates for each cultivar under controlled greenhouse conditions using special 10 dm³ vegetation pots with soil moisturized to 30 % and 45 % of total moisture capacity (MC) and plants grown at the soil moisture of 70 % MC as a control.

The amount of dry matter accumulated by plant leaves, stems, side branches, inflorescences and seeds was registered in different growth phases by sampling 10 plants of each cultivar from plots (3 replicates) followed by drying the samples at 105 °C in a SM 50/250-1000 ShS drying chamber (SM Klimat, Russia). Harvest index was calculated as a percent of the seed weight to the total plant dry weight.

The rates of photosynthesis (RP) and transpiration (RT) were estimated in intact plants in real time using a Li-COR-6400 portable gas analyzer (Li-COR Bioscience, USA) according to the attached manual.

The experimental data statistical processing was performed using Micro-

soft Excel.

Results. Weather during the study has been contrasting. The growing season of 2010 was characterized by high daytime temperatures and a pronounced shortage of rainfall, whereas in 2011 and 2013 it was more favorable for buckwheat as a heat-loving and moisture-loving crop.

1. Dry weight and efficacy of seed formation in 13 buckwheat (*Fagopyrum esculentum* Moench) cultivars studied for the years of experiments (breeding crop rotation, Orel region)

Parameter	2010	2011	2012	2013	On the average
Dry weight of aboveground parts at harvesting, g/plant:					
average for cultivars	3.22	5.18	6.89	6.04	5.33
range	2.51-4.18	3.91-6.21	6.47-6.88	4.65-7.10	4.57-5.90
Harvest index, %:					
average for cultivars	16.2	27.1	25.4	26.5	23.8
range	10.4-24.7	18.7-36.0	20.9-32.4	14.1-46.5	19.1-30.7

Note. Please refer to Methods section for cultivar description (local forms, modern cultivars and cultivars derived in 1970s)

Studies demonstrated that the dry matter accumulation in buckwheat plants averaged 6.04 g under moderate moisture and optimum air temperature (in 2011-2013), reaching 7.10 g when the weather was favorable (Table 1). But under the extreme conditions (the year of 2010) with high temperatures and moisture deficiency, total plant productivity declined not less than 1.9-fold. With this, the efficacy of assimilate use for seed formation dropped especially sharply. Thus, in 2010 the harvest index was 16.2 % being 1.6 times less than in the years of 2011-2013 which were more favorable in humidification and temperature (see Table 1).

As a result, plant seed productivity under the arid conditions in 2010 was very low averaging 0.52 g/plant, or 33 % of this value for 2011-2013 (Fig. 1). With this, seed weight decreased more significantly than the weight of vegetative organs. Under the pronounced lack of moisture and high temperatures, buckwheat seed productivity was 3.0 times lower, and the dry weight of vegetative organs was 1.9 times lower compared to the more favorable years. Seed productivity in buckwheat cultivars ranged from 0.33 to 0.87 g in 2010, from 0.73 to 2.43 g in 2011, from 1.32 to 2.20 g in 2012, and from 0.77 to 2.58 g in 2013.

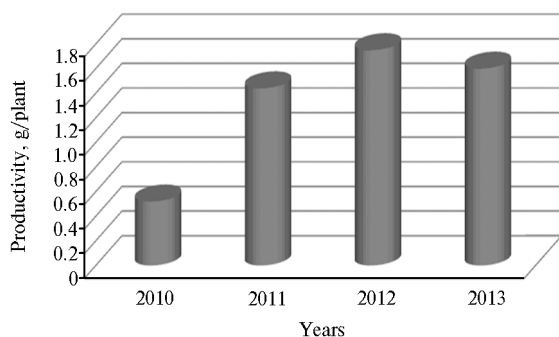


Fig. 1. Buckwheat (*Fagopyrum esculentum* Moench) seed productivity for the study years (averages for 13 cultivars of various breeding periods; breeding crop rotation, Orel region). Please refer to Methods section for cultivar description (local forms, modern cultivars and cultivars derived in 1930-1970s).

Differences between the aboveground organs for the dry matter accumulation may be due to the entomophilous pol-

lination and to the capability of maintaining high vegetative growth intensity almost throughout the growing season, including reproductive development. The last feature is typical for this crop that adversely affects seed formation [12, 18].

According to our data, in modern buckwheat cultivars, the number of seeds per plant varied almost 2 times greater than the weight of 1000 seeds, with 23.6 to 52.4 g for the first parameter, and 27.2 to 28.5 g in the second one, the later being within the experimental error. Due to such a high dependence of

seed formation on weather, the number of seeds formed per buckwheat plant in the dry year of 2010 was 51.5 % lower on average compared to 2011 and 2013, while their sizes were almost unchanged. The weight of 1000 seeds in 13 buckwheat cultivars studied averaged 28.5 ± 1.2 g in 2010, 27.2 ± 1.4 g in 2011, and 28.4 ± 1.3 g in 2013. In other words, seed yield is largely limited by the processes of seed formation. The low rate of fertile pollen under extreme weather, a characteristic feature of buckwheat as a cross-pollinated entomophilous crop, may be one of the reasons [20].

It should be noted that the stability of buckwheat seed formation is hardly increased via breeding [21], and the crop is widespread (from the Southern China subtropical areas to the northern border of agriculture lands), at the low physiological adaptations, mainly due to the population polymorphism in the growing period duration [22]. As a result, the species fertility is provided by long-term mass flowering at the very low seed formation efficacy, particularly only 10 % of flowers form seeds [18, 23].

In this regard, active work to improve seed formation productivity is held through the selection of the specified trait in cultivar populations [24, 25]. It is believed that the breeding of such type may be mostly efficient in hybrid populations involving buckwheat cultivars from the mountainous regions of India and Southeast Asia for which sharp fluctuations in weather conditions are typical [26]. Creation of self-pollinating buckwheat forms is another approach [27, 28]. It is assumed that creation of autogamous varieties would primarily reduce the buckwheat dependence on pollination by bees. Interest in the development of autogamous buckwheat increased sharply after the discovery of the wild self-pollinating *F. homotropicum* Ohnishi in the mountains of Southern China which is closely related to common buckwheat *F. esculentum* Moench [29]. As a result of successful crossbreeding, fertile interspecific hybrids have been reported in a number of laboratories, and their genetics is now being studied in detail [30-33]. A particular interest is due to the adaptive ability to regulate the time of seed formation in the wild type lacking in crop buckwheat that has been discovered by us [34]. The attempts to create self-pollinated common buckwheat cultivars based on this source material have not been successful so far mainly due to the difficulties of overcoming the inherent buckwheat inbreeding depression and poor adaptability of interspecific hybrids to temperate climate conditions [35]. However, this approach is very promising.

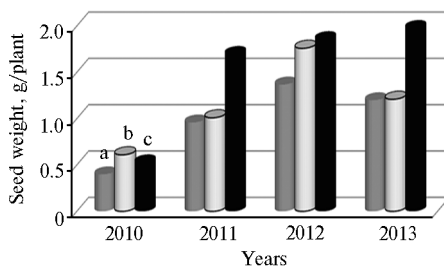


Fig. 2. Seed production in different buckwheat (*Fagopyrum esculentum* Moench) cultivars for the study years: a — local cultivars (k-406, k-1709, VIR collection, St. Petersburg); b — Kalininskaya, Bogatyr', and Shatilovskaya 5 cultivars (bred in 1930-1970s); c — modern cultivars Chatyr-Tay, Batyr, Devyatka, Dizain, Demetra, Dozhdik, Dikul', and Bashkirskaya krasnostebel'naya (breeding crop rotation, Orel region).

Apparently, more attention should be paid to the stable seed formation at the adverse weather factors to improve its efficiency in buckwheat, as this parameter tends to decrease. As a result, the dry weight variability of aerial plant parts (seeds especially) grows. During our study, the range of genotypic variability for seed weight per plant was 0.41-1.37 g in local populations, 0.61-1.76 g in old cultivars, and 0.53-1.85 g in modern cultivars. In the arid year of 2010, modern cultivars had almost no differences in seed production compared to the local and old ones, whereas this value was on average 67.5 % greater in the years of 2011-2013 with relatively favorable temperature

and water regime (Fig. 2).

In other words, modern buckwheat cultivars, like many other crops, have a pronounced advantage over their predecessors mainly in the favorable, but not in the extreme conditions. The weak development of the plant root system can also be considered a possible cause. According to results obtained by A. Lakhanov et al. [36], the proportion of roots formed in the total plant weight in buckwheat cultivars is significantly lower compared to the ancestral forms (*F. homotropicum* and *F. esculentum* ssp. *ancestrale*).

The low sustainability of reproduction in modern buckwheat cultivars may be caused by the high dependence of photosynthesis in plant leaves on the external factors which results in a dramatic reduction in yield under unfavorable conditions [37]. Photosynthetic crop productivity is known to depend significantly on the environmental factors such as temperature, light, moisture, and on the species and cultivar adaptive specificity [38-43]. This is clearly evidenced by our results. Thus, in the arid year of 2010 with a dry and hot weather almost throughout the whole growing season, the rate of photosynthesis in the leaves at seed filling was reduced by an average of 32.1 %, the dry weight of the aerial organs decreased by 46.7 %, and the seed weight was 67.5 % lower compared to the years of 2011-2013 (Fig. 3). The limits of RP genotypic variation (in $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were 4.65 to 10.80 in 2010; 9.81 to 14.38 in 2011; 14.74 to 17.8 in 2012, and 7.92 to 12.9 in 2013.

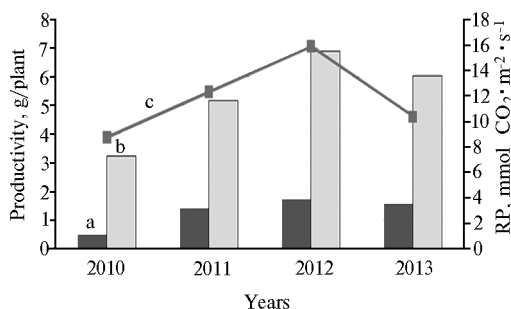


Fig. 3. Productivity and the rate of photosynthesis (RP) in leaves of 13 buckwheat (*Fagopyrum esculentum* Moench) cultivars: a, b — seed productivity and total aerial biomass, respectively; c — RP curve (blooming +10 days; breeding crop rotation, Orel region).

In acute drought, the situation is further getting worse. A model pot experiment demonstrated that at soil moisture of 30 % MC of the total moisture capacity the rate of photosynthesis in buckwheat leaves decreased 4.4 times on average, and seed yield was 41.8 % lower as compared to those obtained at optimal moistening. At the same time, a significant reduction in both parameters was primarily observed in modern varieties. While in k-1709 local cultivar the rate of photosynthesis decreased by 66.1 %, in Dikul' and Dozhdik cultivars the reduction averaged 78.8 % (Table 2).

2. Photosynthesis (RP) and transpiration (RT) rates in buckwheat (*Fagopyrum esculentum* Moench) leaves of different cultivars depending on soil moisture (pot experiment, 2013, blooming +30 days)

Cultivar	RP, $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$		RT, $\text{mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$		Leaf temperature, °C	
	control	experiment	control	experiment	control	experiment
k-1709 (local form)	6.22	2.11	2.80	0.96	20.2	21.3
Bogatyř' (cultivar of the group derived in 1930-1970s)	6.51	1.03	2.64	0.55	24.2	25.1
Dikul' (modern cultivar)	6.70	1.73	3.26	0.66	25.0	25.5
Dozhdik (modern cultivar)	8.23	1.37	2.81	0.65	22.2	23.7
Average	6.92	1.56	2.88	0.71	22.9	23.9
HCP ₀₅	1.69	1.47	1.12	0.52	0.23	0.22

Note. Control — 70 % of the total moisture capacity (MC), experiment — 30 % MC.

In our opinion, these differences may be due to an increased capacity of local cultivars for transpiration which provides appropriate leaf tempera-

ture and an increased uptake of water from the soil under the water deficit. A relatively high positive correlation between the rates of photosynthesis and transpiration ($r = 0.68$; $P_0 < 0,05$) was observed in all buckwheat samples during the study.

In our experiments, the activity of gas exchange in buckwheat leaves varied significantly within cultivar populations as well. Thus, the analysis of 159 Dikul' cultivar plants demonstrated the RP range in the leaves of 0.2 to 14.8 $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Thus, the rate of photosynthesis was from 12.0 to 14.5 $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in 15 %, from 9.0 to 12.0 in 26%, from 3.0 to 9.0 in 41 %, and from 0.2 to 3.0 $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in 18 % of the examined plants. The findings provide a conclusion of a targeted buckwheat breeding for the rate of photosynthesis not only by hybridization, but also by a massive selection in a particular cultivar population, which will level the plants in their ability to provide assimilates for themselves thus increasing the total population productivity.

Thus, the analysis of the crop adaptability problem shows that resistance to adverse environmental factors in modern cultivars has decreased significantly as a result of breeding aimed primarily at providing the maximum productivity [10-13]. Creation of self-pollinating cultivars based on autogamous forms may be the solution. Difficulties associated with the emerging inbreeding depression that accompanies any attempt to obtain cross pollination based autogamous material are almost inevitable but can be overcome as shown by our experiments. Hybridization with *F. homotropicum* can significantly improve the viability of self-pollinated inbred crop buckwheat lines [34, 35]. Another approach is to increase ecological plasticity and stability of the reproduction to ensure high and stable yields. In this, breeding for increased activity and efficacy of photosynthesis remains a reserve [44, 45].

So we are the first to demonstrate no significant increase in the stability and adaptability of photosynthesis, seed production and seed formation as a result of buckwheat breeding. In our experiments, the rate of photosynthesis and dry matter accumulation, as well as the efficient use of assimilates for seed formation under the dry conditions were on average 38.4 % lower compared to those in the years that were favorable for moisture conditions and temperature. Modern cultivars demonstrated high rates of photosynthesis and formed high productivity under the favorable conditions only, but under stress had no advantages compared to cultivars derived in earlier breeding periods and to local forms. The leaf photosynthetic rate in buckwheat plants was found to be a widely varying genotypic trait (from 4.65 to 17.80 $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), which makes it possible to select the forms for this parameter both by hybridizing and using mass selection within an individual cultivar population.

REFERENCES

1. Zhuchenko A.A. *Resursnyi potentsial proizvodstva zerna v Rossii* [Resources for grain production in Russia]. Moscow, 2004.
2. Jain H.K. Eighty years of post Mendelian breeding for crop yield: nature of selection pressures and future potential. *Indian J. Genet. Plant Breed.*, 1986, 1: 30-53.
3. Richards R.A. Selectable traits to increase crop photosynthesis and yield of grain crops. *J. Exp. Bot.*, 2000, 51: 447-458 (doi: 10.1093/jexbot/51.suppl_1.447).
4. *Razvitiye innovatsionnoi deyatel'nosti v rastenievodstve* /Pod redaktsiei V.I. Nechaeva [Innovations in crop production. V.I. Necharv (ed.)]. Moscow, 2010.
5. Sandukhadze B.I., Kochetygov G.V., Rybakova M.I., Bugrova V.V. *Vestnik OrelGAU*, 2012, 3: 4-8.
6. Molchan I.M., Il'ina L.G., Kubarev P.I. *Selektsiya i semenovodstvo*, 1996, 1-2: 36-51.
7. Fernandez-Martinez J.M., Dominguez J., Perez-Vich B., Velasco L. Update on breeding for resistance to sunflower broomrape. *Helia*, 2008, 31: 73-84 (doi: 10.2298/HEL0848073F).

8. Fernandez-Escobar J., Rodriguez-Ojeda M.I., Flonso L.C. Distribution and dissemination of sunflower broomrape (*Orobanche cumana* Wallr.) race F in Southern Spain. In: *Proc. 17th Int. Sunfl. Conf. Cordoba*, Spain, 2008: 231-236.
9. Amelin A.V. *Vestnik OrelGAU*, 2012, 3: 10-15.
10. Shevelukha V.S. *Vestnik RASKHN*, 1993, 4: 16-21.
11. Amelin A.V. *Seleksiya i semenovodstvo*, 1999, 2: 15-21.
12. Fesenko N.V., Fesenko N.N., Romanova O.I. et al. *Teoreticheskie osnovy selektsii. Tom 5. Genofond i seleksiya krupyanykh kul'tur. Grechikha* /Pod redaktsiei V.A. Dragavtseva [Theoretical bases for breeding. V. 5. Gene pool and breeding cereals. Buckwheat. V.A. Dragavtsev (ed.)]. St. Petersburg, 2006.
13. Strel'nikov E.A., Antonova T.S. *Materialy shkoly molodykh uchenykh «Ekologicheskaya genetika kul'turnykh rastenii» (Krasnodar, 24-26 sentyabrya 2014 goda)* [Proc. Meeting of young scientists «Ecological genetics of cultivated plants», Krasnodar, September 24-26, 2014]. Krasnodar, 2014: 122-133.
14. Zhuchenko A.A. *Materialy Vserossiiskoi nauchno-proizvodstvennoi konferentsii «Introduktsiya netraditsionnykh i redkikh sel'skokhozyaystvennykh rastenii» (24-28 iyunya 1998 goda)* [Proc. All-Russia Conf. «Introduction of unconventional and rare agricultural plants», June 24-28, 1998. V. 1]. Penza, 1998, t. 1: 7-25.
15. Goncharenko A.A. *Materialy Vserossiiskoi nauchno-prakticheskoi konferentsii «Puti povysheniya ustoichivosti sel'skokhozyaystvennogo proizvodstva v sovremennykh usloviyakh» (13-15 iyulya 2005 goda)* [Proc. All-Russia Conf. «The current ways to improve sustainability in the agriculture», July 13-15, 2005]. Orel, 2005: 46-56.
16. Grabovets A.I., Fomenko M.A. *Zernobobovye i krupyanye kul'tury*, 2013, 6(2): 41-47.
17. Parakhin N.V., Amelin A.V. *Vestnik OrelGAU*, 2014, 5(50): 92-102.
18. Daai Z., Jinfeng G., Yiping Q., Cui L., Qinqin L., Pengke W., Xiaoli G., Baili F., Pu Y., Yan C. Preliminary study on fecundity of common buckwheat under controlled conditions. *Proc. 12th Int. Symp. on buckwheat (August 21-25, 2013)*. Slovenia, Laško, 2013: 172-174.
19. Martynenko G.E., Shipulin O.A., Fesenko A.N., Biryukova O.V. V sbornike: *Novye sorta sel'skokhozyaystvennykh kul'tur — sostavnaya chast' innovatsionnykh tekhnologii v rastenievodstve (nauchnye materialy Shatilovskikh chtenii, posvyashchennykh 115-letiyu Shatilovskoi SKHOS, 12-13 iyulya 2011 goda)* [In: New varieties as a part of innovations in crop production (materials of meeting devoted to 115 anniversary of Shatilovskaya experimental station, July 12-13, 2011)]. Orel, 2011: 165-173.
20. Zeller F.J. Buchweizen (*Fagopyrum esculentum* Moench): Nutzung, Genetik, Zuchtung. *Bodenkultur*, 2001, 3(52): 259-276.
21. Fesenko A.N., Biryukova O.V., Shipulin O.A., Fesenko I.N. *Zemledelie*, 2014, 4: 43-45.
22. Demidenko N., Logacheva M., Penin A. Comparison of abiotic stress response systems between *Arabidopsis thaliana* and *Fagopyrum esculentum*. *Proc. 12th Int. Symp. on buckwheat (August 21-25, 2013)*. Slovenia, Laško, 2013: 72-73
23. Kadirova L., Sitnykov A. Reproductive biology of buckwheat. *Proc. 11th Int. Symp. on buckwheat (July 19-23, 2010)*. Orel, 2010: 331-339.
24. Inoue N., Hagiwara M. Relationship between the harvest index and duration of each developmental stage of shoot apex in common buckwheat. *Fagopyrum*, 2000, 17: 51-56.
25. Inoue N., Kumagai H., Hagiwara M. Improvement of fertilization rate by mass selection in common buckwheat. *Fagopyrum*, 2002, 19: 49-53.
26. Naseem M., Dutta M., Shah S., Kumar P. Assessment of agro-morphological, physiological and genetic diversity among buckwheat cultivars. *Proc. 11th Int. Symp. on buckwheat (July 19-23, 2010)*. Orel, 2010: 94-101.
27. Campbell C.G. Present state and future prospects for buckwheat. *Proc. 9th Int. Symp. on buckwheat (August 18-22, 2004)*. Czech Republic, Prague, 2004: 26-29.
28. Woo S.H., Suzuki T., Mukasa Y., Morishita T., Yun Y.H., Park C.H. Present status, future breeding strategy and prospects for buckwheat. *Proc. 12th Int. Symp. on buckwheat (August 21-25, 2013)*. Slovenia, Laško, 2013: 25-26.
29. Ohnishi O. Distribution and classification of wild buckwheat species. 1. *Cymosum* group. *Fagopyrum*, 2010, 27: 1-8.
30. Campbell C.G. Buckwheat crop improvement. *Fagopyrum*, 2003, 20: 1-6.
31. Fesenko N.N., Fesenko I.N., Ohnishi O. Homostyly of two morphologically different lineages of *Fagopyrum homotropicum* Ohnishi is determined by locus S4, which is an S-locus related gene in the linkage group. *Fagopyrum*, 2006, 23: 11-15.
32. Fesenko I.N., Fesenko A.N. Genetic basis of interspecific diversity of floral display size between cultivated outcrosser *Fagopyrum esculentum* Moench and wild selfer *F. homotropicum* Ohnishi. *Fagopyrum*, 2011, 28: 17-21.
33. Woo S.H., Kim S.H., Tsai K.S., Chung K.Y., Jong S.K., Adachi Taiji, Choi J.S.

- Pollen-tube behavior and embryo development in interspecific crosses among the genus *Fagopyrum*. *J. Plant Biol.*, 2008, 52: 302-310.
34. Fesenko A.N., Fesenko I.N. *Vestnik OrelGAU*, 2013, 2(41): 2-5.
 35. Chrungoo N.K., Kreft I., Sangma S.C., Devadasan N., Dohtdong L., Chetri U. Genetic diversity in himalayan buckwheats: a perspective for use in crop improvement programmes. *Proc. 12th Int. Symp. on buckwheat (August 21-25, 2013)*. Slovenia, Laško, 2013: 198-211.
 36. Lakhanov A., Napolova G., Napolov V., Kolomeychenko V. System of donor-acceptor relations between organs of buckwheat plants. *Proc. 11th Int. Symp. on buckwheat (July 19-23, 2010)*. Orel, 2010: 241-245.
 37. Kasajima S., Itoh H. Effect of shading during different growth phases on yield parameters of common buckwheat cv. Kitawasesoba in the northern region of Japan. *Fagopyrum*, 2011, 28: 43-46.
 38. Thompson L. Weather variability, climatic change and grain production. *Crop. Sci.*, 1975, 41: 535-541 (doi: 10.1126/science.188.4188.535).
 39. Tarchevskii I.A. V sbornike: *Fiziologiya fotosinteza* [In: Physiology of photosynthesis]. Moscow, 1982: 118-129.
 40. Kraft S.E., Dharmadhikari P. Variation in the relationship between corn yield and climate in a sample of counties in Illinois 1951-1980. *Transactions of the Illinois State Academy of Science*, 1984, 3-4: 219-228.
 41. Mirakilov Kh.M., Abdullaev Kh.A., Karimov Kh.Kh. *Izvestiya Akademii nauk Respubliki Tadjikistan. Otdelenie biologicheskikh i meditsinskikh nauk*, 2009, 1(166): 49-61.
 42. Monteith J.L., Moss C.J. Climate and efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 1977, 281: 277-294 (doi: 10.1098/rstb.1977.0140).
 43. Slattery R.A., Ort D.R. Photosynthetic energy conversion efficiency: setting a baseline for gauging future improvements in important food and biofuel crops. *Plant Physiol.*, 2015, 168: 383-392 (doi: 10.1104/pp.15.00066).
 44. Nichiporovich A.A. *Energeticheskaya effektivnost' fotosinteza i produktivnost' rastenii* [The energy efficiency of photosynthesis and plant productivity]. Pushchino, 1979.
 45. Zhu X.-G., Long S.P., Ort D.R. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Curr. Opin. Biotechnol.*, 2008, 19: 1-7 (doi: 10.1016/j.copbio.2008.02.004).