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Maintenance of inflorescence size variability within common buckwheat (*Fagopyrum esculentum* Moench) cultivars of various origin: the phenomenon and its possible causes

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Background. Intrapopulation polymorphism usually can be interpreted as a result of balancing selection, but the basic mechanisms of such selection are not always clear. Earlier we documented a wide variation in the inflorescence size within one of the most genetically uniform common buckwheat (*Fagopyrum esculentum* Moench) cultivar 'Skorospelaya 86', with larger sizes controlled by recessive alleles of multiple genes. The objective of the present work was to analyze the variation within a set of buckwheat cultivars representing different morphological types of the crop, and try to make out possible mechanisms that underlie it.

Material and methods. A set of buckwheat cultivars of various origin and belonging to different morphological types were analyzed. The size of inflorescences was assessed as a number of their iterative subunits, i.e., partial floret clusters (PFCs). The number of mature seeds in the entire inflorescence and various PFCs was also counted.

Results and conclusions. All the cultivars were variable, with the range at the species level from 6 to 24 PFCs. Accumulation of the genes determining a larger inflorescence seems to be simply explained: larger inflorescences tended to produce more seeds than smaller ones. However, it is not so easy to explain the maintenance of the inflorescence size variability, i.e., why the alleles determining small inflorescences were not lost during the artificial selection for higher seed productivity. Probably, such polymorphism may be useful for maintaining heterosis at the population level.

Keywords: morphological type, partial floret cluster, variability, balancing selection

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ГЕНЕТИКА КУЛЬТУРНЫХ РАСТЕНИЙ И ИХ ДИКИХ РОДИЧЕЙ

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Поддержание изменчивости по размеру соцветия у сортов гречихи обыкновенной (*Fagopyrum esculentum* Moench) различного происхождения: явление и его возможные причины

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Актуальность. Внутрипопуляционный полиморфизм обычно можно интерпретировать как результат балансирующего отбора, но механизмы, лежащие в основе такого отбора, не всегда ясны. Для гречихи обыкновенной характерен широкий полиморфизм по размеру соцветия, который был обнаружен даже у одного из наиболее генетически однородных сортов ‘Скороспелая 86’. Крупное соцветие контролируется рецессивными аллелями множества генов, то есть это вторичный признак, возникший, по-видимому, в результате окультуривания. Аллели, определяющие более мелкие соцветия, тоже поддерживаются в сортовых популяциях. Целью настоящей работы было проанализировать изменчивость в пределах сортов гречихи, представляющих разные морфологические типы культуры, и попытаться выяснить возможные механизмы, лежащие в ее основе.

Материалы и методы. Проанализирован ряд сортов гречихи разного происхождения и разных морфологических типов. Размер соцветия оценивали как количество его повторяющихся субъединиц, то есть элементарных соцветий (ЭлС). Также подсчитывали количество зрелых семян во всем соцветии и различных ЭлС.

Результаты и заключение. Все сорта были полиморфны по анализируемому признаку. Диапазон изменчивости на видовом уровне составил от 6 до 24 ЭлС. Накопление генов, определяющих более крупные соцветия, объясняется просто: более крупные соцветия имеют тенденцию формировать больше семян. Однако трудно объяснить сохранение изменчивости по размеру соцветия, то есть почему аллели, определяющие маленькое соцветие, не были утрачены в ходе искусственного отбора на более высокую семенную продуктивность. Вероятно, такой полиморфизм может быть полезен для поддержания гетерозиса на популяционном уровне.

Ключевые слова: морфологический тип, элементарное соцветие, изменчивость, балансирующий отбор

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Introduction

Maintaining polymorphism within populations for non-neutral traits reveals some mechanisms of the balancing selection whose nature is usually a fundamental question in evolutionary biology (Delph, Kelly, 2014; Gulisija, Kim, 2015). Within-population polymorphism in cultivated species represents a special issue, as it is likely to contribute to their yieldability, but contradicts typical trends toward reduction in the genetic diversity of cultivated plants, i.e., genetic erosion provoked by selecting variants most suitable for agriculture (Dyer et al., 2014; Fu, 2015). Understanding the mechanisms of diversity maintenance could improve breeding approaches to cultivated species.

Common buckwheat (*Fagopyrum esculentum* Moench) is a species with functional dimorphic heterostyly providing obligate insect-mediated cross-pollination (Fesenko, 1983). All buckwheat cultivars are characterized by prolonged plentiful flowering. White or slightly pink flowers of 8–10 mm in diameter are united in partial floret clusters, or partial inflorescences; they are subunits of sufficiently long inflorescences developing in leaves axils. The cultivars grown in Russia over the past century showed a significant increase in the average weight of a thousand seeds (M_{1000}): from 18–22 g to 25–30 g, sometimes up to more than 30 g (large-grain cultivars). Cultivars with the largest grain are characterized by a slight decrease in the number of inflorescences on the shoots, which is regarded as the physiological determination of growth (Fesenko et al., 2018). Nevertheless, all contemporary buckwheat cultivars have retained the proneness to prolonged flowering. A buckwheat flower lives for one day, and then it either dies off or forms a single seed within three weeks. Only 10.5–18.7% of flowers set seeds. Seed filling is highly sensitive to environmental stressors, and usually only 57.8–68.0% of young seeds complete their development (Fesenko et al., 2018). This phenomenon may be explained by prolonged overlapping in the development of vegetative and generative structures of buckwheat plants (Fesenko, 1983).

Buckwheat domestication and breeding were accompanied by an increase in the size of inflorescences, i.e., the number of partial floret clusters (PFCs) in the inflorescence, due to the accumulation of recessive plus-alleles of multiple genes, which factually means mutations with a minor effect, increasing the quantitative characteristics of the trait (Fesenko I.N., Fesenko A.N., 2011). In addition, in cultivar populations, unlike closely related wild species, a broad polymorphism in the number of PFCs in inflorescences was documented (Fig. 1). For example, plants of *F. esculentum* cv. 'Skorospelaya 86', which was included in the experiment on the genetic analysis of the size of inflorescences, formed from 9 to 22 PFCs in the inflorescence; the C9139 line of the wild autogamous species *F. homotropicum* Ohnishi, participating in the same experiment, was characterized by very small polymorphism for this trait (7–10 PFCs) (Fesenko I.N., Fesenko A.N., 2011). *F. esculentum* and *F. homotropicum* are closely related, and in their interspecific hybrids some traits with single-gene control segregate in Mendelean manner (Fesenko N.N., Fesenko I.N., 2015). It should be noted that cv. 'Skorospelaya 86', according to the metameric structure of the branching zone (i.e., the number of vegetative nodes) on the main stem and branches, looked like an almost homozygous line (Fesenko I.N., Fesenko A.N., 2011).

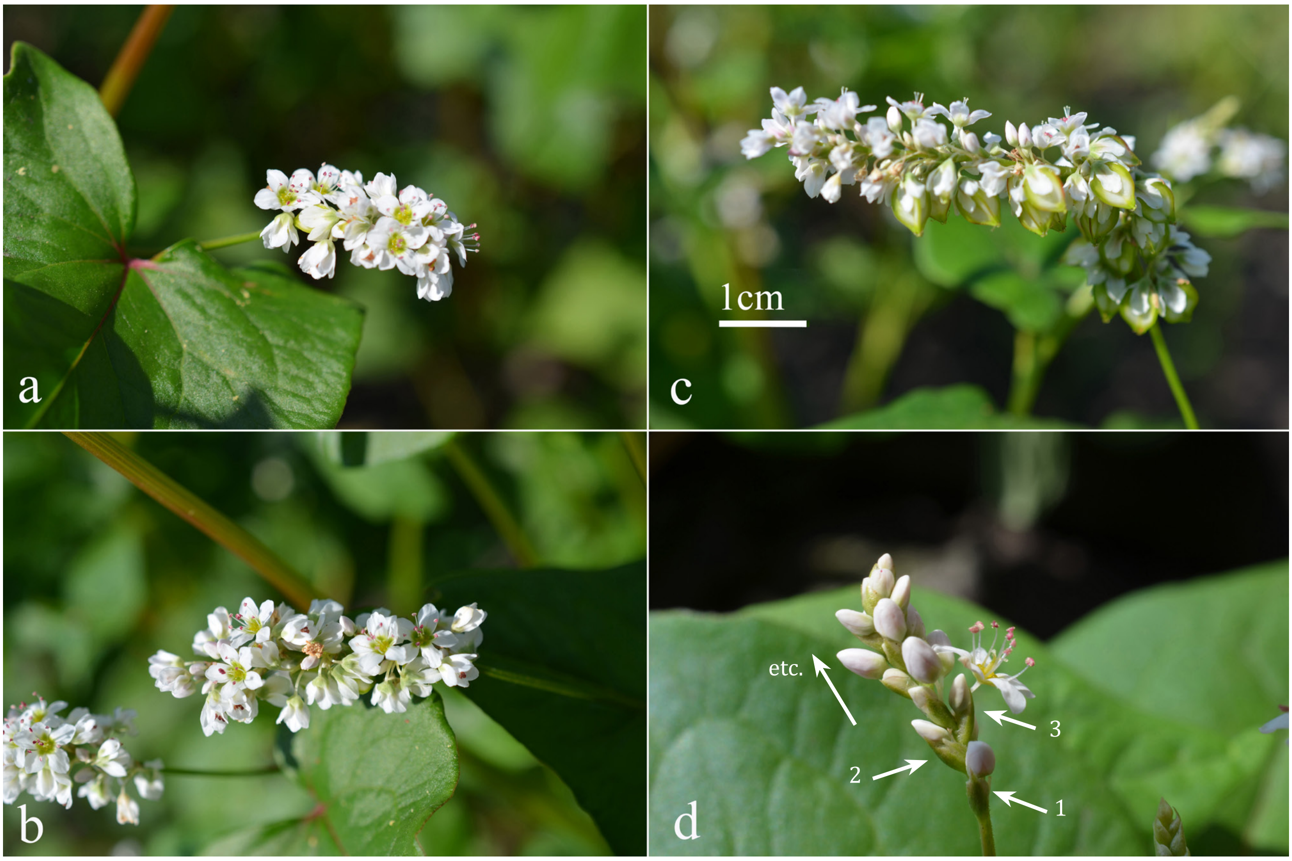

Figure. Common buckwheat inflorescences: a – small; **b** – medium; **c** – large (scale bar only for a, b, and c); **d** – the numbering order of partial floret clusters in an inflorescence of buckwheat

Рисунок. Соцветия гречихи обыкновенной: a – мелкое; **b** – среднее; **c** – крупное (масштаб только для a, b и c); **d** – порядок нумерации элементарных соцветий в соцветии гречихи

Common buckwheat breeding successfully used several forms that were morphologically (and physiologically) different from the originally domesticated populations (“traditional” type), characterized by the indeterminate type of growth and shoots terminating with “umbels”. Contemporary cultivars are sufficiently diverse, each belonging to one of four types, including the “traditional” one (Fesenko et al., 2018). One of them includes plant forms with the determinate growth habit, i.e., restricting the development of the generative zone of shoots to 2–5 inflorescences, without a possibility of forming additional inflorescences: the shoot ends in a lateral-like inflorescence. The second morphological type is characterized by physiological limitation of the generative zone growth (earlier cessation of the development of the generative zone, but without clear terminating, in terms of morphology). The third morphological type manifests limited secondary branching, when 0 to 1 vegetative nodes are formed on the upper branch, instead of two vegetative nodes in other types of cultivars (Fesenko et al., 2018).

We analyzed several groups of buckwheat cultivars, representing all the main morphological types, i.e., obtained using very different materials and different breeding approaches. Despite some differences among the groups of cultivars in their variation ranges, they manifest high levels of polymorphism in the inflorescence size within each of them. Plants with the largest inflorescences are found within the group of determinant cultivars. It has been shown that within one and the same group of cultivars, larger inflorescences, on average, usually produce more seeds, but these additional seeds in most cases are formed in PFCs located closer to the base of the inflorescence, but not in additional PFCs. The objective of the article was to describe and discuss the results of studying this phenomenon.

Materials and methods

Abbreviations and brief characteristics of the morphological types (Fesenko et al., 2018)

IGH – indeterminate growth habit. The cultivars of this type demonstrate potentially unlimited development of shoots. Morphologically, they are similar to buckwheat landraces from Orel Province.

KS – an unusual type of cultivars, named after cv. ‘Krasnostreletskiy’, the first cultivar of such type. Main characteristics of these cultivars are large seed size and physiological determination of growth, i.e., earlier cessation of the generative zone development, but without clear mutation-derived changes in morphology.

LSB – limited secondary branching. The LSB-type plants are characterized by reduced numbers of vegetative nodes on upper branches (0–1, instead of 2–3 in non-LSB plants). Commercial cultivars of the LSB type include a significant share of such plants, usually more than 25%.

DGH – determinate growth habit. DGH-type cultivars have reduced numbers of inflorescences on all shoots (2–5 inflorescences vs. potentially unlimited shoot development in the IGH type). The trait is determined by the recessive mutation *d* (*det*) (Fesenko, 1983).

Plant material

Plant materials are shown in Table 1.

Seeds of all improved cultivars used in the experiment (except for the cultivars developed at the Federal Scientific Center of Legumes and Groat Crops, previously All-Russian Research Institute of Grain Legumes and Groat Crops) were supplied from the collection of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources, St. Petersburg, Russia.

Experimental approaches

The material for analyses was collected from plots for variety testing, 10 m^2 each. Sowing dates were as follows: May 22 in 2017, May 21 in 2018, and May 22 in 2019. The sowing rate was 300 seeds/m^2. Plants for analyses were selected randomly.

Since any plant consists of iterative units (for example, vegetative and generative nodes on the main stem, or partial floret clusters in an inflorescence) (White, 1979), we have used the number of such units (i.e., partial floret clusters) in an inflorescence to characterize its size.

The number of partial floret clusters (PFCs) and the number of seeds per each PFC were assessed in the first inflorescence on the main stem of every plant. To characterize each accession (cultivar or local population), 19–24 plants were analyzed. In several cases, the material of the same cultivar was collected 2–4 times from different plots in the field. The data were added to the statistics to describe the morphological types. To optimize the data presentation, we summarized the numbers of seeds in every part of the inflorescence, consisting of three PFCs each (counting from the base): 1–3, 4–6, 7–9, etc. Significance levels of detected differences were verified using *t*-statistics.

Results

Size and seed productivity of the inflorescence: differences among the groups of cultivars

We analyzed a set of cultivars and landraces representing almost all morphological types of cultivated buckwheat in Russia. The cultivars had been developed by six different breeding centers during almost a century of breeding efforts. In addition, two landraces from Orel Province were included in the analysis.

Buckwheat cultivars of all morphological types were variable in the number of partial floret clusters (PFCs) (Table 2). The ranges of variation were similar in most cases. Only the DGH group differed from the others. The largest inflorescences were found in this group, up to 24 PFCs in size; the average number of PFCs also was higher than in any other group of cultivars ($t = 2.87–9.87$; $P = 0.01–0.001$).

In 2017 and 2018, the DGH group significantly exceeded all others in the number of seeds per inflorescence; in 2019, DGH cultivars produced more seeds per inflorescence than IGH landraces and IGH improved cultivars ($t = 3.09$ and 2.59; $P = 0.001$ and 0.01, respectively), but no significant differences were observed with LSB and KS cultivars ($t = 0.06$ and 1.92, respectively). An explicit and significant difference between the LSB and DGH groups in the size of their inflorescences and, on the other hand, similarity of these groups in the number of seeds per inflorescence, suggested that seed productivity per inflorescence not always depended on the number of PFCs forming the inflorescence.

In 2017, cultivars of the LSB group produced larger inflorescences than KS cultivars ($t = 4.04$; $P = 0.001$), and a higher average number of seeds per inflorescence compared to both IGH landraces and IGH improved cultivars ($t = 2.89$ and 4.25; $P = 0.01$ and 0.001, respectively). Inflorescences of KS cultivars, on average, were larger, albeit insignificantly ($t = 1.49$), compared to IGH landraces, and smaller compared to all other groups ($t = 3.09–9.24$; $P = 0.01–0.001$); their seed number per inflorescence was larger than in IGH landraces ($t = 2.11$; P = 0.05) and IGH improved cultivars ($t = 4.09$; $P = 0.001$).

Table 1. Populations and cultivars of *Fagopyrum esculentum* Moench included in the experiment

Таблица 1. Популяции и сорта *Fagopyrum esculentum* Moench, задействованные в работе

Cultivar type	Cultivar, accession	Catalogue No.	Year of registration	Region
IGH landraces		406		Orel Province
		1709		Orel Province
IGH improved cultivars	‘Bogatyr’[1]	3785	1938	Orel Province
	‘Shatilovskaya 5’[1]	4177	1967	Orel Province
	‘Kalininskaya’[2]	3930	1954	Tver Province
	‘Aromat’[3]	4399	1985	Orel Province
KS	‘Agidel’[4]	4535	2001	Bashkortostan
	‘Inzerskaya’[4]	4536	2002	Bashkortostan
	ˈIlishevskaya’[4]	4563	2008	Bashkortostan
	ˈBashkirskaya Krasnostebelnaya’[4]	4560	2009	Bashkortostan
	‘Kazanka’[5]	4509	1989	Tatarstan
	‘Karakityanka’[5]	4540	1991	Tatarstan
	‘Kama’[5]	4518	1993	Tatarstan
	‘Saulyk’[5]	4541	1997	Tatarstan
	‘Cheremshanka’[5]	4540	2001	Tatarstan
	‘Chatyr-Tau’[5]	4548	2005	Tatarstan
	‘Batyr’[5]	4561	2008	Tatarstan
	‘Kuibyshevskaya 85’[6]	4446	1985	Samara Province
LSB	‘Ballada’[3]	4398	1985	Orel Province
	‘Esen’[3]	4473	1993	Orel Province
	ˈMolva’[3]	4511	1997	Orel Province
DGH	‘Sumchanka’[3]	4397	1985	Orel Province
	‘Dozhdik’[3]	4469	1998	Orel Province
	‘Dikul’[3]	4523	1999	Orel Province
	‘Devyatka’[3]	4539	2004	Orel Province
	‘Dialog’[3]	4549	2008	Orel Province
	‘Druzhina’[3]	4602	2014	Orel Province
	‘Dasha’[3]	4610	2018	Orel Province

Note: originators: 1 – Shatilovo Agricultural Experiment Station, Orel Province; 2 – Research Institute of Agricultural Land Reclamation, Tver Province; 3 – Federal Scientific Center of Legumes and Groat Crops, Orel; 4 – Bashkir Research Institute of Agriculture, Ufa; 5 – Tatar Research Institute of Agriculture, Kazan; 6 – N.M. Tulaykov Research Institute of Agriculture, Samara

Примечание: оригинаторы: 1 – Шатиловская сельскохозяйственная опытная станция, Орловская область; 2 – НИИ сельскохозяйственного использования мелиорированных территорий, Тверская область; 3 – Федеральный научный центр зернобобовых и крупяных культур, Орел; 4 – Башкирский НИИСХ, Уфа; 5 – Татарский НИИСХ, Казань; НИИСХ им. Н.М. Тулайкова, Самара

Table 2. Numbers of partial floret clusters and seeds per inflorescence in the groups of cultivars representing different morphological types (MT)

Таблица 2. Число элементарных соцветий и семян в соцветии в группах сортов разного морфологического типа (MT)

MT	Year	Number of partial floret clusters (PFCs)		Seeds per inflorescence
		Mean ± SE	Range	X ± m
IGH landraces	2017	11.48 ± 0.41	(6–16)	2.67 ± 0.28
	2018	10.90 ± 0.52	(3–19)	1.88 ± 0.36
	2019	9.33 ± 0.45	(4–16)	6.00 ± 0.62
IGH improved cultivars	2017	11.73 ± 0.25	(5–18)	2.25 ± 0.22
	2018	9.69 ± 0.32	(4–18)	2.72 ± 0.26
	2019	10.06 ± 0.29	(4–20)	6.89 ± 0.37
KS	2017	10.83 ± 0.15	(5–18)	3.34 ± 0.15
	2018	9.60 ± 0.18	(4–18)	2.62 ± 0.15
	2019	10.05 ± 0.18	(4–18)	7.27 ± 0.33
LSB	2017	12.52 ± 0.39	(6–19)	3.90 ± 0.32
	2018	11.26 ± 0.43	(4–18)	2.71 ± 0.27
	2019	10.12 ± 0.38	(5–16)	8.18 ± 0.58
DHG	2017	13.93 ± 0.30	(6–23)	5.33 ± 0.30
	2018	13.31 ± 0.33	(4–24)	4.69 ± 0.29
	2019	12.39 ± 0.24	(4–24)	8.14 ± 0.31

In 2018, LSB cultivars exceeded those of the KS and IGH groups in their average inflorescence size ($t = 3.56$ and 2.93; $P = 0.001$ and 0.01, respectively), but in the number of seeds per inflorescence they did not surpass any of the other groups. On average, IGH landraces developed larger inflorescences than the KS group or IGH improved cultivars, but there were no significant differences between them in seed productivity per inflorescence.

Does a larger inflorescence produce more seeds?

Partial floret clusters (PFCs) are very differently involved in seed production. For example, from 46.4 to 73.8% of seeds in an inflorescence are developed within the first to third PFC. The PFCs from the first through the ninth produce from 88.8 to 98.9% of all seeds per inflorescence, with the first twelve PFCs usually producing almost all the seeds in an inflorescence (95.8–100%) (Table 3).

In 2018, the difference in seed numbers per inflorescence between the large (13–24 PFCs) and the medium-sized (10–12 PFCs) inflorescences of the DGH group was 56% ($t = 3.02$; $P = 0.01$), although the PFCs 13th to 24th yielded only 4.1% of the seeds; in 2019, seed productivity of the inflorescences with 13–18 PFCs was 20% higher than of those with 10–12 PFCs ($t = 2.34$; $P = 0.02$), although the PFCs 13th to 18th produced only 2.3% of the seeds (Tables 3 and 4).

In 2019, the inflorescences of the KS group with 13–18 PFCs were on average 30% more productive than those with 10–12 PFCs, but the contribution of the PFCs 13th to 18th to the productivity was only 1.4%.

The most illustrative example was obtained in 2017 from the local landrace populations: the average productivity of larger inflorescences (with 13–16 PFCs) was 1.5 times higher than that of the inflorescences comprising no more than 12 PFCs, despite the fact that no seeds were formed in the PFCs 13th to 16th.

Thus, larger inflorescences sometimes show better seed productivity than smaller ones in plants of the same population, and sometimes these differences are statistically significant. However, such an increase in the inflorescence productivity was not, as a rule, associated with the formation of additional seeds in additional PFCs. The physiological basis of this phenomenon remains unclear.

Discussion

Variations in the inflorescence/floral display size within a genus comprising species with alternative mating systems is sometimes explained in terms of the reproduction costs concept proposed by O. T. Solbrig (1979): cross-pollination has advantages, but usually requires some additional resources to ensure pollen transfer between plants (Krizek, An-

Table 3. Seed setting within different partial floret clusters (PFCs) in the groups of cultivars representing different morphological types (MT)

Таблица 3. Завязывание семян в разных элементарных соцветиях в группах сортов разного морфологического типа (МТ)

MT	Year	Number of seeds (mean ± SE) in the PFCs:				
		1st to 3rd	4th to 6th	7th to 9th	10th to 12th	13th to 24th
IGH landraces	2017	1.88 ± 0.22	0.60 ± 0.13	0.13 ± 0.05	0.08 ± 0.08	
	2018	1.30 ± 0.19	0.30 ± 0.10	0.15 ± 0.09	0.08 ± 0.08	0.05 ± 0.05
	2019	3.23 ± 0.31	1.95 ± 0.24	0.67 ± 0.19	0.15 ± 0.09	
IGH improved cultivars	2017	1.63 ± 0.19	0.46 ± 0.08	0.14 ± 0.06	0.03 ± 0.03	
	2018	1.90 ± 0.17	0.56 ± 0.09	0.18 ± 0.05	0.05 ± 0.03	0.03 ± 0.03
	2019	3.64 ± 0.18	2.14 ± 0.15	0.87 ± 0.10	0.19 ± 0.05	0.05 ± 0.03
KS	2017	2.61 ± 0.08	0.86 ± 0.06	0.32 ± 0.04	0.05 ± 0.02	
	2018	1.80 ± 0.10	0.60 ± 0.06	0.17± 0.03	0.03 ± 0.01	0.01 ± 0.01
	2019	3.24 ± 0.13	2.44 ± 0.12	1.14 ± 0.09	0.34 ± 0.06	0.10 ± 0.04
LSB	2017	2.58 ± 0.12	0.88 ± 0.10	0.33 ± 0.06	0.07 ± 0.03	
	2018	2.02 ± 0.17	0.56 ± 0.11	0.10 ± 0.04	0.05 ± 0.03	
	2019	4.10 ± 0.25	2.68 ± 0.25	1.10 ± 0.18	0.25 ± 0.08	0.05 ± 0.05
DGH	2017	2.79 ± 0.15	1.39 ± 0.13	0.66 ± 0.10	0.38 ± 0.09	0.10 ± 0.04
	2018	2.36 ± 0.12	1.23 ± 0.11	0.57 ± 0.07	0.33 ± 0.06	0.19 ± 0.06
	2019	3.78 ± 0.14	2.38 ± 0.11	1.23 ± 0.09	0.56 ± 0.07	0.19 ± 0.04

derson, 2013; Howard, Barrows, 2014; Oliveira et al., 2021). For example, wild species with insect-mediated cross-pollination tend to develop some features providing pollinators' targeting (Dart et al., 2012), since their plants are usually located separately, i.e., at some distance from one another. A showy floral display is considered as one of the main adaptations to implement such targeting (Howard, Barrows, 2014). For common buckwheat monocenoses, however, the pollinators' concentration is sufficient for successful pollination of all flowers. Therefore, larger inflorescences in buckwheat, likely being a result of domestication (Fesenko I.N., Fesenko A.N., 2011), is hardly a consequence of selection for the attractiveness to insects. Low seed productivity can be extremely rarely (almost never) associated with a lack of pollinators (Fesenko, 1983). Thus, the large inflorescence may well be a consequence of the selection for seed productivity, based on some other mechanisms.

Our research showed that large inflorescences had more chances to produce some additional seeds. Therefore, the accumulation of the alleles determining a larger inflorescence seems to be simply explained: on average, larger inflorescences tend to produce more seeds than smaller ones. This tendency is especially clear in cultivars with a determinate growth habit, which produce the largest inflorescences. But this difference is associated with an unclear physiological mechanism, since most additional seeds in larger inflorescences have been formed near their base (in PFCs from 1st to 12th). Probably, the size of the inflorescence can influence the strength of photosynthesis product attraction (sink strength). The photosynthesis intensity is well known to have feedback regulation by sink strength (Kaschuk et al., 2012; Amelin et al., 2020). Probably, stronger sink strength in larger inflorescences ensures their better seed productivity, in spite of the fact that upper PFCs almost do not participate in seed production.

But what is (are) the mechanism(s) maintaining the polymorphism in the size of inflorescences in cultivated common buckwheat, i.e., why are the genes determining smaller inflorescences not eliminated from populations? *A priori*, the improvement of commercial cultivars through breeding reduces genetic polymorphism. In our study, however, all the analyzed cultivars manifested very wide variability in the inflorescence size. Most of those cultivars showed almost the same range of the variation. An exception was the cultivars with a determinate growth habit (DGH), forming on average the largest inflorescences and having the widest range of variation. The breeding of buckwheat cultivars with a determinate growth habit started in the 1960s (Fesenko, 1983). The first of them, 'Sumchanka', was released in 1985. At present, buckwheat cultivars of this type have the widest factual acreage in Russia (Fesenko A.N., Fesenko I.N., 2019), truly representing a real-time example of the observed inflorescence microevolution. Obviously, the genetic variability of buckwheat was sufficient for such a rapid shift.

So, how to explain the maintenance of the inflorescence size variability? In other words, why have the alleles determining small inflorescences been not lost during the selection for seed productivity? The mechanisms underlying balancing selection are usually considered to be associated with advantages of heterozygosity in individual plants within a population. Such long-term polymorphism in common buckwheat was identified for some biochemical traits. For example, all common buckwheat cultivars maintained polymorphism in the composition of storage proteins in seeds, which was visu-

Table 4. Seed productivity per inflorescence depending on the inflorescence size within the groups of cultivars representing different morphological types (MT), and the shares of seeds formed within the PFCs from 14th to 24th

Таблица 4. Семенная продуктивность соцветия в зависимости от его размеров в группах сортов разных морфологических типов (МТ) и доля семян, образующихся в элементарных соцветиях с 14-го по 24-е

MT	Year	Number of plants	Inflorescence size (number of PFCs)	Number of seeds, (mean ± SE)	(*t*-test)		Seeds in the PFCs ≥ 13th, %
					t	*P**	
IGH landraces	2017	17	10–12	2.12 ± 0.44			
		13	13–16	3.54 ± 0.55	2.02	0.05	0
	2018	15	10–12	1.13 ± 0.31			
		13	13–19	2.92 ± 0.86	1.96	0.05	3.2
	2019	11	10–12	7.00 ± 1.23			
		6	13–16	8.17 ± 2.69	0.40		0
IGH improved cultivars	2017	37	10–12	2.76 ± 0.34			
		31	13–18	3.35 ± 0.37	1.17		0
	2018	29	10–12	3.34 ± 0.54			
		13	13–18	3.62 ± 0.65	0.33		1.1
	2019	35	10–12	7.83 ± 0.54			
		26	13–20	9.31 ± 1.04	1.26		0.7
KS	2017	116	10–12	3.97 ± 0.21			
		58	13–18	4.57 ± 0.32	1.57		0
	2018	86	10–12	2.65 ± 0.25			
		36	13–18	3.44 ± 0.50	1.41		0.4
	2019	95	10–12	7.87 ± 0.48			
		44	13–18	10.27 ± 0.94	2.27	0.05	1.4
LSB	2017	20	10–12	4.20 ± 0.61			
		30	13–19	3.77 ± 0.48	0.55		0
	2018	16	10–12	3.19 ± 0.47			
		22	13–18	3.09 ± 0.50	0.15		0
	2019	23	10–12	9.13 ± 1.08			
		11	13–16	10.18 ± 0.98	0.72		0.6
DGH	2017	31	10–12	4.90 ± 0.51			
		79	13–23	6.03 ± 0.42	1.71	0.10	1.9
	2018	46	10–12	3.33 ± 0.42			
		88	13–24	5.19 ± 0.45	3.02	0.01	4.1
	2019	77	10–12	7.68 ± 0.46			
		123	13–24	9.25 ± 0.49	2.34	0.02	2.3

Note: * – *P*-values are given for statistically significant differences

Примечание: * – значения *P* указаны для вариантов, где различия достоверны alized using SDS PAGE (Lazareva et al., 2007). The adaptive significance of this polymorphism is not yet clear. It should be noted that electrophoretic patterns of seed storage proteins are sometimes quite conservative at the species level. For example, the self-pollinator *F. tataricum* is polymorphic in only one position in the pattern of seed proteins (Lazareva, Fesenko, 2007); the isozyme polymorphism in this species is also significantly narrower than that of *F. esculentum* (Ohnishi, 1998). Presumably, all the polymorphisms, including that in the inflorescence size, can also be parts of the system providing heterosis, although there are no direct evidences to support this hypothesis.

Despite the tendency that larger inflorescences produce more seeds, the relationship between the size of inflorescences and seed productivity in buckwheat cultivars is ambiguous. How can the changing inflorescence size (in any direction) influence the seed productivity of buckwheat cultivars? This question has no unambiguous answer. Improved cultivars of new morphological types can develop, on average, both larger (determinant) and smaller (KS-type) inflorescences compared to the traditional type. All the cultivars were competitive in the variety trials. Apparently, the practical effectiveness of changing the average size of inflorescences in a population using artificial selection depends on the physiological characteristics of particular materials.

Conclusion

This article presents the data illustrating that all common buckwheat cultivars manifested polymorphism in the inflorescence size, assessed as a number of partial floret clusters, i.e., elementary units forming an inflorescence in buckwheat. The cultivars were not selected for this trait. We described it and tried to understand why the polymorphism is maintained. Larger inflorescences tended to produce a higher number of seeds; however, those "additional" seeds were developed mainly within the first 12 floret clusters, counting from the base. In "additional" floret clusters of larger inflorescences, seed development was observed only sporadically. Thus, the genes determining larger inflorescences should be accumulated in populations as a result of the increased seed productivity in larger inflorescences. However, the genes determining smaller inflorescences are also present in all the analyzed populations. We discuss possible mechanisms of the balancing selection maintaining this polymorphism. Perhaps, it is important for maintaining heterosis at the population level. Otherwise, the genes that determine smaller inflorescences would have been eliminated and not maintained in all the studied buckwheat cultivars of various origin.

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