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BUCKWHEAT – A GENOMIC, TRANSCRIPTOMIC AND PROTEOMIC VIEW

Matúš Kučka[1], Katarína Ražná[1], Simona Čerteková[1], Milan Chňapek[2], Lucia Mikolášová[2], Zdenka Gálová[2], Želmíra Balážová[2]*

Address(es):
[1] Institute of Plant and Environmental Sciences, Faculty of Agrobiology and Food Resources, Slovak University of Agriculture, Tr. A. Hlinku 2, 94976 Nitra, Slovakia.
[2] Institute of Biotechnology, Faculty of Biotechnology and Food Sciences, Slovak University of Agriculture, Tr. A. Hlinku 2, 94976 Nitra, Slovakia.

*Corresponding author: zelmira.balazova@uniag.sk

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ABSTRACT

Buckwheat is a pseudocereal from the *Polygonaceae* family. Two species from this family are commercially exploited – common buckwheat and tartary buckwheat. Buckwheat comes from China, although in recent years, the highest production has been noted in Russia. With its nutritional composition (mainly rutin), it has a beneficial effect on human health. Rutin is mainly contained in the flowers and leaves of buckwheat, and it has antidiabetic, neuroprotective and antioxidant properties; it improves blood pressure and lowers cholesterol levels. In addition to rutin, buckwheat contains bioactive peptides that serve as trypsin inhibitors and have antioxidant and antimicrobial properties. Buckwheat found its use mainly in the field of food and feed production. Amplification polymorphism detection techniques are currently used for the genomic analyses of buckwheat, with 8,884 available markers that include 756 loci. The most frequently used type of molecular markers in buckwheat is the microsatellite markers, which form tandem repeats of short nucleotide motifs. The total number of microsatellites in the tartary buckwheat genome is 37,572, with a frequency of 83.25 microsatellites per 1 Mb. Based on their genetic variability, the buckwheat varieties can be divided into the European and Asian groups, with a lower diversity among the varieties in the European group. Genomic analyses can reveal the genetic relatedness or differences between the individual varieties, as well as losses in genetic purity. The transcriptomic analyses are primarily devoted to the expression of genes responsible for the synthesis of flavonoids, but also those involved in the plant's defense mechanisms, development etc. Molecular analyses revealed that the expression of genes supporting the synthesis of rutin can be favorably influenced by light, darkness, methyl jasmonate, abscisic acid etc. Some buckwheat genes were introduced into *Arabidopsis*, which subsequently showed improved properties, for example, resistance to drought. These findings not only enhance our understanding of buckwheat at a fundamental level but also hold practical significance for breeding programs focused on enhancing nutritional and agronomic traits in buckwheat varieties.

Keywords: buckwheat, genomics, transcriptomics, proteomics, microRNAs, molecular markers

INTRODUCTION

Buckwheat is a pseudocereal from the *Polygonaceae* family. It can be distinguished quite easily from other genera in the *Polygonaceae* family by the central location of its embryo in the achenes. Buckwheat is a small genus that includes less than 30 species, which are divided into main groups based on their morphological features and molecular systematics: *cymosum* and *urophyllum* (Tab. 1). The *cymosum* group is characterized by long cotyledons and anthers partially covered by the perianth, while the species in the *urophyllum* group have cotyledons and their anthers are completely covered by the perianth (**Ohnishi and Matsuoka, 1996; Ohsako and Li, 2020**). In the last 30 years, the number of buckwheat species has doubled, mainly thanks to the new species from China and Japan (**Ohsako and Li, 2020**). However, morphological and molecular analyses have revealed that some species were misinterpreted, such as *Fagopyrum hailuogouense* J. R. Shao, M. L. Zhou & Q. Zhang (**Zhou *et al.*, 2015a**), which is morphologically identical to *Bistorta pergracilis* Hemsl. (**Jin *et al.*, 2018**).

Based on the molecular and genetic analyses, it was found that most species of buckwheat belong to the *urophyllum* group. In contrast, the *cymosum* group contains only four species, two of which are cultivated – common buckwheat (*Fagopyrum esculentum* Moench) and tartary buckwheat (*Fagopyrum tataricum* Gaertn.), and two are wild – *F. cymosum* Meisn. and *F. homotropicum* Ohnishi (**Ohsako and Li, 2020**). Of all species of buckwheat, only *F. esculentum* and *F. tataricum* can be used for regular consumption. The tetraploid wild species *F. cymosum* is also sporadically used as a vegetable or feed for livestock. The diploid species *Fagopyrum cymosum* is believed to be the progenitor of Tatar buckwheat and common buckwheat, which is also termed edible buckwheat (**Mazza and Oomah, 2003**). Moreover, the assessment of genetic diversity using microsatellite markers revealed that *F. esculentum* Moench has two wild relatives – *F. esculentum subsp. ancestrale* and *F. homotropicum*, while *F. homotropicum* diverged multiple times from *F. esculentum* subsp. *ancestrale* (**Ohsako *et al.*, 2017**). Another study suggests that *F. esculentum ssp. ancestrale* is a hybrid species formed by spontaneous hybridization between *F. cymosum* and *F. esculentum* (**Cheng *et al.*, 2020**).

Unlike common buckwheat, tartary buckwheat has a certain resistance to frost, so it is mainly grown in mountainous areas where other plants may be at risk of frost damage. tartary buckwheat can be cultivated at an altitude of 400 to 4400 m but is mostly planted at 1500 to 3000 m. It is grown mainly in the Chinese and Indian parts of the Himalayas, in Nepal, Bhutan, Pakistan, and also in the eastern part of the USA, the northern part of Canada, Japan, Russia, South Korea and some parts of Europe. Currently, China is the largest producer of tartary buckwheat with up to 400,000 tons per year from an area of 2,000-3,000 km^2, primarily in the provinces of Yunnan, Sichuan, Guizhou, and Chongqing, which are located in the southwest of China (**Zhou *et al.*, 2018; Mazza and Oomah, 2003**).

Common buckwheat represents more than 90% of the world's production of all species of buckwheat. There are early and late ripening types, Japanese and European types, or summer and autumn types. Various varieties or cultivars may exist within a given type – short or tall, with grey or black triangular-shaped seeds and white or pink flowers.

However, in general, buckwheat varieties are divided into two main groups according to the place of occurrence:

1) Buckwheat varieties grown in Korea, Japan, Southern China, India and Nepal. These varieties form tall and strong plants that mature late in the season and are sensitive to the photoperiod.
2) Buckwheat varieties grown in Europe and Northern China. The varieties in this group, on the contrary, are short; they mature early in the season and are not sensitive to the photoperiod (**Mazza and Oomah, 2003**).

The individual types of buckwheat have a variable growth period. While common buckwheat typically grows from May to August and tartary buckwheat from May to September, some species grow from July to November (for example *F. qiangcai*, *F. macrocarpum*, *F. rubifolium*, *F. gracilipedoides*), others from June to November (for example *F. gracilipes*, *F. luojishanense*, *F. caudatum*), from May to December (*F. cymosum*), from August to November (*F. lineare*) or from April to November (*F. urophyllum*). They also differ in plant height, the tallest species being *F. cymosum* (50 - 300 cm), *F. urophyllum* (180 - 225 cm), and the smallest including *F. leptopodum* (6 - 60 cm), *F. jinshaense* (14, 2 – 31.8 cm) and *F. macrocarpum* (5 – 75 cm). Several species occur primarily on rocky slopes (for

example *F. gracilipedoides, F. leptopodum, F. gilesii, F. lineare* and *F. homotropicum*) or near agricultural areas (for example, *F. rubrifolium, F. gracilipes and F. luojishanense*) (**Wen *et al.*, 2021**).

Table 1 Classification and grouping of some species of buckwheat with the corresponding number of chromosomes (**Ohsako and Li, 2020; Ohnishi and Matsuoka, 1996**)

Group	Species	Number of chromosomes	Author
Cymosum	*F. esculentum*	16 (n)	Moench
	F. tataricum	16 (n)	Gaertn.
	F. cymosum	16,32 (n,2n)	Meisn.
	F. homotropicum	16,32 (n,2n)	Ohnishi.
Urophyllum	*F. urophyllum*	16 (n)	Bur. et Franch
	F. lineare	16 (n)	Sam.
	F. leptopodum	16 (n)	Diels
	F. statice	16 (n)	H. Léveillé
	F. rubifolium	32 (2n)	Ohsako et Ohnishi
	F. gracilipes	32 (2n)	Hemsl.
	F. gracilipedoides	16 (n)	Ohsako et Ohnishi
	F. capillatum	16 (n)	Ohnishi
	F. gilesii	16 (n)	Hemsl.
	F. pleioramosum	16 (n)	Ohnishi
	F. jinshaense	16 (n)	Ohsako et Ohnishi
	F. callianthum	16 (n)	Ohnishi
	F. jinshaense	16 (n)	Ohsako et Ohnishi
	F. macrocarpum	16 (n)	Ohsako et Ohnishi A.J.Li
	F. tibeticum	48 (2n)	Adr.Sanchez & Jan.M.Burke
	F. pugense	16 (n)	T. Yu
	F. densovillosum	16 (n)	J.L.Liu
	F. luojishanense	16 (n)	J. R. Shao
	F. qiangcai	16 (n)	D. Q. Bai
	F. longzhoushanense	16 (n)	J. R. Shao
	F. crispatifolium	32 (2n)	J.L.Liu

Origin and occurrence of buckwheat

Buckwheat is believed to have originated from Central and Northeast Asia. It was most likely cultivated in China as early as the middle of the 4th millennium BC. It originated in southwestern China, where it was grown as an additional crop alongside the main agricultural crops such as millet and rice (**Mazza and Oomah, 2003**). However, linguistic evidence confirms that buckwheat was cultivated with barley long before millet and rice in eastern Bhutan (**Hyslop and Guedes, 2021**). The oldest micro- and macrofossils of buckwheat – a total of 26 – also come from China.

In most cases, these are pollen and starch granule fossils to a lesser extent. The oldest fossil probably dates back to 5500 years ago. According to the findings, it is assumed that the progenitor of buckwheat was first domesticated and only later expanded to the north of China due to the movement of the first farmers (**Hunt *et al.*, 2018**). However, this contradicts other archaeological and palynological records, in which it is assumed that the cultivation and domestication of buckwheat occurred in the north and not in the southwest of China (**Yao *et al.*, 2023**). Polymorphism detection techniques revealed that the direct progenitor of common buckwheat was the buckwheat population originating from the Sanjiang region of China (**Konishi *et al.*, 2005**). The findings also show that buckwheat expanded from China via two main routes. The first route led from China to Korea and from Korea to Japan. The second route went from China to Bhutan, Nepal, Kashmir, Karakoram and Hindu Kush (**Murai and Ohnishi, 1996**). According to ancient documents, it was found that buckwheat was primarily used as a medicine in traditional Chinese medicine, but in Japan, it gradually became a popular food crop and is part of traditional Japanese cuisine. Nowadays, buckwheat is only consumed in a few regions in China (**Tatsumi and Marui, 2012**). Buckwheat came to Europe through the Himalayas, the Caucasus, Russia and Turkey in the 14th and 15th centuries and North America in the 17th century. The greatest peak in the worldwide cultivation of buckwheat was reached at the beginning of the 19th century. Since then, we have observed a decrease in the rate of cultivation. From 1995 to 1999, approximately 2.7 million tons were grown yearly, with China and the former Soviet Union accounting for 58% of global production (**Mazza and Oomah, 2003; Hunt *et al.*, 2018**). According to the data from FAO (The Food and Agriculture Organization of the United Nations), Russia (919,147 tons) and China (502,369 tons) were the largest producers of buckwheat in 2021. Other important producers include Ukraine (105,780 tons) and the USA (82,359 tons). Poland and France were also important in the past, but no data were available for 2019-2021 **(Tab 2)** (**http://www.fao.org/about/en**).

Tab 2 Buckwheat production in tons in the individual years (https://www.fao.org/faostat/en).

Country	1961	1971	1981	1991	2001	2011	2019	2020	2021
China	1,500,000	2,000,000	2,600,000	2,500,000	1,250,000	780,000	512,961	503,988	502,369
Russia	-	-	-	-	573,981	800,375	785,702	892,160	919,147
USSR	745,000	1,000,000	476,000	1,217,000	-	-	-	-	-
Ukraine	-	-	-	-	387,600	281,600	85,020	97,640	105,780
France	55,660	18,990	7,200	29,700	58,872	91,400	-	-	-
USA	19,596	18,000	48,000	95,000	67,362	79,618	82,056	82,182	82,359
Japan	42,800	19,500	18,000	19,700	26,000	32,000	42,600	44,800	40,900
Canada	26,496	54,974	52,800	23,300	16,300	-	18,000	8,900	7,600
Poland	59,000	49,000	130,405	39,197	58,661	92,985	-	-	-
Brazil	500	9,500	50,000	47,000	49,074	57,000	64,015	64,692	65,427

Notes: Data are not available for some years.

Nutritional composition of buckwheat

Buckwheat groats contain 55% starch, 12% protein, 4% lipids, 7% fiber, 2% soluble carbohydrates, 2% ash and 18% other compounds, which include organic acids, phenols, tannins, phosphorylated carbohydrates, nucleotides and nucleic acids (Fig. 1) (**Steadman *et al.*, 2001**).

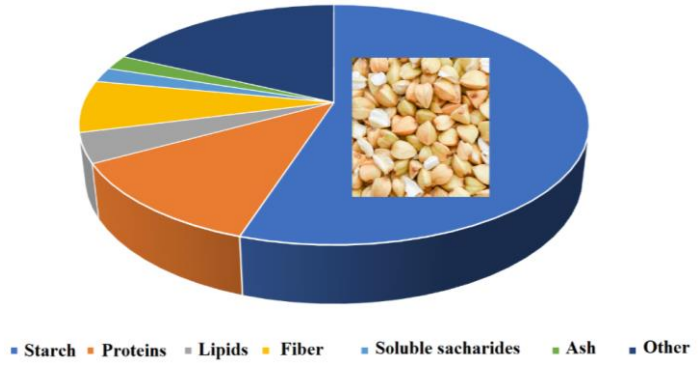

Figure 1 Nutritional composition of buckwheat groats (**Steadman *et al.*, 2001,** modified)

There are differences in the chemical composition of buckwheat products, such as peels, groats, flour and wholemeal flour (**Table 3**). The highest proportion of proteins, fats, and rutin can be found in whole grain flour, and the highest proportion of carbohydrates is in groats (**Vojtíšková *et al.*, 2012**).

Table 3 Differences in the chemical composition of individual buckwheat products (**Vojtíšková *et al.*, 2012**).

Buckwheat product	Moisture (%)	Crude protein amount (%)	Starch content (%)	Fat content (%)	Rutin (mg per g)
Peels	6.1	3.5	57.2	0.6	0.1
Groats	8.3	13.1	69.5	3.4	0.1
Flour	11.5	12.9	67.9	4.1	0.1
Wholemeal flour	11.9	14.4	61.6	4.1	0.6

Buckwheat proteins are composed of well-balanced amino acids and have a high biological value. Groats intended for consumption have a high content of lysine, isoleucine, tryptophan, valine, histidine and phenylalanine. A big advantage is that they do not contain gluten and are suitable for the nutrition of people with celiac disease (**Sytar *et al.*, 2018**). Buckwheat seeds also contain bioactive peptides with a unique composition of amino acids and apart from their nutritional value, they also have several other benefits (**Zhou *et al.*, 2015**). For example, tartary buckwheat contains peptides with the following amino acid sequences: Gly-Glu-

Val-Pro-Trp, Tyr-Met-Glu-Asn-Phe and Ala-Phe-Tyr-Arg-Trp with a molecular weight of 586.65; 702.79 and 741.85 Da, which have potent antioxidant abilities. The third peptide has the strongest effects, which can best bind hydroxyl radicals and inhibit lipid peroxidation **(Luo *et al*., 2020**).

Another example is the FtTI polypeptide from tartary buckwheat, which weighs 14 kDa and consists of 86 amino acid residues containing two disulfide bonds. FtTI is a trypsin inhibitor with inhibitory activity against phytopathogenic fungi (**Ruan *et al*., 2011**). Trypsin inhibitors are another important component of bioactive peptides. Buckwheat contains seven main trypsin inhibitors, divided into permanent inhibitors of 6,000 to 7,000 Da (BTI I, IIa, IIb and IIIa) and temporary inhibitors (10,000 to 11,500 Da): BTI IIc, BTI IIIb1 and BTI IIIb2. These inhibitors play a key role in maintaining mitochondrial homeostasis by directly targeting mitochondria and inducing mitochondrial fragmentation and mitophagy (**Li, 2023**). In addition to these effects, bioactive peptides exhibit antimicrobial activity against gram-positive and gram-negative bacteria and antitumor activity. They are also involved in lowering blood pressure and cholesterol levels and are also effective in the treatment of diabetes. Buckwheat peptides are also promising in the food and pharmaceutical industry (**Zhou *et al*., 2015**).

Although buckwheat groats only contain 4% fat, their big advantage is the high proportion of unsaturated fatty acids with a predominance of linoleic and oleic acids. Palmitic acid has the highest proportion of saturated fatty acids (**Sinkovič *et al*., 2020**). The flowers of common and tartary buckwheat contain volatile essential oils. Twenty-eightvolatile essential oil constituents have been identified in common buckwheat, most of which (more than 90 %) are nonanoic acid, (E)-3-hexen-1-ol, and benzothiazole. In tartary buckwheat, only 14 volatile essential oil components have been identified, of which the majority (over 85%) are 2-pentadecanone, eugenol, 1,2-benzene carboxylic acid, bis(2-methyl propyl) ester and (E, E)-farnesyl acetone. Individual volatile oils have been found to have a broad-spectrum antibacterial activity. *Xanthomonas vesicatoria* is an example of a bacteria sensitive to these oils. Volatile oils are also characterized by antioxidant properties (**Zhao *et al*., 2018**). Buckwheat also abounds in minerals K, P, Ca, Fe, vitamin B, and E (**Vojtíšková *et al*., 2012**). While the proteins, lipids, soluble carbohydrates and minerals are located in the embryo in the grain, starch can be found in the central endosperm (**Steadman *et al*., 2001**).

Flavonoids are among some other important components contained in buckwheat. Altogether six flavonoids were identified in the buckwheat seeds: rutin, orientin, vitexin, quercetin, isovitexin and isoorientin. While all the above flavonoids are present in the seed coat, only rutin and isovitexin are present directly in the seeds. The total flavonoid content of the seed hulls can reach concentrations of up to 74 mg per 100 g of dry matter, as opposed to the seeds, where concentrations are around 18 mg per 100 g of dry matter. Processing the seeds and then separating them from the husks thus loses some of their nutritional value (**Dietrych-Szostak and Oleszek, 1999**). The amount of rutin in the common buckwheat grains ranges from 0.05 to 1.35%, while the quercetin content is lower – ranging from 0.01 to 0.17%. Tartary buckwheat has a high rutin content of 0.14 to 1.35%. The highest rutin content was found in the tartary buckwheat seeds from Sichuan, China (**Bai *et al*., 2015**). The highest rutin content in common buckwheat was found in its flowers (above 83 mg per g of dry matter) and leaves (over 69 mg per g of dry matter) (**Vojtíšková *et al*., 2012**).

Buckwheat also contains a fluorescent and phototoxic substance called fagopyrin. At the moment, there are no reliable quantitative data on the toxicity of fagopyrin, but it can be generally assumed that the consumption of buckwheat seeds, flour and teas in normal quantities should not cause any issues; however, the diets consisting of buckwheat sprouts, herbs and especially flowers can cause fagopyrism (**Benković and Kreft, 2015**).

Effects of buckwheat on human health

As mentioned in the previous chapter, buckwheat contains a large number of substances that have a positive effect on human health. Buckwheat has been proven to have antioxidant properties (**Abbasi *et al.*, 2015**). After including buckwheat grains in the human diet as a main dietary component, buckwheat is a preventive measure against high blood pressure, dyslipidemia and hyperglycemia (**Zhang *et al*., 2007**). Buckwheat bran extract was found to be the most effective against diabetes (**Hosaka *et al*., 2011**). Studies have shown that buckwheat can inhibit the activity of the sucrase enzyme in mice, which causes mice to develop lower blood glucose levels one hour after sucrose consumption. In addition, there are substances in buckwheat that exhibit antimicrobial activity; for example, three compounds were isolated from the methanolic extracts of buckwheat hull (6,7-dihydroxy-3,7-dimethyl-octa-2(Z),4(E)-dienoic acid (1), 6,7- dihydroxy-3,7-dimethyl-octa-2(E),4(E)-dienoic acid (2), and 4,7-dihydroxy-3,7-dimethyl-octa-2(E),5(E)-dienoic acid (3)), which in the amount of 500 μg exhibit antimicrobial activity against *Staphylococcus aureus* (**Cho *et al*., 2006**). Also, there is the potential of using buckwheat for antitumor activity. The species *F. cymosum* Meisn has been used in China for some time to treat various lung diseases, including cancer. It was found through experiments that the extract from *F. cymosum* has inhibitory effects on cancer cells in other human body parts such as the liver, colon, leukocytes or bones. Buckwheat extracts have no effect on the prostate, cervical, ovarian, and brain cancer cells, and the *F. cymosum* extract is not recommended for breast cancer cells (MCF-7) because it stimulates the growth of these cells (**Chan, 2003)**.

Rutin is the most important compound concerning human health; the small intestine relatively poorly absorbs it, and most is only absorbed in the large intestine. An important role in the absorption of rutin is played by human intestinal bacteria, which use the ß-glucosidase and α-1-rhamnosidase enzymes to transform rutin into quercetin, which is more biologically available (**Tuyishime *et al*. 2018**). Rutin has the following effects on human health:

a) It prevents inflammation induced by UV light: When investigating the effects of rutin on the fibroblasts irradiated by UV light, it was found that rutin reduced the pro-inflammatory response induced by UV radiation, the formation of ROS, and it also increased the activity and levels of antioxidants and prevented protein modifications, especially the formation of the tyrosine derivatives (**Gegotek *et al*., 2017**).
b) Rutin also has antidiabetic effects: Rutin was administered orally with pioglitazone for three weeks in the experiments with rats in which type 2 diabetes was deliberately induced. The rat's body weight, plasma glucose level, glycosylated hemoglobin, pro-inflammatory cytokines and liver condition significantly improved. Rutin treatment also improved the beta islet structure and reversed hepatocyte hypertrophy. In the future, rutin may serve as a diabetic modulator in combination with standard antidiabetic drugs (**Niture *et al*., 2014**).
c) Rutin also has neuroprotective effects: A wide range of neurodegenerative diseases, including Alzheimer's disease, Parkinson's disease, and Huntington's disease, share common mechanisms such as neuronal loss, apoptosis, mitochondrial dysfunction, oxidative stress and inflammation. Several *in vivo* and *in vitro* studies have revealed that rutin can alleviate various neurodegenerative processes leading to the above diseases. Rutin causes a reduction of pro-inflammatory cytokines, improves antioxidant enzyme activities, reduces the mRNA expressions of pro-apoptotic genes, restores the activity of mitochondrial complex enzymes, and is involved in the plasticity and survival of neurons in the CNS (**Enogieru and Haylett, 2018**).
d) Together with quercetin, it also improves blood pressure: Animals with a high-salt diet showed an increased systolic, diastolic, pulse and mean arterial blood pressure. Groups of rats treated with rutin and quercetin for two weeks showed significant changes in the values of the above indicators compared to those with a high-salt diet. The rutin and quercetin treatment was more effective than high blood pressure drugs, which contain nifedipine as an active substance and have negative side effects (**Olaleye *et al*., 2014**).
e) Rutin also lowers cholesterol levels: Male rats were fed a high-cholesterol diet followed by rutin alone or combined with lovastatin for four weeks to study the hypocholesterolemic effects of rutin on plasma lipid levels. Feeding the animals a high-cholesterol diet resulted in high hypercholesterolemia and increased serum LDL cholesterol (LDL-C) levels. Rutin – administered alone or in combination with lovastatin – significantly reduces total cholesterol and LDL-C levels, and it also significantly reduces liver enzymes and body weight in animals fed a high-cholesterol diet (**Ziaee *et al*., 2009**).

Exploitation of buckwheat

Buckwheat is primarily grown as a food for human consumption and animal feed, but it can also be used as green manure, a source of buckwheat honey or a crop to suppress weeds (**Campbell *et al*., 1997; Bhardwaj and Hamama, 2020**).

Buckwheat is eaten in different ways in different countries. Buckwheat noodles are typical for Japan, while buckwheat flour is mixed with wheat flour to make pancakes, cereals and pasta in Europe and North America. Buckwheat groats, used to make soups and porridges, are traditional in Russia and Poland. In Sweden, buckwheat is used as a filling when preparing fish. In Southeast Asia, buckwheat is used as a staple food in preparing unleavened bread – chapati, and paratha is made when buckwheat flour is mixed with potatoes (**Campbell *et al*., 1997**). Vinegar and various alcoholic and non-alcoholic beverages, such as buckwheat beer and tea, are also produced from buckwheat. In addition, buckwheat sprouts are consumed as fresh vegetables or preserved (**Cai *et al*., 2016**).

The buckwheat biomass has a higher protein concentration than other feeds (approximately 21%), but the oil content (6%) is lower than, for example, in soybean feed. The concentrations of minerals P, K, Ca, Mg and Zn are higher than in alfalfa hay. Based on the above, buckwheat appears desirable forage, especially during the summer when other crops, such as corn or soybean, die due to drought (**Bhardwaj and Hamama, 2020**). The effects of buckwheat as feed for ruminants were investigated in the experiments with an artificial rumen (Rusitec). It was found that buckwheat feed has no effect on the composition and concentration of short-chain fatty acids. When fresh buckwheat was used, the ammonia concentration in the rumen was reduced, and the estimated growth efficiency of microbial nitrogen was increased. Silage buckwheat did not exhibit these effects. Fresh buckwheat also reduced the number of bacteria in the incubated liquid, while silage buckwheat reduced the level of the holotrich protozoa. Buckwheat had no

effect on the production of methane. It was also found that partial substitution of corn silage with buckwheat silage had no adverse effects on feed intake, milk yield or milk composition and appeared to be suitable for the nutrition of ruminants (**Amelchanka *et al*., 2010**).

Buckwheat is a fast-growing crop, which allows it to suppress weeds by shading and preventing them from accessing nutrients and soil moisture. For this reason, it is used as a cover crop, which is planted before or alongside a slower-growing crop such as legumes. In addition, the buckwheat plant contains substances that have an allelopathic effect on weeds. Even the non-living parts of the plant retain this effect for up to 30-60 days. Buckwheat can absorb soil-based inorganic phosphorus better than other plants because its roots secrete substances during the growth phase that allow phosphorus to be dissolved and processed. Buckwheat roots have a high storage capacity for inorganic phosphorus. When buckwheat is introduced into the soil, it quickly breaks down, making phosphorus and other nutrients available to other plants. Moreover, buckwheat improves soil quality by improving the structure of topsoil, making it more friable, improving its slope and increasing the water infiltration rates (**Valenzuela and Smith, 2002; Possinger *et al*., 2013**).

Buckwheat honey mainly contains carbohydrates – primarily the monosaccharides such as glucose and fructose, with the fructose content slightly higher. In contrast to other types of honey, buckwheat honey has a relatively high amount of proteins (1.83 $mg.g^{-1}$), which indicates its high nutritional value. It also contains minerals such as Mg, Ca, Na, K, Fe, Mn, Zn, B and others, which favorably affect the vital functions of the human body. Buckwheat honey also contains phenolic compounds, mainly p-hydroxybenzoic acid, chlorogenic acid and p-coumaric acid. Buckwheat honey shows antibacterial activity against *Staphylococcus aureus* and *Pseudomonas aeruginosa* and exhibits antioxidant activity (**Deng *et al*., 2018**). Recent research has also found that phenols and oligosaccharides in buckwheat honey benefit the human gut by selectively promoting the growth of native probiotic bacteria and suppressing the growth of pathogenic bacteria (**Jiang *et al*., 2020**).

Genomic characteristics of buckwheat

Common buckwheat is an interesting crop, and several programs are dedicated to its breeding. A draft of the buckwheat genome composition was created to accelerate the molecular breeding programs using next-generation sequencing (NGS). After the collection of short reads, altogether, 387,594 sequences were determined as the draft genome. The total length of the common buckwheat genome sequences was 1.177 Gb, i.e. approximately 1.2 Gb. The genome contains 286,768 coding sequences, including those related to transposable elements with a total length of approximately 0.213 Gb; which constitutes 18% of the genome (**Yasui *et al*., 2016**). The tartary buckwheat genome is considerably shorter. Its length is approximately 0.489 Gb. This length contains 33,336 genes that are transcribed into mRNA (**Zhang *et al*., 2017**). It is assumed that the genome length between common buckwheat and tartary buckwheat is mainly due to the high content of transposable elements in the genome of common buckwheat (**Penin *et al*., 2021**). The ability of buckwheat to tolerate high levels of abiotic stress has been attributed to the expansion of several genes involved in signal transduction, gene regulation and membrane transport (**Zhang *et al*., 2017**). Flow cytometry also revealed that the genome length can vary significantly between buckwheat species. The longest genome was determined in *F. urophyllum* – 1.85 Gb, *F. pleioramosum* – 1.47 Gb, and on the contrary, *F. statice* had the shortest genome – 0.65 Gb. Also the genome length of tartary buckwheat detected by whole-genome shotgun sequencing differs slightly from flow cytometry's (0.489 Gb to 0.53 Gb) (**Nagano *et al*., 2000**).

Current studies are also devoted to extranuclear DNA, i.e. in the chloroplasts and mitochondria of buckwheat. The chloroplast genome of tartary buckwheat is 159,272 kb long, so it is slightly shorter than the chloroplast genome of common buckwheat (159,999 kb). The chloroplast genome of both species has the same orientation, order and content of genes, and variability only occurs in the frequency of tandem and palindromic repeats and the connecting regions. The nucleotides and amino acids of both genomes have coding sequences that show a 98% homology, and four genes (*rpo*C2, *ycf*3, *acc*D, and *clp*P) have a high synonymous value (Ks) (**Hong and Cho, 2018**). The chloroplast genome of *Fagopyrum esculentum ssp. ancestrale*, a progenitor of common buckwheat, is similar to the chloroplast genome of spinach in gene ordering and composition. However, these genomes differ in the presence of an intron in the *rpl2* gene, a shift mutation in the *rpl23* gene and an extended inverted repeat region in a way to include the *ycf1* gene in the buckwheat genome. Phylogenetic analysis has confirmed that the *Caryophyllales* group, including buckwheat and asterids, are sister relatives (**Logacheva *et al*., 2008**). The *F. dibotrys* species has a chloroplast genome of 159,9 kb. This genome has a tetrahedral structure and consists of a pair of inverted repeat regions separated by a large single-copy region. According to the analyses, the chloroplast genome of *F. dibotrys* contained 131 genes, including 80 protein-coding genes, 28 tRNA genes and four rRNA genes. The phylogenetic analyses of the chloroplast genome showed that *F. dibotrys* and *F. tataricum* are closely related (**Wang *et al*., 2018**).

The buckwheat's mitochondrial genome comprises ten circular chromosomes with a total length of 404 kb. It contains all the genes typical of plant mitochondrial genomes and long inserts originating in plastids (approximately 6.4% of the total length of the mitochondrial genome). When the genetic diversity of buckwheat mitochondrial and plastid genomes in 11 buckwheat cultivars with the wild ancestor *F. esculentum ssp. ancestrale* was characterised, diversity among the cultivars was surprisingly low. There were only 1-2 variations in the plastid genome and 3-6 variations in the mitochondrial genome.

Conversely, the divergence between the cultivars and *F. esculentum ssp. ancestrale* is significantly higher: in the mitochondrial genome, variability was identified in 220 positions and 159 positions in the plastid genome. The SNP in the plastid genome is enriched with non-synonymous substitutions, especially in the genes involved in photosynthesis – *psb*A, *psb*C and *psb*H (**Logacheva *et al*., 2020**).

After sequencing the buckwheat genome to design the microsatellite markers, it was found that the total number of microsatellites in the buckwheat genome is 37572, with a frequency of 83.25 microsatellites per 1 Mb. The most frequently occurring dinucleotide microsatellites were AT/TA (65.85%). From the total number of microsatellites, they managed to design 26,549 markers, of which 2,643 were gene microsatellite markers. These microsatellite markers were physically mapped to eight chromosomes of tartary buckwheat, and the first physical map was constructed with an average density of 58.82 markers per Mb. The numerous novel microsatellite markers and their location on the physical map provide a valuable resource for studying diversity, constructing genetic maps, functional gene mapping, and exploring QTL (**Fang *et al*., 2019**).

Genomic analyses of buckwheat using molecular markers

Genomic analyses make it possible to identify important genes in a crop and analyze the population structure. Different types of genetic markers have been developed for *Fagopyrum esculentum* Moench. Morphological and allozyme markers were used from the 1980s until the beginning of the 21st century, enabling the construction of linkage maps. The studies using these markers have shown that *Fagopyrum esculentum* Moench most likely originated from the Sanjiang region of China. The end of the 1990s and the beginning of the 21st century marked the advent of PCR technology, which enabled the creation of advanced markers. However, PCR-based markers were not initially able to analyze the whole buckwheat genome, and this was only made possible by the subsequent development of next-generation sequencing techniques. Currently, 8,884 markers have been proposed, spanning 756 loci. These markers have been used for genomic selection to increase yields (**Yasui, 2020**).

Buckwheat breeders are trying to improve the buckwheat genome to improve its morphological and physiological characteristics. To this aim, mutations in the genome were introduced, which were formed evolutionarily, i.e. by random changes during the crossing. Moreover, recombination using interspecies hybridization and selective selection of promising individuals from populations was also used (**Taranenko *et al*., 2018**).

Using SSR (Simple Sequence Repeat) markers, it was found that the uncontrolled production of common buckwheat in Bosnia and Herzegovina led to the loss of genetic purity of the 'Darja' variety. In the future, these problems can be avoided by using certified buckwheat material (**Grahic et al., 2017**).

Using 10 SSR markers and 32 morphological markers (e.g. plant height (cm), number of internodes, stem color, leaf color, and others), it was found that among 3 buckwheat cultivars ('Čebelica', 'Darja' and 'Goluba'), the highest relatedness is found in 'Goluba' and 'Čebelica' (**Grahic *et al*., 2018**).

Using 7 SCoT (Start Codon Targeted) (primers and an annealing temperature of 50 °C, it was possible to demonstrate polymorphism in 17 buckwheat cultivars. Based on hierarchical cluster analysis, it was found that the genetically closest varieties to each other are Russian Ballada and Austrian Bamba, and the variety from the USA (Madawaska) is the most different from all varieties (**Balazova *et al*., 2018**).

The DNA markers corresponding to single- to four-nucleotide polymorphism, which made it possible to distinguish two varieties of buckwheat from Japan – "Manten-Kirari" and "Hokkai T8", were developed based on the RNA polymorphism because 17.76 GB of sequences of RNA of the 'Manten-Kirari' variety were sequenced using next-generation sequencing methods. Of these sequences, 11358 contigs were generated de novo, and 8 DNA markers were subsequently created from them. A total of 8 DNA markers are needed to distinguish the variety "Manten-Kirari" from "Hokkai T8", and only three markers are needed to distinguish "Manten-Kirari" from tartary buckwheat, and only two from common buckwheat (**Katsu *et al*., 2019)**.

Additionally, 18 gene-specific STS (Sequence-Tagged Site) markers were developed and subsequently tested on 91 buckwheat samples to analyze the allelic diversity at these loci. The plant material came primarily from the Indian part of the Himalayas. Of the total number of 27 loci, only 18 were able to amplify the PCR product after adding STS markers. Apart from 4 STS markers, the majority only showed moderate polymorphism. These 4 STS markers – BW10, BW12, BW22 and BW27 – showed high polymorphism and can be used for further genomic analyses (**Archak *et al*., 2017)**.

Equally important are the markers that can detect the loci and the genes occurring on them, which are related to resistance to premature germination (PHS). PHS is the pre-harvest or premature germination that damages the nutritional composition of the plant. PHS is most likely to increase with global warming. A total of 300 markers were generated using the whole-genome next-generation sequencing

(NGS) techniques, from which 100 markers associated with PHS tolerance were developed using the NGS-based bulk segregation analysis (NGS-BSA). With the help of these markers, genetic maps were subsequently developed that allow rapid detection of polymorphisms (**Takeshima *et al*., 2021**).

The S locus was studied by **Mizuno and Yasui (2019),** who determined the genotypes of common buckwheat by sequencing and found that buckwheat showed a high nucleotide diversity (0.0065) compared to other distantly crossed plants. Based on single-nucleotide polymorphism, the common buckwheat varieties were divided into the European and Asian groups, with lower diversity (0.0055) between the individual varieties in the European group and low differentiation between the Asian and European groups. These results indicate the genetic differences that formed during the spread of buckwheat from Asia to Europe and the recent intensive cultivation and selection of buckwheat varieties in Europe.

Bashir *et al*. (2021) investigated the polymorphism of common buckwheat from the Jammu, Kashmir and Ladakh regions. The polymorphism of 52 genotypes of common buckwheat was investigated using 15 SSR markers, which identified 143 alleles, most of which were polymorphic with an average of 9 alleles per primer. Of these 15 SSR markers, only seven could be amplified by PCR in tartary buckwheat, which were then used to study the genetic variability of 110 genotypes of tartary buckwheat.

Common buckwheat has two progenitors: *F. esculentum subsp. ancestrale* and *F. homotropicum*. In order to determine the genetic diversity among these species, **Ohsako *et al*. (2017)** used SSR markers. In total, 174 alleles were detected in the 11 loci in 9 samples of *F. esculentum subsp. ancestrale* and 7 samples *of F. homotropicum*. *F. esculentum subsp. Ancestrale* contained more alleles per locus (6–26, with an average of 14.27) than *F. homotropicum* (2–8, with an average of 5.09). The total genetic diversity for each locus was also higher in the samples of *F. esculentum subsp. ancestrale* (0.673 – 0.941) than in *F. homotropicum* (0.320 – 0.783). Based on the microsatellite variability, the populations of *F. esculentum subsp. ancestrale* were divided into northern and southern groups. The northern group included five populations: three from Tibet (C0142, C2013 and C0206) and two from Yunnan (C0413 and C0203), and the southern group included three populations from Yunnan (C9802, C2021 and C9138) and one population from southern Sichuan (C9803). The populations from the southern group were mixed with *F. homotropicum*, forming a monophyletic group. Overall, the diversity of the *F. homotropicum* populations is half that of *F. esculentum subsp. ancestrale*.

Tartary buckwheat is a more nutritious crop than common buckwheat, but its processing is significantly more complicated due to the difficult dehulling of the grains and their separation from the peels. For this reason, there is an effort to develop such varieties of tartary buckwheat that would employ more accessible methods for dehulling the grains. In order to identify the gene that determines easy dehulling, recombinant XJ-RIL buckwheat lines were used, created by crossing the easy-to-peel variety Rice (a variety of the wild-growing common buckwheat and cultivated tartary buckwheat) and tartary buckwheat of the Jin-qiaomai 2 variety. Using the SNP markers, a genetic map consisting of 8 linkage groups containing 122,185 SNPs (Single Nucleotide Polymorphisms) covering 1444.15 cM, with an average distance of 0.35 cM between the neighbouring markers, was constructed. In total, nine quantitative trait loci (QTL) were identified that affect the genes related to easy grain dehulling. A major and reliable locus for the TGW genes that affect the peel type was mapped to the 38.2–39.8 cM region in chromosome 1, and it was found to be responsible for 23.6–47.5% of the phenotypic variation (**Shi *et al*., 2021**).

Facho *et al*. (2019) looked at the genetic diversity of buckwheat in the Pakistani part of the Himalayas. They analyzed a total of 21 common buckwheat and 15 tartary buckwheat samples from 7 different districts of Gilgit-Baltistan using the SSR markers. Substantial differences were identified between common buckwheat and tartary buckwheat (FST = 0.331), indicating that they do not cross with each other. The common buckwheat samples revealed a higher genotypic diversity (1.00) than tartary buckwheat (0.983).

The investigation of the genetic polymorphism of 5 varieties of common buckwheat using the ISSR (Inter Simple Sequence Repeat) markers was done by **Klykov *et al*. (2019)**. After the amplification with ISSR markers, 106 products were generated, of which 105 were polymorphic and one monomorphic product. Intraspecific polymorphism ranged from 50% (Izumrud) and 50.94% (Bashkirskaya krasnostebelnaya) to 75.47% (Cheremshanka). According to the results of the ISSR analysis, the Izumrud, Krasnoznamennaya Bashkirskaya, and Kitawasesoba 1 varieties show the most remarkable genetic differences and are therefore recommended for breeding to create new genotypes with a high content of flavonoids.

Transcriptomic analyses of buckwheat

Zhang *et al*. (2018) investigated the effect of light on the expression of genes involved in the synthesis of flavonoids in buckwheat. The transcription factor FtMYB116 can be found among these genes, which binds directly to the promoter region of flavonoid-3'-hydroxylase (F3'H) and induces its expression, thereby promoting the synthesis of rutin. This transcription factor can be induced by blue and red light. This study suggests that red and blue light support the increase of flavonoid content in buckwheat, with blue light with a wavelength of 470 nm being the most effective, followed by red light (670 nm), and red light with a wavelength of 735 nm.

Black tartary buckwheat is also termed a "black pearl" because it contains higher levels of rutin than ordinary tartary buckwheat. Using the RNA-seq technology, approximately 48.4 million reads were generated and sequenced into 57,800 genes. By analyzing these genes, it was found that, compared to common buckwheat, black tartary buckwheat has a higher content of genes encoding phenylalanine ammonia lyase (PAL), chalcone synthase (CHS) and chalcone isomerase (CHI), which serve for the synthesis of flavonoids and the gene encoding quercetin 3-O-glucosyltransferase (UF3GT), which serves for the synthesis of rutin. On the contrary, the genes encoding flavonol synthase (FLS), which correspond to the synthesis of kaempferol and quercetin, were identified at a lower level. For this reason, black tartary buckwheat has a higher rutin content and a lower quercetin content than ordinary tartary buckwheat **(Yao *et al.* 2017)**.

The R2R3-MYB transcription factors that regulate flavonoid metabolism and trichome formation, as both flavonoids and trichomes play an important role in plant defence mechanisms, have been investigated by **Huang *et al*. (2019)**. They managed to discover the FtMYB8 transcription factor whose coding region is 729 bp long, and after expression, an MYB protein with a length of 242 amino acids is formed. In addition, they found that the highest expression of *FtMYB8* at each developmental stage is in buds and roots, and the lowest in leaves and stems. While darkness has no significant effect on the expression of this gene, UV-B exposure leads to a rapid accumulation of *FtMYB8* mRNA. Methyl jasmonate and abscisic acid also have a significant effect on *FtMYB8* expression.

Sun *et al*. (2019) analyzed the transcription factor FtMYB31 in trtary buckwheat, which, similar to *FtMYB8*, belongs to the group of R2R3-MYB transcription factors. FtMYB31 positively regulates the synthesis of flavonoids in tartary buckwheat, and can increase the expression of the *CHS*, *F3H* and *FLS* genes in a heterologous system and thus positively influence the accumulation of rutin and total flavonoids in the plant.

The transcriptome analysis of two varieties of common buckwheat revealed the mechanism by which anthocyanins accumulate in the cotyledons and flowers of common buckwheat (**Fang *et al*. 2019)**. The HHTQ variety of common buckwheat has distinctly red cotyledons, leaves and petals in the different growth stages, while the Beizaosheng variety has green leaves and white flowers. In total, two types of anthocyanins were identified – cyanidin 3-O-gulcoside and cyanidin 3-O-rutinoside. The highest levels of these anthocyanins were found in the cotyledon of the HHTQ cultivar, with the total anthocyanin levels in the flowers of the HHTQ cultivar being 7.51 times higher than those of the Beizaosheng cultivar, and 5.12 times higher in the cotyledons than those of the Beizaosheng cultivar. Subsequently, 9050 genes with different expression levels involved in anthocyanin biosynthesis were identified by RNA-seq.

The genes belonging to the bZIP family of transcription factors in tartary buckwheat were identified by **Liu *et al*. (2019a)**. These transcription factors are important in light signals, seed maturation, cell elongation, flower development, stress, and other biological processes. In total, 96 *FtbZIP* genes were discovered in tartary buckwheat, which were divided into 11 groups based on their genetic relatedness to 70 *AtbZIP* genes from *Arabidopsis thaliana.* Evolutionary analyses revealed that, the *FtbZIP* genes of buckwheat are most closely related to those of soybean.

Li *et al*. (2019) investigated FtbZIP83, which belongs to the group of bZIP transcription factors and improves the drought and high salt tolerance of trtary buckwheat. The induction of this gene can be triggered by abscisic acid, polyethylene glycol and NaCl. This gene can be transformed into *Arabidopsis thaliana* by *Agrobacterium* strain GV3101, with the modified plants having increased drought and salt tolerance.

A total of 247 miRNAs were identified in common buckwheat, including up to 15,403 potential target genes. Significant increases or decreases in the expression of 49 miRNAs (31 conserved and 18 novel miRNAs) were observed between different developmental stages. These miRNAs may play an important regulatory role in common buckwheat seed development (**Hongyou et al., 2020**). On the contrary, 230 miRNAs were identified in tartary buckwheat, with 25 miRNAs differentially expressed during different seed development stages. 65 mRNA targets of these miRNAs were identified. **(Li *et al*. 2021).** The highest expression levels among the known miRNAs were observed in fta-miR159, which is consistent with previous findings of **Li *et al.* (2020),** who reported that fes-miR159 was the most abundant miRNA in the common buckwheat transcriptome. The miR159 family members have been shown to participate in crucial biological processes, such as seed development and germination in Arabidopsis, rice and wheat **(Zhao *et al.* 2017; Millar *et al.* 2019; Jiang *et al.* 2022; Niazi *et al.* 2022).** **Peng *et al.* (2014)** also observed an increase in the miR159 expression levels during seed development in rice. **Li *et al.* (2021)** also identified miR156, miR160, miR166, miR167, miR168, miR395, miR396, miR397, miR398, miR399 and miR408 as the potential regulators of seed development in tartary buckwheat. In a study by **Song *et al.* (2022),** the impact of various salinity conditions on the miRNA regulation patterns in tartary buckwheat was investigated. The authors analyzed the transcriptomes of 4 cultivars of tartary buckwheat seedlings (two cultivars and their mutants that have undergone natural mutagenesis in saline-alkali soil). Out of the 770 known miRNAs and 264 novel miRNAs identified in this study, 19 miRNAs were reportedly affected by salt stress, including miR156-z,

miR157-x, miR172-x, and miR393-y. Many of the genes cleaved by these miRNAs were classified as transcription factors and associated with metabolic processes, cellular processes and biological regulation. It has also been suggested that miR157-x plays an important role in enhancing salt tolerance in mutant plants **(Song *et al.* 2022).**

However, the development of common buckwheat seeds is affected by miRNAs and other genes. **Hongyou *et al*. (2019)** investigated the molecular mechanisms involved in the development of common buckwheat seeds. Nine libraries were constructed for three common buckwheat samples, which were analyzed using RNA-seq at different developmental stages. A total of 248.53 million reads were generated, narrowed down to 242.86 million after the removal of the adapter sequence and low-quality reads. From the total number of identified genes (54,582), a total of 4619 genes were identified in three different developmental stages of common buckwheat with different expressions in the individual stages. These genes included those responsible for the Ca^{2+} signal transduction pathway (genes encoding the calmodulin-like proteins CML and calmodulin-binding proteins CBL, genes responsible for the cation exchange with Ca^{2+} CCX...), hormone signal transduction pathways (auxin, abscisic acid, ethylene, jasmonate, cytokinin...), transcription factors (mainly FAR1, C2H2, AP2, bHLH, MYB and others) and genes related to starch synthesis. Eighteen of these genes were identified as key candidate genes for seed size, and qRT-PCR confirmed their identification. Seed size is a critical factor in determining crop seed yield.

Liu *et al.* (2019a) analyzed heat shock transcription factors (FtHsf), which help organisms resist high temperatures and regulate plant growth and development. In total, 29 *FtHsf* genes were identified in tartary buckwheat on eight chromosomes. Their expression produces proteins ranging in size from 216 (FtHsf5) to 503 amino acids (FtHsf17). Most *FtHsf* genes contain only one intron, and only four genes (*FtHsf2, FtHsf5, FtHsf6* and *FtHsf9*) contain two introns. The expression levels of FtHsf varied significantly in the tissues and developmental stages, suggesting that individual genes may have different functions. Three *FtHsf* genes were significantly expressed in fruits (*FtHsf18, FtHsf19, FtHsf22*) and seven *FtHsf* genes (*FtHsf10, FtHsf9, FtHsf6, FtHsf15, FtHsf4, FtHsf16, FtHsf5*) in flowers. Except for two *FtHsf* genes (FtHsf20/FtHsf5), other genes showed high expression in leaves, and most *FtHsf* genes had high expression in the stem. The analyses revealed that the expression of almost all *FtHsf* genes changed during three different developmental stages.

The GRAS transcription factors responsible for plant growth and development were analyzed by **Liu *et al*. (2019b)**. In total, 47 *FtGRAS* genes were identified on eight chromosomes from the tartary buckwheat genome, which differ from each other in the distribution of their expression products. Based on the similarity of the amino acid sequences of FtGRAS proteins in tartary buckwheat and the GRAS proteins in *Arabidopsis thaliana*, the *FtGRAS* genes of tartary buckwheat were divided into 10 groups: LAS, SCL4/7, HAM, SCR, DLT, SCL3, DELLA, PAT1, SHR and LISCL. The LISCL group had the highest amount of *FtGRAS* genes (19), while the SCL4/7, LAS and DLT groups only had one *FtGRAS* gene each.

Increasing the concentration of salts in the soil is a current trend with adverse effects on agricultural production. For this reason, **Wu *et al*. (2017)** conducted a study on how salt concentrations affect tartary buckwheat. Salt content can significantly influence the physiological activities of tartary buckwheat. Further analyses revealed that tartary buckwheat activates the metabolism of carbohydrates and amino acids and various signal transduction and translation events under stress caused by a high concentration of salts. Using the PlantTFcat online tool, 93 families of transcription factors were identified, many of which serve as the plant's defence mechanism against abiotic stress. The most represented transcription factors were “C2H2” (15.2%), “WD40” (9.2%), “MYB-HB” (6.2%), “CCHC” (5.7%), “PHD” (4.8%), “bHLH” (3.9%), “AP2-EREBP” (3.4%) and “bZIP” (3.1%).

Similar research was also conducted by **Lu *et al*. (2018)**, who identified 55 families of transcription factors, of which the following had the highest representation: "bHLH" (8.57%), "ERF" (6.99%), "bZIP" (5.59%), "C2H2" (5.51%), "MYB" (5.24%), “NAC” (4.63%), “WRKY” (4.2%) and the factors related to “MYB” (5.33%). Also, 43,772 transcriptomic sequences were screened, from which 2503 potential SSR markers were identified. Trinucleotide (55.49%) was the most frequent type of SSR, followed by dinucleotide (30.40%). Of the trinucleotide SSR markers, most markers had a repeat unit count of five.

Song *et al*. (2021) using RNA-seq, found 42 unigenes in four varieties of tartary buckwheat, that had different expression after the exposure to NaCl solution for 48 hours. They deduced that these differentially expressed genes could play a role in the response of tartary buckwheat to a saline environment.

The Trihelix transcription factors in tartary buckwheat, which play a role in response to light, leaf development, seed maturation, resistance to biological and abiotic stress, and others, were analyzed by **Ma *et al*. (2019)**. In total, 31 Trihelix genes were identified using the BLAST method on seven chromosomes (chromosome 6 does not contain the Trihelix genes), except for two genes located in the chloroplasts – all others were located in the nucleus. Based on the phylogenetic relationship with 29 Trihelix genes from Arabidopsis thaliana, the Trihelix genes of tartary buckwheat were divided into five groups: *GT-1, GT-2, SH4, GTγ* and *SIP1*.

Proteomics analyses of buckwheat

Proteomics is a scientific discipline that deals with the structure, biochemical and cellular functions of all proteins in the organism. It studies mutual interactions of proteins with subsequent determination of their expression in different cells of a given organism, their subcellular localization in different organelles, post-translational modification, as well as the relationship between structure and their function. The proteome can be examined using two-dimensional electrophoresis or ionization mass spectrometry techniques, including matrix-assisted desorption/ionization (MALDI) and electrospray ionization (ESI).

The research on plant proteome was also focusing on buckwheat seeds. Buckwheat seeds contain 12-15% proteins, of which 70% are globulins, 12.5% albumins, 2.9% prolamins and 8.0% glutelins (**Suzuki *et al.* 2020**; **Chrungoo and Chettry, 2021**). The buckwheat seed albumins show a sedimentation coefficient of 2S and a molecular weight (MM) in the range of 8 to 12 kDa. One of the characteristic traits of these proteins is that disulfide bonds do not connect them. The 2S albumins are also found in the seeds of dicots, and are similar to 2S albumins from wheat and trypsin inhibitors and α-amylases from cereals. The 2S albumins are also found in legumes, where they are linked by disulfide bonds (**Shewry and Pandya, 1999**; **Radovic *et al*. 1999**). **Javorník and Kreft (1984)** separated the common buckwheat albumins using SDS–PAGE into eight electrophoretic bands whose molecular weight ranged from 17 to 67 kDa. The above results are from the results of **Guo and Yao (2006)**, who determined five main bands with a molecular weight of 64, 57, 52, 41 and 38 kDa in the non-reduced albumin fraction in tartary buckwheat. The secondary structure of buckwheat albumins is expected to consist of 2% α-helices, 46% β-sheets, and 52% irregular structure **(Janssen *et al.*, 2017)**. 13S globulin, which contains 5.9% lysine and 2.3% methionine, is the main storage protein of buckwheat seeds. Its molecular weight ranges from 280 to 390 kDa, and it consists of 6 non-identical monomers. The monomers interact in a non-covalent way, and each consists of a smaller (16 to 29 kDa) basic subunit linked to the larger (30 to 47 kDa) acidic subunit by disulfide bonds. Compared to other plant proteins, the buckwheat 13S globulin has a significantly higher ratio of lysine to arginine and methionine to arginine. The protein with a molecular weight of 26 kDa, which shows a 5.9% representation of lysine and 2.3% representation of methionine, is the basic subunit of the 13S globulin. The gene encoding this protein can be an interesting research object for breeders to improve the amino acid imbalance in cereals, which are generally deficient in lysine **(Chettry and Chrungoo, 2021)**. It has been shown that the secondary structure of 13S globulin is composed of 34.5% β-sheets, 20.0% β-helices, 16.0% α-helices and 14.4% random coils **(Choi *et al.*, 2006; Tang 2009)**.

The globulins in tartary buckwheat were characterized less extensively compared to common buckwheat. Based on SDS–PAGE, the globulins in buckwheat were separated into major globulin with MM 443 kDa. The globulin structure in buckwheat is made up of 25% α-helices, 30% β-sheets and 45% aperiodic structure, while the structure of 2S globulin is made up of 14% α-helices, 29% β-sheets and 57% aperiodic structure **(Janssen et al., 2017)**.

Skerritt (1986) separated the prolamin fraction of common buckwheat by SDS-PAGE and found that the proteins with MM in the range of 10 to 28 kDa were the dominant fraction. Smaller protein bands with MM in the range of 32-80 kDa were also defined. **Nałecz *et al.* (2009)** separated buckwheat prolamins into five subfractions by two-dimensional (2D) SDS-PAGE with molecular weights of 50 kDa (pIs 6.0 - 7.3), 39 kDa (pIs 6.2 - 6.8), 32 kDa (pIs 5.9), 31 to 59 kDa (pl 5.5) and 22 kDa (pIs 5.9 - 6.6). A 2D electrophoresis is a useful tool for detecting buckwheat prolamins, especially due to the lack of information about their sequencing in the databases, which prevents their direct identification using peptide-based mass spectrometry **(Nałecz *et al.*, 2009, Janssen *et al.*, 2017)**.

In SDS-PAGE, the tartary buckwheat prolamins showed two minor and two major protein bands with molecular weights of 14 and 20 kDa, as well as 15 and 17 kDa, which are not affected by the reducing agent. Two more bands with MM 26 and 29 kDa were observed under reducing conditions **(Guo and Yao 2006)**. The low proportion of prolamins and absence of α-gliadins, which is a key factor for the gluten-free nature of buckwheat seed proteins, makes buckwheat a healthy alternative in the diet of patients with gluten metabolism disorders, such as celiac disease, non-celiac gluten sensitivity and dermatitis herpetiformis **(Gálová *et al.*, 2019a; Rajnincová *et al.*, 2019)**.

The commonly grown buckwheat varieties show a high degree of glutelin polymorphism. Glutelins consist of 3 to 5 subunits linked by the disulfide bonds, and their MM ranges from 43 to 66 kDa **(Gao *et al.*, 2008)**. The tartary buckwheat seed glutelins separated in SDS-PAGE appear as faint and difficult-to-identify bands. Despite this, it is possible to distinguish nine electrophoretic subfractions with MM ranging from 12 to 66 kDa with a low degree of polymorphism **(Guo and Yao 2006, Janssen *et al.*, 2017).**

Until recently, the breeding of Tatary and common buckwheat aimed to achieve a high yield, reduced allergenic protein content and resistance to adverse agroecological environmental conditions. It has been proven that people with multiple allergies can also develop intolerance to buckwheat **(Luthar *et al.*, 2021)**, which may be due to proteins with a low molecular weight of 18–29 kDa in the seed embryo. So far, however, no studies have been published on the allergenicity of proteins in the endosperm and the aleurone layer **(Jin *et al.*, 2020)**.

The buckwheat grain embryo is a rich source of protein; therefore, breeding buckwheat with larger embryos is a possible strategy to increase the protein content of both tartary and common buckwheat seeds. Recently, special attention has been devoted to optimizing the nutritional quality of tartary and common buckwheat seeds to increase the protein content and achieve an optimal representation of amino acids. Lysine is the limiting amino acid that determines other amino acids' use in human nutrition. According to **Eggum (1980)**, common buckwheat contains 5.1% lysine in its protein, while wheat contains 2.6%, corn 2.8% and barley 3.7%. Compared to legumes, the representation of lysine in soy is 5.99% and 6.04% in beans. Considering the above, the biological value of buckwheat protein reaches 93%, and it is a mere 68% in soy and 51.1% in beans. The lower biological value of soy and bean proteins is due to the lower representation of sulfur-containing amino acids (methionine, cysteine). It has been proven that by using micro-particle-induced X-ray emission (micro-PIXE) it is possible to detect the sulfur content in different buckwheat seed structures (Pongrác et al., 2020; Lutar et al., 2021).

Although buckwheat seeds are a good source of high-value proteins, they also contain certain anti-nutritional substances, such as protease inhibitors, which reduce the digestibility of buckwheat proteins **(Kreft *et al.* 2016)**. Polyphenols, which are naturally present in tartary and common buckwheat, including rutin and quercetin, reduce the actual digestibility of proteins **(Gálová *et al.*, 2019; Kalinová *et al.*, 2019)**. **Ikeda *et al.* (1986)** states that phenolics and other common secondary metabolites have significant inhibitory effects on the *in vitro* peptidic and pancreatic digestion of globulin. It could be expected that the breeding of tartary and common buckwheat could focus on a lower content of polyphenols, which would increase the nutritional value of proteins. On the other hand, it should be noted that this could also negatively affect the polyphenol-protein complex and its benefits in the area of prevention of human diseases **(Wieslander *et al.* 2012)**.

CONCLUSION

Buckwheat is a pseudocereal originally from China, and it is currently grown mainly in Russia and China. In addition to being a honey crop, it is mainly used in the food and fodder production. It is classified as a functional food due to its unique nutritional composition. It contains a relatively large amount of proteins with valuable amino acids, so it is a suitable alternative for vegans, and it is gluten-free, which means people with celiac disease can consume it. Of the non-nitrogen substances, it abounds in starch and lipids with a high content of unsaturated fatty acids, vitamins, minerals and flavonoids, which have invaluable effects on human health. It has been found that rutin, which is mainly contained in tartary buckwheat, has a positive effect on diabetes, cholesterol levels, blood pressure and various neurodegenerative diseases. The buckwheat genome is being researched in an attempt to improve buckwheat properties, be it better resistance to adverse conditions or higher nutritional content, especially higher rutin content. Whole genome analyses with sequencing, SNP markers, but especially SSR markers, are currently used for the genomic analyses of buckwheat. The draft genome composition of common buckwheat and tartary buckwheat has been determined, revealing differences in genome length and the presence of transposable elements. The genomic studies have also shed light on the chloroplast and mitochondrial genomes of different buckwheat species, highlighting their similarities and differences. Molecular markers, including SSR markers and SNP markers, have been developed for buckwheat, enabling the analysis of population structure, genetic purity, relatedness among cultivars, and the identification of important genes. These markers have been important in genomic selection, genetic mapping, and exploring resistance traits. The genetic diversity among buckwheat varieties and populations has been assessed, providing valuable information for breeding programs. Using the whole genome next-generation sequencing (NGS) techniques, the markers associated with tolerance to premature germination have been developed. These markers were then utilized to construct genetic maps, facilitating the rapid detection of polymorphisms. Transcriptomic and proteomic analyses have provided valuable insights into the molecular mechanisms underlying the synthesis and regulation of flavonoids, anthocyanins, and other important compounds in buckwheat, focusing not only on gene expression related to flavonoid metabolism and defense reactions against stress but also on monitoring various biological events such as seed ripening, flower development, and cell elongation. Research is also focused on comparing the expression of genes before and after the exposure to stress to determine which genes influence the given type of stress. Many studies have identified key genes, transcription factors, and microRNAs involved in the biosynthesis pathways of secondary metabolites in buckwheat. The expression of these genes is influenced by various factors, such as light, temperature, salt stress, and hormone signaling. Additionally, the identification of transcription factors and their expression patterns has shed light on their roles in plant growth, development, and response to environmental stresses. These findings not only contribute to the basic understanding of buckwheat biology but also have practical implications for breeding programs aimed at improving buckwheat varieties with enhanced nutritional and agronomic traits. Future research in this field will continue to unravel the complexity of gene expression and regulatory networks in buckwheat, further widening its potential as a valuable crop.

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