REVIEW

Revisiting the versatile buckwheat: reinvigorating genetic gains through integrated breeding and genomics approach

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Abstract

Main conclusion **Emerging insights in buckwheat molecular genetics allow the integration of genomics driven breeding to revive this ancient crop of immense nutraceutical potential from Asia.**

Out of several thousand known edible plant species, only four crops-rice, wheat, maize and potato provide the largest proportion of daily nutrition to billions of people. While these crops are the primary supplier of carbohydrates, they lack essential amino acids and minerals for a balanced nutrition. The overdependence on only few crops makes the future cropping systems vulnerable to the predicted climate change. Diversifying food resources through incorporation of orphan or minor crops in modern cropping systems is one potential strategy to improve the nutritional security and mitigate the hostile weather patterns. One such crop is buckwheat, which can contribute to the agricultural sustainability as it grows in a wide range of environments, requires relatively low inputs and possess balanced amino acid and micronutrient profiles. Additionally, gluten-free nature of protein and nutraceutical properties of secondary metabolites make the crop a healthy alternative of wheat-based diet in developed countries. Despite enormous potential, efforts for the genetic improvement of buckwheat are considerably lagged behind the conventional cereal crops. With the draft genome sequences in hand, there is a great scope to speed up the progress of genetic improvement of buckwheat. This article outlines the state of the art in buckwheat research and provides concrete perspectives how modern breeding approaches can be implemented to accelerate the genetic gain. Our suggestions are transferable to many minor and underutilized crops to address the issue of limited genetic gain and low productivity.

Keywords Buckwheat · Genetic gain · Gluten free · Nutritional security · Underutilized crops

Introduction

Even though agricultural productivity has witnessed significant increases in the second half of the twentieth century, just over 12 crops provide 75% of the world's food supplies and three major crops, rice, wheat and maize provide 50% of global dietary requirements (FAO 2005). The narrow agricultural portfolio raises serious questions on how effectively major crops alone can contribute towards food security and poverty alleviation. The shrinking portfolio of species used in agriculture also reduces the ability of farmers and ecosystems to adapt to new environments, needs and opportunities. Addressing this concern requires broadening the focus of research and development to include a much wider range of crop species. Supplementation of major cereals with pseudocereals possessing better nutritive value and nutraceutical

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properties would be a potential strategy to improve dietary diversification to combat hidden hunger.

Buckwheat is one such versatile pseudocereal, grown over centuries for its grain (food & feed) and greens (vegetable & fodder). There are three cultivated species in the genus *Fagopyrum* (*F. esculentum*, *F. tataricum* and *F. cymosum*) (Fig. 1) which are predominantly diploids with 16 chromosome pairs and a small genome size of 1.2 Gbp and 48 Gbp for *F. esculentum* and *F. tataricum*, respectively (Yasui et al.

2016; Zhang et al. 2017). Common buckwheat (*F.esculentum*) is a widely cultivated species from Asia to Europe, North America and South Africa, whereas tartary buckwheat (*F.tataricum*) and *F.cymosum* are mainly confined to highlands of southwest China and Himalayas (Ohnishi 1998; Zhou et al. 2016). By virtue of its rich nutrient composition, there has been an increased interest in consumption of buckwheat as functional food such as naengmyeon (Korean cold noodles), Chinese noodles, Japanese soba and as an

Fig. 1 Phenotypes of three cultivated species of buckwheat. **a** Field view of *F. esculentum*. **b** Inflorescence of *F. esculentum*. **c** Field view of *F. tataricum*. **d** Inflorescence of *F. tataricum.* **e** Field view of *F. cymosum.* **f** Inflorescence of *F. cymosum*
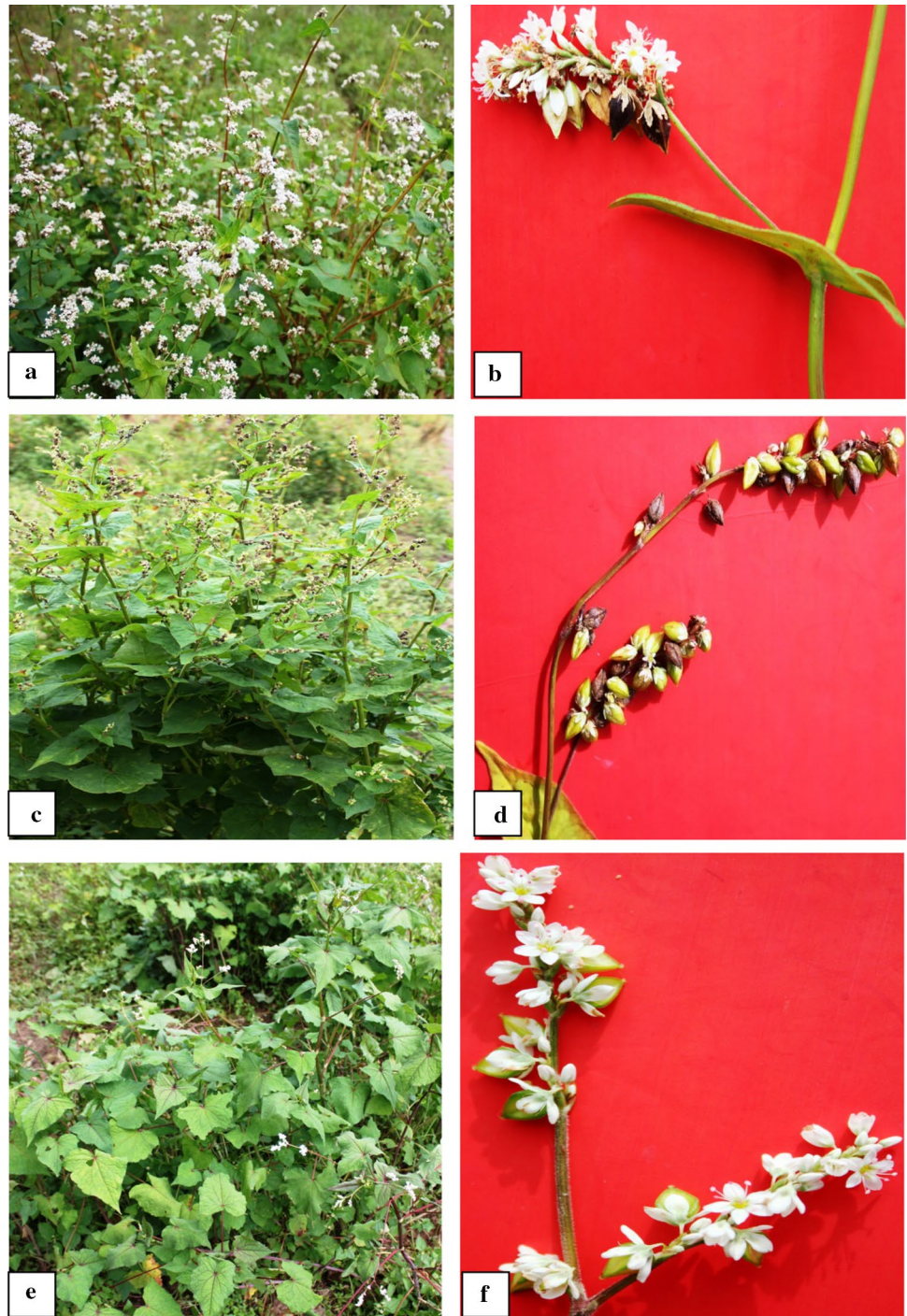
ingredient of cake, bread, pasta and pancake mixes in Asia, Europe, North America and Canada (Campbell 1997; Lee et al. 2016). The nutritional superiority over major cereals in terms of balanced amino acid profile of seed protein (Table 1) and bioactive flavonoids of diverse pharmaceutical uses makes it a highly valuable crop. Moreover, buckwheat has agricultural superiority over other commercial crops attributed to its ability to adapt under marginal and less input demanding cultivation including fragile hill and mountain regions (Zhou et al. 2016). Despite its immense agricultural value, global area under buckwheat cultivation and production in the last five decades have declined or remained stagnated compared to major cereals (Fig. 2). The continuous downfall in buckwheat area and production may be attributed to the lack of concentrated crop improvement efforts compared to major cereals. Appreciable genetic gain through conventional breeding has not been achieved in buckwheat due to a number of bottlenecks such as unsynchronized flowering; low seed yield and an inherited out-breeding mechanism (self-incompatibility) peculiar to common buckwheat
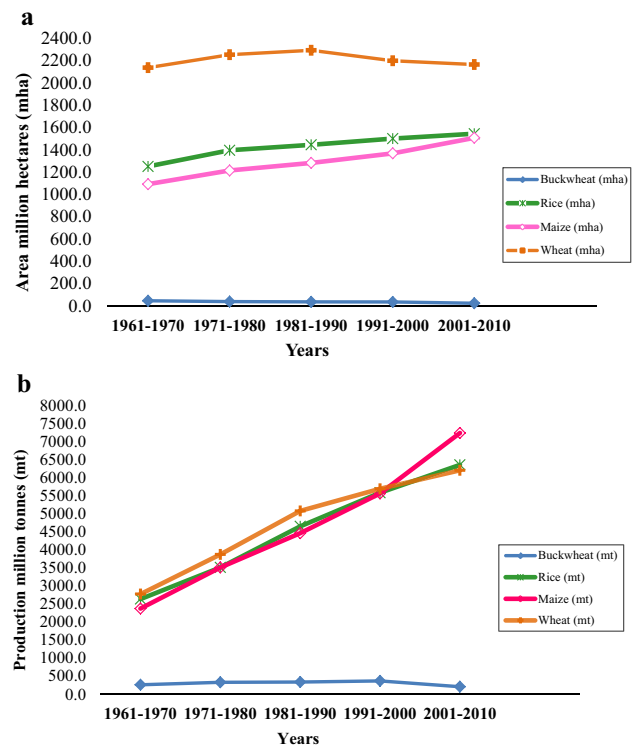
Fig. 2 Comparison of global trends in cultivation of buckwheat and three major cereals (FAOSTAT 2018). **a** The figure illustrates trends in area under cultivation over the last five decades. **b** The figure illustrates trends in production over the last five decades

(Neskovic et al. 1995; Woo et al. 1998). In this context, integration of cutting-edge biotechnological and 'omics' tools with conventional breeding technique is the key to leverage buckwheat genetic improvement. In the recent years, substantial advances have been made in buckwheat genetics that may assist in projecting it as a golden crop of future cropping systems. In the present article, we summarize the importance of buckwheat as a healthy alternative food as well as its origin, history, genetic resources, breeding, biotechnological and genomic advancements. We also provide concrete perspectives how to take benefits from emerging molecular breeding techniques to revive this ancient crop of immense agricultural value.

Phylogeny, origin and history

The genus *Fagopyrum* belongs to family Polygonaceae and includes 26 described species that includes diploids ($2n = 16$) and tetraploids ($2n = 4\times = 32$), of which *F.esculentum* is most important and widely cultivated (Zhou et al. 2018). All the species of the genus *Fagopyrum* are native to Asia and included into two groups: the big achene group (*cymosum* group) comprising eight; and the small

Table 1 Nutritional composition of buckwheat in comparison to three major cereals. Data from Campbell (1997), Kumar et al. (2016)

Nutrients	Buckwheat	Rice	Wheat	Maize
Proximate composition (per 100 g grain)				
Energy (Kcal)	355	345	346	365
Crude protein (%)	12.0	6.8	11.8	9.4
Total carbohydrates (g)	72.9	78.2	71.2	74.3
Total fiber (%)	17.8	4.5	12.5	7.5
Fat (g)	7.4	1.5	2.5	4.7
Moisture (%)	11.0	13.7	12.8	10.4
Minerals and trace elements (mg per 100 g grain)				
Calcium	110	10	30	7
Iron	4.0	0.7	3.5	2.7
Magnesium	390	65	138	127
Phosphorus	330	160	298	210
Manganese	3.4	0.5	2.3	1.9
Zinc	0.8	1.3	2.7	2.3
Potassium	450	268	284	287
Essential amino acids (% of total protein)				
Lysine	5.9	3.8	2.6	1.9
Methionine	3.7	3.0	3.5	3.2
Tryptophan	1.4	1.0	1.2	0.6
Leucine	6.7	8.2	6.3	13.0
Vitamins (mg per 100 g grain)				
Thiamine	3.3	0.06	0.5	0.4
Riboflavin	10.6	0.06	0.2	0.2
Niacin	18.0	1.9	5.5	3.6
Tocopherols	40.0	–	–	–
Pantothenic acid	11.0	–	–	–
Choline	440	–	–	–

achene group (*urophyllum* group) comprises sixteen species (Ohnishi and Matsuoka 1996). The species of the *cymosum* group have large lustreless achene partially covered with persistent perianths, whereas the species of the *urophyllum* group have small lustrous achenes completely covered with persistent perianths (Ohnishi 2016). The large achenes buckwheat group comprised of *F. esculentum*, *F.tataricum*, *F.homotropicum* and *F.cymosum*. The allotetraploid perennial species *F.cymosum* and its two diploid varieties *F.cymosum* var. *pilus* and *F*.cymosum var. *megaspartanium* of the large achene group form the cymosum complex (Chen 1999). These are closely related and readily cross within the complex (Ohnishi 2016). Reports based on meiotic behavior of hybrid chromosomes (Chen 2001), allozyme analyses (Chen et al. 2004) and DNA polymorphism (Ohsako and Ohnishi 2000; Li et al. 2013) revealed that *F. megaspartanium* and *F.pilus* of *cymosum* complex may be the progenitors of common buckwheat (*F. esculentum*) and tartary buckwheat (*F.tataricum*) respectively.

Buckwheat is one of the oldest domesticated crops from Asia. The centre of origin of buckwheat is thought to be in Central and Western China (Ohnishi 1988; Ohnishi and Konishi 2001). In China, the oldest findings of buckwheat came from a grave of Western Han Dynasty, where seeds of *F.esculentum* were dated first–second century old (Li and Yang 1992). The distribution suggests that cultivated buckwheat was probably introduced to Asian countries from northern and southern China about 3000 years ago by both land and sea routes (Nagatomo 1984; Murai and Ohnishi 1996). In Europe, widespread cultivation of buckwheat started only in the middle ages but archaeological records of collected seeds date back to the first or second century (Ohnishi 1993).

Botanical description

The buckwheat plant is an annual or perennial herb growing 0.5–2.5 m tall characterized by hollow, branched or unbranched reddish colour stems bearing either white or pink flowers (Zhou et al. 2018). The plants are generally characterized by large cordiform petiolate leaves with ovate-triangular to triangular blades (Joshi and Paroda 1991). Buckwheat is short duration and fast growing crop and completes the life cycle from seeds to seeds in 70–90 days (Campbell 1995). Buckwheat possesses a shallow taproot system extending up to 1–2.0 m. depth and constitutes 3–4% of total plant biomass (Woo et al. 2016). The shallow root system makes the buckwheat plant susceptible to extreme moisture stress conditions, which usually occur in delayed planting conditions (Campbell 1997). The inflorescence is a raceme in which flowers are densely clustered at the end of branches (Joshi and Paroda 1991). The flowers are perfect

but incomplete and vary from white, light green, pink to dark pink in colour (Cawoy et al. 2009). The two main cultivated species of buckwheat namely common buckwheat (*F.esculentum*) and Tartary buckwheat (*F.tataricum*) can be easily discriminated through floral morphology and pollination behavior (Woo et al. 2010). In general, common buckwheat is characterized by dimorphic flowers, producing either a pin type (long pistil and short stamen) and thrum type (short pistil and long stamen) flowers, which leads to self incompatibly, whereas tartary buckwheat is comprised of homomorphic flowers, capable of self-fertilization (Woo et al. 2010, 2016). However, genotypes bearing only one type of flower with pistils and stamens of similar length have been reported in *F.esculentum* (Marshall 1969; Fesenko and Antonov 1973). The pistil is characterized by a unicellular superior ovary and a single style with knob-like stigma surrounded by eight stamens (Campbell 1997). Generally, both the species are characterized by triangular nut shaped; winged seeds and vary in colour from brown, silver grey to black (Farooq and Tahir 1987). However, seeds of tartary buckwheat taste bitter compared to seeds of common buckwheat due to the presence of high content of rutin (Rana et al. 2016).

Growth, development and agronomic attributes

In general, buckwheat completes its life cycle in 70–90 days (Campbell 1997); under unfavorable conditions it may extend up to 130–150 days (Michiyama and Hayashi 1998). Although buckwheat can grow in wide range of environmental conditions, it performs best in moist and cool climate. It prefers well-drained sandy soils but thrives well in drained marshland, marginal land and acidic soils (pH < 5) (Hore and Rathic 2002). Sowing time is one of the essential parameter for optimum buckwheat production and it depends on various agro-climatic conditions particularly temperature. For proper growth of the plant, the optimum temperature range is 18–23 °C. While low temperature (below 10 °C) generally delays or inhibits the flowering (Bjorkman 2000), high temperature (above 30 °C) is reported to cause abortion of ovule and embryo sac malformation (Gang and Yu 1998). It has been observed that exposure of buckwheat plant to frost conditions for 4 to 6 h to temperatures between − 1 and − 3 °C during emergence and at the end of growing season generally ceases the growth and leads to heavy yield losses (Kalinova and Moudry 2003). If conditions are favorable, seedling emerges 4–5 days after sowing and plants show profuse vegetative growth from 3rd to 6th week. Transition from vegetative to reproductive phase occurs from 6th to 7th week and seed filling begins in the 8th week. The grain matures 10–12 weeks after sowing (Radics and Mikohazi

2010). Buckwheat has been reported as facultative short day plant (Quinet et al. 2004). The optimum time of harvesting in buckwheat is 10–12 weeks after planting when 70–75% of the seeds have reached physiological maturity, and the plants have shed most of their leaves (Farooq et al. 2016). Due to indeterminate growth habit of buckwheat, seeds of all stages namely mature seeds, immature seeds and fertilized flower can be observed during the harvesting period on the same plant (Farooq and Tahir 1982). The optimum temperature and moisture content for drying is about 45 °C and 16%, respectively (Olson 2001).

The nutrient requirement of buckwheat is fairly low and it has been reported that 44 kg nitrogen, 22 kg phosphorus and 40 kg potassium or 1500 kg farmyard manure per hectare are sufficient to produce 1 tonne of buckwheat grain (Radics and Mikohazi 2010). Overall, buckwheat is a low input crop that needs little fertilizer, but requires proper management for high yields during seedling establishment and at seed harvest.

Buckwheat: a wonder grain as human food

From the nutritional perspective, buckwheat is an excellent source of high-quality protein and dietary fibre with rich micronutrient density than that of world's major cereal grains (Campbell 1997; Table 1). Especially in low-income food deficit countries, buckwheat based food products could play a vital role in dietary diversification for the prevention of nutritional disorders.

Grains, leaves and inflorescences of buckwheat have different nutritional potential. The average protein content in buckwheat grains ranges from 10 to 15%, which is comparable with major cereals (Eggum et al. 1980; Saturni et al. 2010). However, it has a particularly favorable composition in essential amino acids and its protein quality is much higher than ordinary food sources like wheat, rice and maize (Bonafaccia et al. 2003b). Most cereal grains are generally deficient in essential amino acids while, buckwheat is rich in lysine (Table 1) and therefore, has a well-balanced composition of amino acids. Similarly, the concentration of major sulphur containing amino acid, methionine is comparatively higher in buckwheat (3.7% of total protein) (Table 1) than most of the pulses protein. Compared to seeds, protein quality of buckwheat sprouts is very high with biological values above 90% (Zhang et al. 2012). Recently, Sytar et al. (2018) characterized the amino acid profile of buckwheat sprouts where novel information regarding high concentration of sulphur containing amino acid methionine in buckwheat sprouts was reported. In addition, buckwheat sprouts are also characterized by very high content of leucine (25–29 g/kg dry weight) in leaves. Furthermore, active accumulation of glutamic acid is observed in early growth stages, which

is associated with higher accumulation of arginine, proline and leucine in leaves and stems of buckwheat sprouts. The abundance of essential amino acids makes buckwheat a good source of high-quality protein and nutritive substitute for some cereals in functional foods as well as conventional feed in the feed mixtures of livestock and poultry (Leiber 2016). Buckwheat protein is mainly composed of easily digestible albumins and globulins (50–60% of total protein), 11–23.8% of alkali-soluble glutelins, which are close to albumins and globulins by their nutritive value, and only 1–7% of alkali-soluble proteins prolamines (Javornik and Kreft 1984; Wei et al. 2003). The low content of prolamines and absence of α-gliadin, makes buckwheat a healthy alternative to gluten-containing grains in diets of patients with celiac disease (Podolska 2016). Gluten-free buckwheat seed flour can be used to improve the nutritional value and digestibility of various food products by enhancing their protein quality and amino acid profile. Digestibility of buckwheat protein is less compared to cereals protein due to the presence of high fibre content (17.8%) (Campbell 1997).

Buckwheat is also valued for its excellent mineral profile and considered an important nutritional source of macronutrients and essential micronutrients such as iron (Fe), manganese (Mn), and calcium (Ca) and potassium (K) (Table 1). It is also a rich source of water-soluble and lipid-soluble vitamins: thiamin, riboflavin, niacin, pantothenic acid and pyridoxine (Bonafaccia et al. 2003a; Table 1). In addition, trace quantity of antioxidant vitamins such a β carotene and tocopherols has also been reported in buckwheat seeds (Wei et al. 1995; Li and Zhang 2001).

Buckwheat: a potential crop with nutraceutical values

While the most widely known health benefit of buckwheat is that the grains are effectively gluten-free, there are several reports of the presence of a variety of nutraceutical properties in its grains, groat and sprouts (Table 2). Consumption of buckwheat based food products is known to reduce the concentration of cholesterol in blood serum and glycemic and insulin indexes (Skrabanja et al. 2001; Stokic´ et al. 2015). Nutraceutical properties of buckwheat are mainly attributed to the presence of six major flavonoids; rutin, quercetin, orientin, homoorientin, vitexin and isovitexin in its leaves, flowers, seeds and sprouts (Fabjan et al. 2003; Morishita et al. 2007; Zielinska et al. 2012; Raina and Gupta 2015) (Table 2). In the past few years, these dietary flavonoids have received tremendous attention from health professionals, nutrition scientists, and consumers for their health benefits (Bystricka et al. 2011; Zielinska et al. 2012). Buckwheat is the only grain crop which contains rutin. Rutin is known to be highly preventive against skin carcinogenesis

Table 2 Nutraceutical properties of buckwheat

Nutrients	Ingredients	Functional properties	Nutraceutical properties	References
Proteins	Globulin, albumin and prolamines	High proportion of essential amino acids	Suppress protein energy malnutrition, gallstone formation and colon carcinogenesis	Kayashita et al. (1999), Tomotake et al. (2006)
Carbohydrates	α-amylase resistant starch, free sugar and oligosaccharides	Low glycemic and insulin indexes	Antidiabetic and prevent body fat accumulation	Skrabanja et al. (2001), Takahama and Hirota (2010)
Micronutrient and trace elements	Selenium, zinc, iron, calcium and magnesium	Cofactors of various enzymes regulating metabolism	Combat osteoporosis, anemia, cancer and AIDS	Zheng et al. (2011)
Carotenoids	β-carotene and lutein	Controls the Antioxidative activities in cells	Prevent humans from oxidative stress and ageing	Tuan et al. (2013)
Dietary Fibers	Water soluble and insoluble fibre	Reduction in serum cholesterol and glucose content	Decreases risk of cardiovascular diseases, gastro-intestinal disorders and constipation	Slavin (2013)
Flavonoids	Rutin, quercetin, orientin, homoorientin, vitexin, isovitexin and fagopyrin	Inhibit antiadipogenic and vasorelaxation activities. Enhance hypotriglyceridemic, anticancerogenic and antifungal activities and work as immune modulators	Positive cardiovascular effects, protection from UV-radiation, glycemic control in type II diabetics, treatment of hormone-dependent tumors and amelioration of renal injury	Kreft et al. (2002), Sytar (Sytar 2015), Sytar et al. (2016)

and inflammation (Nile and Park 2014). These bioactive flavonoids vary between buckwheat species and tartary buckwheat (*F. tataricum*) is reported to contain higher amount of flavonoids particularly rutin (0.8–1.7% dw) compared to common buckwheat (*F.esculentum*) (0.01% dw) (Fabjan et al. 2003; Rana et al. 2016). Sytar (2015) conducted comparative analysis of antioxidant activity and secondary metabolites in inflorescence of three buckwheat varieties viz., common buckwheat (*F. esculentum*), tartary buckwheat (*F. tataricum*) and green-flower buckwheat (*F. esculentum*, forma green flowers). Antioxidant activity in the inflorescence of these buckwheat varieties has been found high and inflorescence of green flower buckwheat was characterized by the highest total phenolic content. Compared to other varieties, inflorescence of *F.esculentum*, forma green flower was reported to have the highest concentration of chlorogenic acid and *p*-anisic acid, which are characterized by strong antitumor activities. Buckwheat is also enriched in an essential trace element selenium (0.0099–0.1208 mg/g), which enhances human resistance to cancer and AIDS but is absent in most other plant foods (Zheng et al. 2011). By virtue of their immense health benefits, various food products of buckwheat such as tea, wine, cookies, pancakes and roasted groats are available in the market. Among these products, tea prepared from buckwheat groats and inflorescence is the most famous health products in Asian and European countries (Qin et al. 2011). The tartary buckwheat tea contains many beneficial trace elements and chlorogenic acid which possess strong antioxidant activities and prevent from hypertension, hyperglycemia and hyperlipidemia (Sytar et al. 2016). Use of buckwheat inflorescence for making organic tea has emerged as a new way of promoting buckwheat products in South Asian countries (Thwe et al. 2013). The numerous potential compounds with unique medicinal properties provide new avenues for buckwheat improvement for nutraceutical development through integrated breeding and genomics approach.

Genetic resources of buckwheat: ex situ conservation and impact

Buckwheat and its wild relatives harbor a wide diversity and considerable efforts have been made for ex situ conservation of genetic resources (Table 3). At present, more than 10,000 diverse accessions of buckwheat genetic resources are being maintained across the world and half of them are preserved in east and south Asian gene banks (Zhou et al. 2018). The Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS) is the largest repository for buckwheat worldwide with more than 2800 germplasm accessions (Zhou et al. 2018; Table 3). While the hot spots of buckwheat diversity are well represented in collections,

Table 3 Buckwheat genetic resources conserved in major gene banks globally

Institute/organization	Country	Total germplasm holding	Major species represented	References
Institute of Crop Sciences, Chinese Academy of Agricultural sciences (CAAS)	China	2804	*F.esculentum* and *F.tataricum*	Zhou et al. (2018)
N I Vavilov All-Russian Institute of Plant Industry	Russia	2116	landraces, cultivars, and wild forms of *F. esculentum* and *F. tataricum subsp. multholium*	www.vir.nw.ru, Zhou et al. (2018)
V Y Yuriev Institute of Plant Production	Ukraine	1600	landraces, cultivars and wild forms of *F. esculentum* and *F. tataricum*	Zhou et al. (2018)
Podillya State Agricultural University	Ukraine	900	*F.esculentum* and *F.tataricum*	Zhou et al. (2018)
National Bureau of Plant Genetic Resources	India	1050	*F. esculentum*, *F. tataricum*, *F. sagittatum*, *F. cymosum*, *F. tataricum* ssp. *Himalianium* and *F. esculentum* ssp. *emerginatum*	Rana et al. (2016)
National Agriculture Genetic Resource Centre	Nepal	511	Indigenous landraces *F.esculentum* and *F.tataricum*	Paudel et al. (2016)
University of Ljubljana	Slovenia	378	Landraces of *F. esculentum,* accessions of *F. tataricum*	Zhou et al. (2018)
National Institute of Agrobiological Sciences	Japan	226	Landraces of *F. esculentum* and varieties of *F. tataricum*	Katsube-Tanaka (2016)
Crop Research Institute	Prague	170	Mostly exotic accessions of *F.esculentum*	Cepkova´ et al. (2009)

gaps exist for wild and weedy species. It is of great importance to make these ex situ collections more comprehensive by enriching them with rare valuable alleles to widen the gene pool and prevent genetic erosion.

To categorize germplasm collections, taxonomic keys and descriptors of buckwheat have been developed by Bioversity International (IPGRI 1994). The large scale and well-documented germplasm characterization studies conducted in China (Yang 1995), India (Joshi and Paroda 1991; Rana et al. 2016), Korea (Choi et al. 1995), Japan (Katsube-Tanaka 2016) and Nepal (Baniya et al. 1995) revealed genetic variations for agro-morphological traits. However, due to their large size, sufficient evaluation data for stress tolerance and nutraceutical traits are not available for these collections. Consequently, these collections remain largely underutilized in breeding program. Their use can be enhanced by developing 'core collection' of reduced sample size (Brown 1989), which represent the complete genetic spectrum of the base collection. By virtue of its reduced size, core collection can be precisely evaluated for economic traits in replications under multi-locations/environments for the identification of trait specific accessions.

Bottlenecks in buckwheat breeding

Common buckwheat is a highly allogamous crop due to the existence of peculiar dimorphic and sporophytic type of self incompatibility, which makes it difficult to breed homozygous and homogenous pure line cultivars and to fix economic traits (Yasui et al. 2016). Artificial hybridization through hand emasculation is cumbersome in common buckwheat due to the complex arrangement of floral structure. Consequently, most of the present day's cultivars of common buckwheat are the bulks of first and second generation selection cycle derived from heterogeneous landraces through temporal and spatial isolation. Although homomorphic, self-compatible common buckwheat lines capable of self-fertilization have been reported (Marshall 1969), their utilization in breeding program is largely restricted due to the occurrence of severe inbreeding depression. This is probably due to the large number of deleterious spontaneous recessive mutants exposed to homozygous state (ss) that normally remain hidden in heterozygous cross pollinating thrum flowers (Ss). In contrast to the common buckwheat, tartary buckwheat is a self-compatible autogamous species (Woo et al. 2010). Therefore, it is much easier to generate large segregating progenies and maintain genetic purity of advanced breeding lines in tartary buckwheat.

To overcome the breeding barriers in buckwheat, efficient hybridization techniques are prerequisite to cross elite lines for broadening the genetic base of cultivars. Mukasa (2011), standardized hot water emasculation in a self-compatible homomorphic common buckwheat strain (42 °C for 5 min) and tartary buckwheat (44 °C for 3 min) for artificial hybridization and large-scale production of hybrids. However, disadvantages of inbreeding depression in self-compatible common buckwheat progenies are more than the advantages of artificial hybridization.

Production constraints and breeding targets

The crop is still considered as a minor food crop of rural low-income communities and has not attracted breeding efforts like major cereals. Buckwheat is less adapted to the modern agroecosystems, which leads to a different primary set of breeding targets compared to major crops. Major breeding objectives in buckwheat include reduced seed shattering, determinate growth habit, synchronized flowering and reduced plant height for mechanical harvest and prevent yield losses due to lodging (Campbell 1997). The shortage of photosynthates during grain filling is one of the fundamental factors for poor seed yielding ability of buckwheat cultivars (Yang et al. 1998). It has been estimated that to enhance the buckwheat seed yield by twofold, the plant requires only 24% of the blossoms presently being produced (Sangma and Chrungoo 2010). Therefore, breeding buckwheat cultivars bearing optimal flowers will be a potential strategy to divert the nutrients towards grain filling that are generally being exhausted for generation of blooms, which the plant does not require anymore. Easy dehulling is another important breeding objective to reduce the drudgery involved in postharvest processing of tartary buckwheat. Availability of easy dehulling types has been reported in the local landraces (Rice buckwheat) (Campbell 1997), which can be used to transfer the trait to high-yielding cultivars. Besides these, early maturity, larger seed size, increased groat percentage, seed coat colour and flower colour are important breeding targets.

In contrast to major crops, buckwheat is relatively free from serious pest infestation and disease incidence. One potential pest is *Rhinoncus sibiricus*, which can cause crop losses up to 30% in common buckwheat (Kuznetsova and Klykov 2012). Apart from this, leaf spot (*Ramularia* spp.), root rot (*Rhizoctonia spp.*) and downy mildew (*Peronospora ducometi*) are known to cause minor crop losses in buckwheat. Resistant sources to these diseases need to be identified in disease screening nurseries. Among abiotic stresses, susceptibility to frost is a major yield constraint in common buckwheat (Zhou et al. 2016). Sources of frost tolerance are not reported in common buckwheat germplasm, while tartary buckwheat is well known for its frost tolerance (Campbell 1995). However, transfer of frost tolerance from tartary buckwheat to common buckwheat is a daunting challenge due to strong crossability barrier between the two species.

Traits for nutraceutical development and knockdown of genes governing self-incompatibility and allergens are need to be included as important targets in the breeding program to make the crop more competitive with major cereals. For instance, abundant genetic variation for flavonoids particularly rutin and quercitrin has been reported in tartary buckwheat (Fabjan et al. 2003). The self-pollinating behavior and easy emasculation in tartary buckwheat provide an opportunity to obtain transgressive segregants for rutin content through selective breeding approach.

Genetic architecture of economic traits

Improving the efficiency of breeding programs requires a better understanding of genetic architecture of breeding targets. While traits such as determinant growth habit (Fesenko 1968), dehulling capacity (Fesenko et al. 2016), shattering habit (Wang et al. 2005) and floral morphology (Woo et al. 1999) follow a simple Mendelian inheritance in buckwheat, other traits such as plant height have more complex genetic architecture (Li et al. 2012). Economically important traits such as anthesis time, seed weight and days to maturity have been reported to have moderate to high heritabilities coupled with high genetic advance in buckwheat (Li et al. 2012; Rana et al. 2016). Genetic studies to determine the mode of inheritance and prevalent gene action controlling the traits of nutritional quality and nutraceutical development are yet to be implemented.

Buckwheat Improvement: synthesis of past breeding efforts

Genetic improvement programs began across the world in the early 1900 with a major emphasis on collection, characterization and conservation of buckwheat accessions. Although a number of cultivars have been released for cultivation across the world, buckwheat breeding programs largely relied on traditional mass selection for common buckwheat and pure-line selection in tartary buckwheat (Campbell 2003). The most successful cultivar development was achieved in Eastern Europe and Russia through incorporation of recessive allele (*det*) controlling determinate growth habit, one of the key traits for breeding high-yielding varieties of common buckwheat (Fesenko et al. 2006). The average yield of buckwheat in Russia was doubled in the last decade after increasing the share of determinate varieties in crop production (Fesenko et al. 2016). Mutation breeding was initiated in the 1970s to induce genetic polymorphism for economic traits; with a primary focus on protein content, amino acid profile, rutin content and seed size (Alekseeva 1984, 1988). Induced mutagenesis followed by family group selection approach led to the development of promising cultivars like Aelita, Lada and Podolyanka (Alekseeva 1984). Anthocyanin pigmentation in vegetative organs of buckwheat has been demonstrated as a reliable and easy phenotypic marker for identifying plants with high content of rutin (Sytar et al. 2014). Anthocyanin pigmentation as

phenotypic marker was reported to be stable over three generations and allowed selection of a genetic line of 'Rubra' cultivar with high rutin content. These findings suggested that colour visual assessment of vegetative organs can be implemented as a reliable genetic marker system into buckwheat breeding programs to speed up the selection for high rutin content by skipping the lengthy and costly laboratory screening for rutin content.

The germplasm collections maintained across the world have shown a wide range of variability for yield and yield-contributing characters (Joshi and Paroda 1991; Rana et al. 2016; Zhou et al. 2018). In India, the release of cultivars Himpriya, Himgiri, VL7, PRB1 and Sangla B1 which are selections from local and exotic germplasm lines, are notable examples of effective utilization of buckwheat germplasm in the breeding program (Rana et al. 2016). Nonetheless, lack of efficient breeding methods and limited research funds are the major reasons for little advances in buckwheat research.

Modern breeding approaches to enhance genetic gain in buckwheat

Hybrid breeding and population improvement

Exploitation of heterosis through hybrid breeding has strongly improved yield potential and yield stability in many crop plants. To introduce hybrid breeding in buckwheat, few tools have to be improved and applied.

One of the essential requirements of hybrid breeding is the availability of at least two populations (heterotic pools) with good agronomic adaptability, while genetically distant enough to exhibit strong heterosis (Breseghello and Coelho 2013). In general, the more divergent are the heterotic pools, the higher will be the manifestation of heterosis in resulting offspring (Kaeppler 2012). The two main agronomically adapted species of buckwheat (*F. esculentum* and *F. tataricum*) are grown separately for a long time are genetically divergent enough to express heterosis, which makes them ideal heterotic gene pools in buckwheat. The exhaustive germplasm characterization studies conducted across the world could provide valuable information to isolate genetically divergent heterotic pools in common buckwheat. In addition, genetic distance data of geographically isolated landraces derived through next-generation molecular markers will facilitate construction of heterotic pools with more precision. This approach is effectively utilized for constructing heterotic pools in wheat (Boeven et al. 2016).

Availability of an efficient crossing technique is a major requirement for large-scale seed production of hybrids so that the cost of seed production does not offset the economic benefit of heterosis. The above-described emasculation techniques (Mukasa 2011) provide possibilities for limited crosses for experimental purpose in buckwheat. Therefore, self-incompatibility should be thoroughly investigated for cost effective hybrid seed production, as genetic male sterility has not been reported in buckwheat. Homozygous S-alleles have been utilized to produce single and double cross hybrids in red clover (Anderson et al.1974). In buckwheat, homozygous homostyle (S^hS^h) and pin (*ss*) inbred lines were developed utilizing self-compatible gene of common buckwheat (Mukasa 2011). Single cross hybrids were produced using homozygous homostyle and pin lines as pollen and seed parents, respectively. The resulting homostyle self-compatible (S^hs) F_1 hybrids exhibited the average grain yield advantage of 10–15% over the standard open pollinated variety of buckwheat. These results suggest that heterosis breeding can be used to increase seed yield in common buckwheat. A major disadvantage of this method is lengthy cycling generations to produce homozygous inbreds through successive selfing. Double haploid technology allows accelerated recovery of absolute homozygous lines, which is well exploited in many crops (Forster and Thomas 2005). With the availability of optimized growth conditions for stable induction and regeneration of gynogenic haploids (Bohanec et al.1993; Bohanec 1995), double haploid technology might become available for inbred development and hybrid breeding in buckwheat.

Population improvement to accumulate the rare desirable alleles at higher frequency into a population is a popular and cost-effective approach in highly allogamous species (Li and Brummer 2012). In general, mass selection without progeny testing is applied in buckwheat population improvement programs (Campbell 1997). However, mass selection with controlled pollination is ineffective for the traits with low heritability (Campbell 2003). Modern population breeding procedures such as recurrent selection and polycross breeding, relying on progeny testing through consecutive rounds of selection and recombination are quite effective for improving traits with low heritability (Breseghello and Coelho 2013). These procedures require efficient pollination mechanism for repeated inter-mating, which is unproblematic in allogamous self-incompatible common buckwheat.

Interspecific hybridization: widening the buckwheat gene pool

Wild and weedy species of genus *Fagopyrum* harbor several agronomic traits that are missing in mainstream gene pool. For instance, higher seed yield, self-pollination ability, frost tolerance, high rutin content and plant vigor are the traits of high economic value but there is only little variation available in common buckwheat (Campbell 1997; Ohnishi 2013). Substantial efforts have been made for interspecific hybridization in buckwheat to transfer these traits in cultivated gene pool (Table 4). However, efforts to

Table 4 Status of interspecific hybridization between the species of large achene *cymosum* group of genus *Fagopyrum*

Interspecific cross	Method used	Result	Reference
F. esculentum (2×) × *F. cymosum* (2×)	Conventional crossing	Embryos of early globular stage only	Shaikh et al. (2002)
F. esculentum (4×) × *F. cymosum* (4×)	Ovule rescue technique	Hybrids (4×) with perennial growth habit	Suvorova (2001)
F. esculentum (2×) × *F. cymosum* (2×)	Ovule rescue technique	Hybrids (2×) characterized by perennial growth habit and heterostyly flower	Hirose et al. (1995)
F. esculentum (4×) × *F. cymosum* (4×)	Embryo rescue	Hybrids (4×) capable of self-fertilization	Rumyantseva et al. (1995
F. esculentum (2×) × *F. cymosum* (2×)	Embryo rescue	Vigorous but self sterile hybrids (2×)	Woo et al. (1999)
[(*F. esculentum* × *F. cymosum*) × *F. homotopicum*] × *F. homotopicum*	Multiple crossing and ovule rescue	Vigorous but sterile trispecies hybrids	Suvorova (2010)
F. tataricum (4×) × *F.cymosum*(4×)	Conventional crossing	Amphidiploid fertile tetraploid (2n = 4× = 32) hybrid. Later designated as a separate species, *F.giganteum*	Krotov and Golubeva (1973)
F. tataricum (4×) × *F. giganteum* (4×)	Conventional crossing	Early maturing, self-fertilizing amphidiploid hybrids (4×). Designated as new man-made species *F.hybridum*	Fesenko and Fesenko (2010)
F. tataricum × *F. esculentum*	Ovule rescue technique	Sterile hybrids (2× and 4×)	Samimy et al. (1996) Hirose et al. (1995), Wang et al. (2002), Niroula et al. (2006)
F. tataricum × *F. esculentum*	Ovule rescue technique	Fertile hybrids (2× and 4×). The fertile hybrids produced F$_1$ and F$_2$ generation	Azaduzzaman et al. (2009)
F. esculentum (4×) × *F. homotopicum* (4×)	Embryo rescue	Fully fertile hybrids (4×)	Campbell (1995)
F. esculentum (4×) × *F. homotopicum* (4×)	Conventional crossing	Fertile hybrids (2× and 4×)	Fesenko et al. (2001), Kim et al. (2002)

develop interspecific hybrids between distant gene pools were largely failed due to the presence of great incompatibility barriers between the species. Advancements in ovule and embryo rescue techniques and molecular methods for handling backcross generations extended the possibilities of the interspecific hybridization of buckwheat. *F. homotropicum* of *cymosum* group is one potential wild species characterized by self-compatible behavior, tolerance to frost and high rutin content. An example for successful transfer is the self-compatible trait of *F. homotropicum* which was transferred to *F. esculentum* to reduce cross pollination (Campbell 1995). The successful hybridization between *F. esculentum* and *F. homotropicum* at diploid level opened new horizons for improvement of common buckwheat. For instance, self-compatible long homostyle common buckwheat breeding line Norin-PL1 was developed by crossing *F. esculentum* cv. Botansoba and *F. homotropicum* accession from Yunnan followed by recurrent backcrossing of F$_1$ hybrid with *F. esculentum* (Matsui et al. 2008). The Norin-PL1 has been recommended as

a parental line for producing self-compatible buckwheat lines in different breeding programs. However, one major drawback of *F. homotropicum* is that it is characterized by high seed shattering leading to severe seed losses.

Interspecific hybridization between *F. esculentum* and *F. tataricum* offers a promising avenue for mutual genetic improvement of the two species. The fertility barriers between the two species have been analyzed, and modern biotechnological tools employed to overcome them (Samimy et al.1996; Hirose et al. 1995; Wang et al. 2002; Niroula et al. 2006). An important step in interspecific hybridization of buckwheat is recovery of fertile diploid and tetraploid hybrids between *F. tataricum* × *F. esculentum* through ovule culture (Azaduzzaman et al. 2009). The effort has resulted in obtaining F$_2$ generation, which was more fertile than parents and F$_1$ hybrid. The first successful attempt allows the consideration that interspecific hybridization between *F. esculentum* and *F. tataricum* will be one of the directions of buckwheat breeding.

Genomics-driven breeding for trait improvement

Despite of its status as an orphan crop and a small research community, recently there have been substantial advances in generating genomic resources of buckwheat. These resources can greatly enhance the genetic gain for polygenic traits with low heritability, which are otherwise difficult to breed through conventional approach. One of the most important resources for genomics-assisted breeding (GAB) is the availability of well assembled reference genome. The most recent high quality reference genomes of common buckwheat and tartary buckwheat have a genome size of 1.2 Gbp (Yasui et al. 2016) and 0.48 Gbp, respectively (Zhang et al. 2017). In addition to these high-quality nuclear assemblies, there are two chloroplast genome sequences in buckwheat (Liu et al. 2016; Wang et al. 2017). These reference genomes of buckwheat facilitated the identification of novel candidate genes predicted to be involved in self-incompatibility mechanism, rutin biosynthesis and abiotic stress tolerance.

Different genome-wide markers have been employed to explore the diversity and phylogenetic studies in buckwheat. However, these are mainly restricted to utilization of traditional non reproducible DNA markers (Nagano et al. 2001; Sharma and Jana 2002a, b; Matsui et al. 2004; Yasui et al. 2004). The numerous, easily assayed and codominant genic and genomic microsatellites are excellent resource of molecular markers across the crop plants. Unlike major cereals, only few microsatellite markers are reported in buckwheat (Konishi et al. 2006; Joshi et al. 2006; Ma et al. 2009). One potential strategy to enrich the microsatellite markers is to use the expressed sequence tags (ESTs) available in other plant species belonging to taxonomically common order of *Fagopyrum* species (Chauhan et al. 2010; Rana et al. 2016). Recently, low-cost genome sequencing facilitated the development of single nucleotide polymorphism (SNPs) markers and high-throughput automated genotyping for crops with small genomes (Bohra et al. 2014). This will be particularly important to assess allelic diversity in ex situ collections and use this diversity to map quantitative trait loci (QTL) by association mapping. Such developments have not reported in buckwheat yet, but these will greatly improve our understanding of the genetic architecture of complex quantitative traits. For instance, detection of SNPs in genotypes bearing contrasting differences for rutin and other flavonoids will be of great significance in molecular breeding of buckwheat.

Genetic maps are another vital genomic resource required for detailed analysis of the association between QTLs and agronomic traits for marker-assisted breeding (MAB) (Chauhan et al. 2010). Genetic maps are available in both *F. esculentum* (Yasui et al. 2004; Pan and Chen 2010) and *F.tataricum* (Xiaolei et al. 2013) and major QTL's governing photoperiod sensitivity (Hara et al. 2011) and stem length (Yabe et al. 2014) were identified. However, constructed

genetic maps remain largely unutilized in tagging important QTLs or genes till date due to the lack of enough informative markers with uniform distributions across all the eight chromosomes. The recently available genome sequences (Yasui et al. 2016; Zhang et al. 2017) will facilitate mapping of numerous markers such as simple sequence repeats (SSRs) and SNPs leading to a more saturated maps with less genetic distance between markers and economic traits in buckwheat.

While considerable progress has been made in generating genomic resources, genetic mapping populations are lacking, which may be attributed to limited breeding efforts in buckwheat. There have been few genetic mapping studies in buckwheat for identifying important QTLs governing quantitative traits (Hara et al. 2011; Yabe et al. 2014). However, reproducibility of genetic measurements in family-based mapping populations (F_2 and F_4) utilized in these studies are limited due to their heterozygous genetic constitution. Recombinant Inbred Lines (RILs), Multiple Advanced Generation Intercross (MAGIC) and Nested Associated Mapping (NAM) enhance mapping resolution and fine mapping of quantitative traits (Korte and Farlow 2013). Therefore, a current need in buckwheat genomic research is development of robust mapping populations to identify genetic determinants (QTLs) of breeding targets. With the advancements in crossing techniques (Mukasa 2011) and interspecific hybridization (Azaduzzaman et al. 2009), next-generation mapping populations (MAGIC, NAM) might become available in buckwheat.

Comparative genomics allows to project map-based orthologous candidate QTLs or genes governing important traits through genomic collinearity and synteny map (Kumar et al. 2016). Using full sequence information of well-explored plant genomes, it is now possible to do comparative genomic analysis to detect rare valuable alleles influencing several important traits in lesser explored crops like buckwheat. Utilizing the genomic synteny and functional similarity with *Arabidopsis* genome, genes governing rutin biosynthesis has been identified in *F. esculentum* and *F.tataricum* (Rana et al. 2016).

Genomic selection for enhancing breeding efficiency of complex traits

Genomic selection (GS) is a promising approach invented to overcome many of the drawbacks of marker-assisted selection (MAS). GS refers to the use of DNA markers to predict genomic estimated breeding values (GEBV) particularly for complex traits with low heritability (Varshney et al. 2013). In contrast to phenotyping and genotyping of a large family-based mapping population in MAS approach, GS can establish marker–trait associations (MTAs) based on a small training population (TP) (Desta and Ortiz 2014). Based on GEBVs, GS can assist in the

selection of genotypes with high heritability or can discard very low performing genotype for the trait under selection (low heritability). Genotypes with superior GEBVs are selected as parents from the training population (TP) and crosses are made to develop candidate population (CP). To exploit the full potential of GS in buckwheat improvement, robust TPs need to be developed from advanced breeding lines for which historical data on their performance has already been compiled.

Genetic gain of GS for polygenic traits were reported to be much higher than MAS and conventional pedigree breeding in maize (Bernardo and Yu 2007; Heffner et al. 2010). In addition, GS has found quite effective in improving genetic gain for grain quality and nutritional traits, which are costly to phenotype through conventional MAS approach (Velu et al. 2016; Nielsen et al. 2016). In buckwheat, potential of GS to complement traditional mass selection has been recently demonstrated (Yabe et al. 2018). The empirical results of pilot GS experiment indicated that genomic prediction could largely accelerate the genetic gain for nutritional traits per generation through early selection and holds great potential for biofortification breeding in sbuckwheat.

Functional genomics approach for gene discovery

Transcriptomics

Transcriptome-based gene expression profiling is a robust functional genomics approach for characterizing the candidate genes regulating various biological processes (Kumar et al. 2016). For lesser explored crops with poorly characterized genomes, like buckwheat, transcriptome assemblies provide comprehensive information about expression patterns of genes and functional polymorphism. This valuable information can be utilized for development of functional markers such as EST-SSRs, SNPs and intron-spanning region (ISR). Comprehensive transcriptome analysis for floral structure (Logacheva et al. 2011), aluminium toxicity (Xu et al. 2017; Chen et al. 2017) and salt tolerance (Wu et al. 2017) has been carried out to explore the underlying gene regulatory mechanism in buckwheat. Transcriptome analysis of seed development at twelve different stages from fertilization to maturation identified 11,676 differentially expressed genes in tartary buckwheat (Huang et al. 2017). These candidate genes provide a rich genomic resource for functional characterization of nutrient content and flavonoid biosynthesis in tartary buckwheat. Since grains of common buckwheat are also rich sources of nutrition, similar global transcriptome analysis are required for functional characterization of genes and gene families responsible for nutrient biosynthesis and regulation.

Proteomics and metabolomics

Proteomics implies to the comprehensive study of structure, expression and function of complete set of proteins. The important areas of plant proteomics include 2-D gel electrophoresis, mass spectrophotometry and gel-free shotgun proteomics approaches (Matros et al. 2011). These rapid advances in proteomics tools are allowing new insights into plant genomes through proteome mapping, comparative proteomics and identification of protein–protein interactions (Varshney et al. 2009). Studies using proteomics to understand grain quality traits have yet to be implemented in buckwheat. Nevertheless, few studies have analyzed leaf and stem proteome of buckwheat sprouts for understanding their light-dependent developmental physiology to facilitate functional genomics analysis (Lee et al. 2016). Comparison of protein composition between sprouts grown under light and dark conditions identified 166 unique cytosolic proteins regulating chlorophyll biosynthesis. Due to its gluten-free nature, buckwheat protein has emerged as a healthy food supplement as gluten is one of the major protein causing allergies. However, buckwheat is reported to cause allergen reactions in Asia and Europe (Heffler et al. 2014). Therefore, absolute quantitative proteomics is recommended for quantifying allergen proteins in buckwheat varieties to definitely classify it as a dietary supplement (Lee et al. 2016). So far, a major lacuna in large-scale genome-wide proteomic study in buckwheat was the unavailability of a well-assembled reference genome sequence. The recent availability of draft genome sequences of buckwheat species (Yasui et al. 2016; Wang et al. 2017; Zhang et al. 2017) will accelerate further understanding of seed proteomics.

Metabolomics is one of the recent "omics" technologies, which refers to identification, characterization and quantification of low molecular weight biomolecules (metabolome) of a biological system (Kumar et al. 2016). It has been well demonstrated that major contributors toward nutraceutical properties of buckwheat grain are secondary metabolites like polyphenols and flavonoids. Therefore, it requires thorough metabolomics studies to identify the best genotypes for human consumption. Metabolic profiling of buckwheat grain has not been reported yet. However, there are reports that have thoroughly investigated metabolome of hairy root culture of tartary buckwheat (Thwe et al. 2013). This study identified a total of 47 secondary metabolites involved in phenylpropanoid biosynthetic pathway by gas chromatography–time-of-flight mass spectrometry (GC-TOFMS). This valuable information on the molecular and physiological processes of phenolic compounds in buckwheat may be integrated with other omics data for understanding underlying gene regulation mechanism. In fact, to implement biofortification breeding in buckwheat it is essential to analyze the

complete seed metabolome and integrate it with transcriptomics and proteomics data of seed tissues.

Gain and loss-of-function approach

Genetic engineering can enrich the buckwheat breeding programs through incorporation of novel genes not available in the mainstream gene pool. Genetic engineering through *A. tumefaciens* and *A. rhizogenes* mediated transformation events is well established in buckwheat (Table 5). In addition, establishment of *in planta* transformation has paved the way for further transgenic development by avoiding lengthy tissue culture cycle and somaclonal variations (Kojima et al. 2000a, b). In vitro hairy cultures capable of producing higher amount of flavonoids have been generated through *A. rhizogenes* mediated transformation events in buckwheat (Park et al. 2011; Gabr et al. 2012; Table 5).

In the recent years, genome editing has emerged as a revolutionary functional genomics approach to address the productivity constraints in various crops (Bortesi and Fischer 2015). Genome editing approaches viz., zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs) and the recent type II clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated protein 9 (Cas9) relying on programmable site-specific nucleases have been developed to modify the plant genomes in a rapid yet precise manner. In contrast to protein guided, complicated ZFNs and TALENs approaches, CRISPR/Cas9 gene editing relying on DNA or RNA sequence homology is easy to implement and received widespread attention (Ma et al. 2016). Till date, no proof of concept for gene editing has been reported in buckwheat. However, the rapid progress in buckwheat transformation has opened avenues for determining gene function through genome editing.

One potential application of genome editing is in the understanding of genetic mechanism underlying rutinosidase activity in tartary buckwheat. The rutinosidase activity hydrolyze the rutin present in buckwheat flour within a few minutes after the addition of water providing extremely bitter taste of bread and confectioneries (Suzuki and Morishita 2016). Precise nucleotide changes in genes encoding rutinosidase enzyme through genome editing could help to understand the molecular mechanism underlying hydrolysis of rutin in buckwheat flour. Furthermore, CRISPR/Cas9-based targeted molecular stacking of rutinosidase inhibiting genes would facilitate development of rutin rich non-bitter functional food products of tartary buckwheat. The tools of genome editing could further be utilized for knockdown of genes encoding allergenic protein in seed proteome of common buckwheat to make it more attractive for food industry.

Conclusion and perspectives

By virtue of its unique nutritional profile and immense nutraceutical properties, buckwheat is projected as the golden crop of future. The available literature on buckwheat research reveal that this pseudocereal has not received much attention as it deserves. The genetic variation available in buckwheat has not made a great impact on development of nutritionally rich cultivars across the world. Therefore, global database and core collection of ex situ accessions for systematic evaluation and unlocking the genetic potential of the buckwheat germplasm has to be developed. Modest progress in interspecific hybridization between the genetically distant buckwheat species suggested that exhaustive efforts are required to overcome the fertility barriers. Recently, considerable reports have appeared on genomic interventions in buckwheat and it is expected that, in years

Table 5 A comprehensive list of different transformation events in buckwheat

| Buckwheat species	Method of transformation	Explant used	Outcome	References
F. esculentum	*Agrobacterium rhizogenes*-mediated	Stem	Transgenic hairy root clones producing high quantity of rutin	Kim et al. (2010)
F. tataricum	*A. rhizogenes*-mediated	Stem	Transgenic hairy root cultures producing high amount of caffeic acid, chlorogenic acid and rutin	Park et al. (2011)
F. esculentum	*A. rhizogenes*–mediated	Excised roots, leaves and stems	Transgenic hairy cultures producing higher quantity of chlorogenic, *p*-hydroxybenzoic, *p*-anisic and caffeic acids	Gabr et al. (2012)
F. esculentum	*A. tumefaciens*-mediated	Cotyledon	Establishment of transformation efficiency	Miljus-Djukic et al. (1992)
F. esculentum	*A. tumefaciens*-mediated	Hypocotyls	Establishment of transformation efficiency	Kim et al. (2001)
F. esculentum	*in planta*	Apical meristem	Establishment of efficient *in planta* transformation protocol	Kojima et al. (2000a, b)
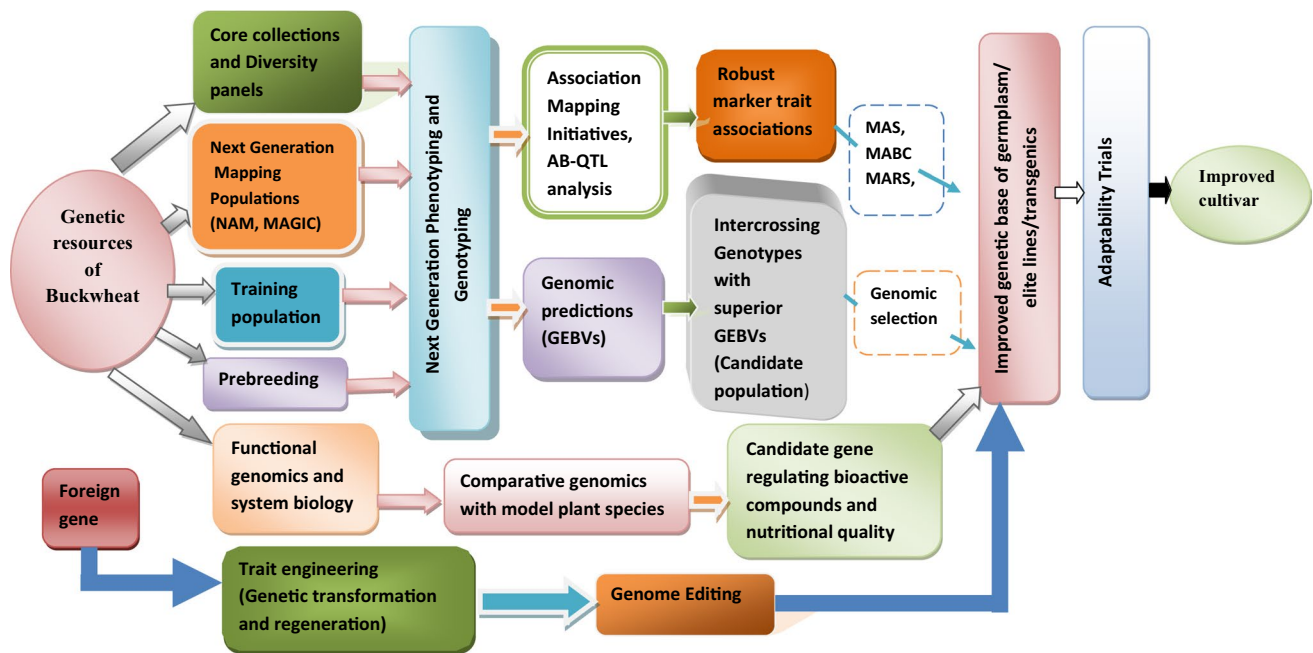
Fig. 3 Schematic representation of an integrative genomics and breeding approach for achieving higher genetic gain in buckwheat

to come, significant developments in the field of buckwheat genomics is going to happen. Many of the wild species within the genus *Fagopyrum* can hybridize with the cultivated species and could serve as a source for missing desirable agronomic traits. The wild relatives *F. cymosum, F. gracilipes* and *F. urophyllum* have higher protein content, total amounts of essential amino acids and dietary flavonoids than cultivated species (*F. esculentum* and *F. tataricum*) and could be a source to new genetic variations for buckwheat improvement. *F. cymosum* is also valued as high-quality forage due to high crude protein content, good palatability and quick regeneration potential and could be a novel source for enhancing feeding value of *F. esculentum* and *F. tataricum*. With the emerging insights in buckwheat molecular genetics, it is high time that genes or allele governing proven traits of importance in wild species should be deployed in breeding programs. Molecular breeding efforts utilizing omics tools in buckwheat lag considerably behind those in other crops. A schematic representation of an integrative genomics and breeding approach for accelerated genetic improvement of buckwheat is proposed in Fig. 3.

Multidisciplinary interventions of the World Vegetable Centre (AVRDC 2008) and Biodiversity International (Gotor and Irungu 2010) in conjunction with local NGOs made a great impact on cultivation, marketing and public awareness among the farming communities for African leafy vegetables, which were once considered as neglected crops of Africa. Similar well-planned and long-term public sector investment for multidisciplinary research activities, jointly by major growing countries are required in

buckwheat. On the whole, enhanced research on biofortification and value addition along with public awareness on nutritive value and government support for marketing could certainly make buckwheat as a golden crop of the future.

Compliance with ethical standards

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