The European Journal of Plant Science and Biotechnology ©2012 Global Science Books

Peculiarities of Common Buckwheat Adaptation to Growing Conditions

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ABSTRACT

All buckwheat populations have a complex structure. They are comprised of 1 or 2 most numerous morphotypes (the adaptive nucleus of a population) and several less abundant ones (insurance morphotypes). The main adaptive element of buckwheat is the number of vegetative nodes per plant. In the first place, this indicator changes at the expense of the vegetative nodes on the main stem. Adaptation of buckwheat to conditions of the East European part of its distribution area was linked with the decrease in the average number of vegetative nodes per stem (from 10.1 in the East Asian populations down to 3.4 in those from the Russian North). The structure of populations is characterized by predominance of SBZ-3, SBZ-4, SBZ-5, SBZ-6 and SBZ-7 morphotypes. Duration of the vegetation period has decreased from 119 down to 66 days, respectively.

Keywords: branching potential, *Fagopyrum esculentum* Moench, genotype × environment interaction, morphotypes

Abbreviations: EEPDA, East European part of the distribution area; **MI**, manifestation index; **SBZ**, stem branching zone; **VIR**, N.I. Vavilov Research Institute of Plant Industry

INTRODUCTION

Common buckwheat (*Fagopyrum esculentum* Moench) is currently cultivated worldwide: in Asia, Europe, South and North Americas, countries of the former USSR and in Australia.

The first written sources mentioning common buckwheat date back to the 5th century AD and have Chinese origin (Krotov 1975). However, the excavations undertaken in 1979 at Xiangyang city of Shaanxi Province made it possible to talk about common buckwheat as a more ancient crop, since it was cultivated and eaten in China already in the 2nd - 1st centuries BC (Li and Yang 1992). The European literary sources that mention common buckwheat start to appear from the late 15th or the early 16th century. According to the archeological data, common buckwheat was known to the peoples inhabiting southern Ukraine in the last years BC or in the 1st century AD, while by the 10th to 12th centuries common buckwheat had spread to the territories currently located in northern Ukraine and southern Belarus (Krotov 1975). Common buckwheat originated from southern China and diffused to northern China, then diffused westward into Europe via the Silk Road (Ohnishi 1991, 1993a, 1993b; Murai and Ohnishi 1995).

The eastern part of the European continent in the 15th century became the secondary area of distribution that formed as a result of land development by the Slavic peoples (Fesenko 2006a) when moving north-eastwards as far as 60° N, from the lands of the present-day Ukraine (48° N). The widening of the area was accompanied by considerable changes in soil and climatic conditions of crop cultivation (Smirnov and Korneychuck 1970). Formation of local populations in different regions of the East European part of the distribution area (EEPDA) was guided by natural selection of those that were fit for local conditions with the minimal human interference. Thus, monitoring of local populations makes it possible to reveal the main factors and mechanisms of the species adaptation, and provides valuable information for crop breeding.

For describing genus *Fagopyrum* plants, experts widely use the *Descriptors for Buckwheat* published by the International Board for Plant Genetic Resources (IBPGR) in 1992. According to the Descriptors, the total number of internodes on the main stem is taken into consideration. The Russian scientists N.V. Fesenko and V.E. Dragunova (1972) suggested that the character number of nodes (number of internodes + 1) should be regarded as the total of two components, namely the number of vegetative nodes and the number of generative nodes (that is, size of the branching zone and the fruiting zone of the stem), these being the most informative and effective in screenings. Very soon after that, expediency of this approach was demonstrated by the Russian and Nepalese experts (Fesenko and Dragunova 1976; Andrianova 1995; Martynenko 1998; Fesenko *et al.* 1998; Rajbhandari and Hatley 1998).

In this relation, the stem branching zone development has been studied to reveal peculiarities of plant morphogenesis in local common buckwheat populations which had formed under conditions of long-term cultivation in diverse ecological zones of the EEPDA, which is in the Volga, Northwestern and Central regions of Russia, in Belarus and Ukraine.

MATERIALS AND METHODS

Accessions of common buckwheat

Accessions of common buckwheat from the global plant genetics resources collection of the N.I. Vavilov Research Institute of Plant Industry (VIR) were analyzed. The examined set included 68 landraces of different geographical origin: from China, Japan, Korea, Russia, Ukraine and Belarus.

Experimental design

The experiments were conducted in the experimental field of the

Received: 18 April, 2012. Accepted: 7 August, 2012.

Original Research Paper

Table 1 Morphogenetic characteristics of buckwheat landrace populations from the East European part of the distribution area and from East Asia.

Region of origin	Number of nodes in SBZ		Branching potential in plants of a population		LB [a]	Average length (days)	
	Average	Extremes	Average	Extremes		Vegetative growth	Growing season
East Asia	10.1 a	9.0-11.5	53.0 a	45.0-65.0	0.0	38	119
Ukraine	5.6 b	3.9-6.8	17.6 b	10.6-22.8	5.2	33	93
Central Region of Russia	4.7 c	4.2-4.9	12.6 c	11.3-14.6	6.8	31	79
Belarus	4.2 d	3.2-4.3	10.0 d	7.6-12.0	14.1	30	68
Volga Region of Russia	4.1 d	3.3-4.2	9.4 d	8.2-12.0	21.9	30	69
Northwestern Region of Russia	3.8 d	2.8-3.6	8.6 d	8.0-9.2	15.1	28	66

[a] limited-branching plants (with a complete or partial reduction of the branching zone in the upper branch), %
* Different letters within a column indicate significant differences according to Student's *t*-test (P<0.05

Table 2 Characteristics of the architecture of the vegetative system in buckwheat landrace populations from different regions of the East European part of the distribution area and from East Asia.

Region of origin	Average number of nodes in SBZ, pcs	Average number of plants with SBZ morphotypes in populations, %												
		SBZ 3	SBZ 4	SBZ 5	SBZ 6	SBZ 7	SBZ 8	SBZ 9	SBZ 10	SBZ 11	SBZ 12	SBZ 13	SBZ 14	SBZ 15
I	10.1			0.4	2.6	5.8	19.6	21.6	8.1	12.6	12.2	8.0	5.6	3.5
II	5.6	4.7	20.4	34.2	31.3	9.4								
III	4.7	10.0	30.8	32.0	19.2	8.0								
IV	4.2	30.5	32.3	26.5	8.3	2.4								
V	4.1	38.5	39.0	18.7	3.1	0.7								
VI	3.8	44.5	34.0	15.7	5.8									

I: East Asia, II: Ukraine, III: Central Region of Russia, IV: Belarus, V: Volga Region of Russia, VI: Northwestern Region of Russia

All-Russian Research Institute of Pulse and Groat Crops (Orel city, the Central Region of Russia) located at 53° N, with the maximum day length of 18 h in June, average monthly temperature of +17.2°C in June, average monthly precipitation of 72 mm and the hydrothermal index of 1.3. The season of the study conducted was average and favourable for common buckwheat in 2009. The sets of accessions were sown during the last week of May on 6 m^2 plots (1 m × 6 m), 30 cm × 10 cm per plant, 200 plants per plot in one replication on gray forest soil. Fertilizers were not used. The number of vegetative nodes on the main stem and first-order branches of 100 typical, well developed plants of each accession were analyzed. Duration of the vegetative growth stage (from seedling emergence to first flower) and vegetation period were recorded.

Statistics

The statistical analysis of experimental data was made using Excel statistics 2010 for Windows. Following ANOVA, significant differences between means were determined using the Student's *t*-test.

RESULTS AND DISCUSSION

General regularities in common buckwheat adaptation

According to the results, adaptation of common buckwheat to conditions of the East European area of its distribution was associated, in the first place, with the shortening of the vegetation period of a population: while the East Asian populations vegetated till the first autumn frosts (119 days, on average), those from the southern part of the East European area of common buckwheat distribution (Ukraine) reached harvesting ripeness within 93 days, on average (**Table 1**). Within the EEPDA, the average length of the vegetation period for a particular population logically decreased according to the South-to-North direction of origin, from 93 days in case of the Ukrainian accession down to 66 days in accessions from the Northwestern Region. The earlier ripening in populations was achieved at the expense of a reduction in the average number of nodes in the stem branching zone (SBZ) (from 10.1 down to 3.4) and of the reduction in the plants' branching potential (from 53.0 down to 8.6). The average number of nodes in SBZ reliably correlated to the vegetative period duration in the populations studied ($r = 0.741$, $P_0 < 0.001$). The correlation coefficient was calculated between the average number of nodes per SBZ in each population and the vegetative period of the plants to match.

From the agrometeorological point of view, populations with diverse duration of the vegetation period differed, in the first place, by their thermal regime requirements expressed as the total average daily temperatures above 10°C (Smirnov and Korneychuck 1970). For the East European varieties belonging to the early ripening group, this figure is 1600°, for the medium ripening ones it is 1800°, and for the late ripening ones it is 2000° and above. The number of vegetative nodes in the stem and in the entire plant had a reliable positive correlation ($r = 0.913$ and $r = 0.792$, respectively) with the yielding ability of a buckwheat population (Fesenko *et al.* 2010), therefore a reduction in the number of vegetative nodes leads to a lower productivity potential in the earlier ripening populations. Besides, the total productivity and the uptake of nutrients by plants increase with later maturity of varieties (Lakhanov *et al.* 2004). Therefore, within the East European populations, Ukrainian populations demonstrate not only the latest maturity (and the highest yielding ability as a consequence), but a higher demand to heat, photosynthetically active radiation, supply of nutritional elements and moisture.

The second important morphogenetic peculiarity of buckwheat landrace populations is their polymorphism in terms of SBZ structure. All the populations are composed of several SBZ morphotypes. This peculiarity is a specific trait. While East Asian populations are composed of a wide range of morphotypes (from 5 to 15 nodes in SBZ), the studied local populations from the EEPDA include a lesser number of morphotypes within a given population that is, with 3, 4, 5, 6 and 7 nodes in the SBZ of a particular population (**Table 2**). The presence of the enumerated SBZ morphotypes in the structure of local populations is an evidence to prove that they are adapted to the conditions in the corresponding regions in the common buckwheat distribution area.

In southern regions well provided with heat, water and high soil fertility, the later ripening SBZ morphotypes with 5, 6, and 7 nodes not only fit the favourable local climatic conditions, but are potentially better prepared for utilizing the local natural resources than early ripening morphotypes. On the contrary, the less demanding plants of early ripening morphotypes SBZ-3 and SBZ-4 have a better advantage in the regions with lower temperatures or less fertile soils.

The number of inflorescences on the stem of different SBZ morphotypes practically did not change, therefore a reduction in the number of nodes in the SBZ leads to an increased generative load on the vegetative node (higher ratio of generative to vegetative nodes on the stem) (**Table 3**).

Table 3 Development of the generative zone of the stem in landrace populations from the East European part of buckwheat distribution area.

Number of populations studied	Number of vegetative nodes per stem		Average number of inflorescences per stem	Generative load per vegetative node
	Average	Extremes		
3	3.9	3.5-4.0	7.7	1.98
9	4.3	4.1-4.5	7.7	1.81
9	4.9	4.6-5.0	7.5	1.54
3	5.4	5.1-5.5	7.6	1.40
4	5.8	5.6-6.0	7.6	1.32

Thus, a reduction in the number of nodes in the SBZ leads not only to a shorter vegetation period, but is also accompanied by relative increased nutrient accumulation in ripening seeds, which ensures more stable seed formation under low-temperature conditions unfavourable for grain filling (Fesenko and Martynenko 1998; Fesenko 2006a).

Selective forces for maintenance of intra-population polymorphism in the number of vegetative nodes

It is demonstrated in **Table 1** that the main mechanism of adaptation in common buckwheat is the variation in the number of vegetative nodes in a plant. When the growing conditions change, two types of adaptive response can be used by plants, these are variation in the number of vegetative nodes either in the stem or in the branches.

Let us consider effectiveness of these responses on the example of common buckwheat populations from the EEPDA. Within each SBZ morphotype range, plants slightly differ in terms of the average branching potential value regardless of the growing region (**Table 4**). In SBZ-3 morphotype for instance, manifestation index (MI) varies in different regions within the 0.93-1.03 range relative to the value displayed in Ukraine. A similar regularity is observed in SBZ-4 morphotypes with MI of 0.77-0.91, and in SBZ-5 morphotypes with MI of 0.87-0.99. A tendency towards a certain reduction of the branching potential in common buckwheat morphotypes in the South-to-North direction is linked with the growing fraction of the limited-branching plants in populations (**Table 1**). In these plants, the number of vegetative nodes in the upper branches is reduced from 2-3 (in the normally branching plants) down to 0-1 (Fesenko 2006b).

An absolutely different regularity is revealed when total numbers of vegetative nodes in plants of different SBZ morphotypes are compared (**Table 4**). If this trait manifestation in SBZ-3 morphotype is taken as 1.0, then in plants of SBZ-4 morphotype it increases up to 1.41-1.76, in SBZ-5 plants up to 2.08-2.48, and up to 2.74-3.06 in SBZ-6 plants.

The noted regularities in plant morphogenesis within one and different SBZ morphotypes have obviously served as one of the causes of the establishment of the existing SBZ structure in common buckwheat populations. With its appearance, adaptive mechanisms of populations have significantly improved.

The initial prerequisite needed for the adaptive processes to function is the sufficient genetic heterogeneity of a population in terms of adaptive characters (Shmalgauzen 1968; Zavadsky 1968; Altukhov 2003). Since common buckwheat lacks special adaptations to ecological stresses (Fesenko 2006a), the strategy of its ecological adaptation is based on 'sensing' favourable weather conditions. In common buckwheat, it is achieved thanks to the presence of biotype groups with different adaptive forms in a population, which are strictly differentiated according to the main adaptive trait, that is, the number of vegetative nodes per plant. This ensures crop conformity to contradictive requirements: to ensure the maximum possible survivability and productivity under normal conditions and retain the capability to adapt to the changing conditions.

Depending on the weather factors fluctuation, the periods favourable for fruit formation coincide with the development rhythm of a plant with this or that SBZ morphotype. It determines the advantage of this morphotype in terms of its contribution to the yield of the population. In the long run, the random variation of weather factors approaches the mean annual rhythm of climatic conditions in a locality, which allows a long-established population to accumulate the SBZ morphotypes that are most productive under these particular conditions. Thus, the life of a population experiences natural selection aimed at increasing its adaptability to regional conditions. The adaptation itself has shaped in populations into a SBZ system comprised of a compact group of the main (modal) SBZ morphotypes with the highest degree of adaptation to growing conditions and an insignificant number of obligatory retained extreme (insurance) morphotypes. Since such structures are the result of natural selection, the population parameters characterize both local conditions (climate and soil) and the amplitude of the predominant weather factors that fluctuate in this locality. This is clearly seen in structural peculiarities of local variety populations in the regional cut.

The highest degree of diversity in terms of SBZ morphotypes is displayed by East Asian populations which grow in the most favourable conditions. As the growing conditions keep worsening, both the number of nodes in SBZ and the SBZ morphotypes diversity keep decreasing. It should be noted that one mechanism (an increase in earliness) was used to solve the problem of adaptation to different unfavourable environmental factors.

Peculiarities of common buckwheat adaptation to conditions of different regions in the East European part of its distribution area

The role of the modal SBZ fraction is most expressed in populations from the Northwestern Region, where heat deficiency serves as the main limiting factor. In this region, even insignificant deviation from the mean annual temperature values represents considerable stress for plants. In this relation, the dominating role here is performed by the earliest SBZ-3 morphotype amounting to 61.6% of a polymorphous population. The second place in terms of importance is occupied by the SBZ-4 morphotype, which amounts in combination with SBZ-3 to 86.5% of a population. Therefore, the dominating role in common buckwheat adaptation to the climatic factor is performed by two earliest morphotypes (**Table 2**). Thanks to them, populations can produce a yield within a short cool summer.

Along with the decreasing heat in the Volga Region, the

Table 4 Vegetative nodes manifestation index in plants within one SBZ morphotype and in different SBZ morphotypes in landrace populations of the East European part of buckwheat distribution area.

Region	Within one SBZ morphotype relative to Ukrainian morphotypes			In different SBZ morphotypes relative to SBZ-3 morphotype			
	SBZ-3	SBZ-4	SBZ-5	SBZ-3	SBZ-4	SBZ-5	SBZ-6
Ukraine	1.0	1.0	1.0	1.0	1.76	2.33	3.06
Central Region of Russia	1.03	0.91	0.92	1.0	1.57	2.08	2.94
Belarus	0.98	0.85	0.91	1.0	1.53	2.17	2.74
Volga Region of Russia	0.97	0.77	0.87	1.0	1.41	2.09	
Northwestern Region of Russia	0.93	0.86	0.99	1.0	1.63	2.48	
Average				1.0	1.58	2.23	2.91

Table 5 Characteristics of modal SBZ morphotypes in landrace populations from the East European part of buckwheat distribution area.

Region	**Modal SBZ types**					**Ripeness group**
	3	**4**	**5**	**6**	**7**	
Ukraine	+	+				early
	+	+	+			mid-season
		+	+	+		mid-late
				+	+	late
Central Region of Russia	+	+	+			mid-season
		+	+			
Belarus	+	+				early
Volga Region of Russia	+	+				early
Northwestern Region of Russia	+	+				early

water supply regime (the influence of continentality factor) acquires an important role. The morphotypes SBZ-3 (49.5%) and SBZ-4 (33.0%) remain the main morphotypes here; however, the specific weight of SBZ-4 has increased, thus mitigating the influence of water deficiency.

A similar structure is characteristic of the varietal samples from Belarus, SBZ-3 (41.2%) and SBZ-4 (37.6%) being the modal morphotypes in it (**Table 2**). However, it got established under the influence of different factors. Local common buckwheat populations were growing on low-fertile sandy loams characterized by a low water-retaining capacity. The temperature regime here is similar to that of the Central Region and is sufficient for the growth of mid-season varieties. However, the deficiency of water and mineral nutrients are the main limiting factors, which have determined formation of early populations with SBZ-3 and SBZ-4 as the leading morphotypes.

Climatic and soil conditions of the Central Region are favourable for vegetation of varieties of the mid-season type, the morphotypes SBZ-3 (22.9%), SBZ-4 (33.4%) and SBZ-5 (28.6%) being the modal ones. The deficiency of both heat and rainfall are the equally strong limiting factors here. An extension of the vegetation period was determined by an increase in the number of the main SBZ fractions up to three at the expense of SBZ-5 addition.

The Ukrainian Region is characterized by the most complex ecological structure of populations. The main factors here are a higher temperature regime and an extended length of the period favouring buckwheat growth. Favourable temperatures and high soil fertility create optimal conditions for plants development, but intensive evaporation causes instability of the water supply of plants. In this relation, water deficiency is the main stress factor here. This is clearly expressed in provinces adjacent to Belarus, where soil fertility and water-retaining capacity are low. That is why a characteristic feature of the structure of local Ukrainian populations is a wide range of modal SBZ morphotypes: SBZ-4 (20.8%), SBZ-5 (30.8%) and SBZ-6 (30.8%) (**Table 2**). These three average values conceal a range of varietal samples with wide diversity in terms of earliness and SBZ structure. The early (SBZ-3 and SBZ-4 modes), mid-season (SBZ-4 and SBZ-5 modes), mid-late (SBZ-4, SBZ-5 and SBZ-6 modes), and late (SBZ-6 and SBZ-7 modes) local populations have formed here (**Table 5**).

CONCLUSION

A specific peculiarity of common buckwheat is a narrow norm of reaction, therefore adaptation to unfavourable environmental factors (e.g., deficiency of heat and moisture, low soil fertility) is achieved by one mechanism, that is, through optimizing the vegetation period duration. A peculiarity of adaptive mechanisms in common buckwheat is the clearly expressed structureless of populations, that is, the presence of a system of SBZ morphotypes differing in the rhythm of development, duration of vegetation, requirements to environmental conditions and in potential productivity. Within the boundaries of the EEPDA, ecological adaptation is ensured by the presence of SBZ-3, SBZ-4, SBZ-5, SBZ-6 and SBZ-7 morphotypes in the structure of populations. In terms of the rhythm of development, the adaptive norm of a population is usually characterized by 2-3 modal SBZ morphotypes. The morphotypes with edge values in the SBZ range perform the insurance function and ensure rapid adaptive transformation of the population in the case of abrupt environmental changes.

ACKNOWLEDGEMENTS

The authors express their gratitude to the late Nikolay Valerianovich Fesenko, a talented buckwheat researcher who has inspired and guided the present work. The authors also wish to thank Dr. István Gondola and Dr. Jaime A. Teixeira da Silva for making extensive improvements to grammar and style.

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