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REVIEW ARTICLE

Beyond the Cereal Box: Breeding Buckwheat as a Strategic Crop for Human Nutrition

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Abstract

While intensification of farming systems is essential for achieving the Millennium Development Goal of "Zero hunger", issues such as availability of nutritious foods would demand increased attention if any long-term form of food security is to be achieved. Since wheat, rice and maize have reached near to 80 percent of their yield potential and reliance on these crops alone would not be sufficient to close the gap between demand and supply, there is a need to bring other climate-resilient and nutritionally dense crops into agricultural portfolio. Buckwheat (*Fagopyrum* spp.) has attracted considerable interest amongst global scientific community due to its nutritional and pharmaceutical properties. The gluten free nature of buckwheat, nutritionally balanced amino acid composition of its grain protein, and high levels of anti-oxidants, such as rutin, makes buckwheat an important crop with immense nutraceutical benefits. However, a key challenge in buckwheat cultivation is the variation in yield between years, which impacts the entire value chain. Current information on buckwheat indicates existence of significant phenotypic variation for agronomic and nutritional traits. However, genetic bottlenecks in conventional breeding restrict effective utilization of the existing diversity in mainstreaming buckwheat cultivation. Availability of high density buckwheat genome map for both the cultivated species viz. *F. esculentum* and *F. tataricum* would add to our understanding of genetic basis of their agronomic traits. The review examines the potential of buckwheat as a strategic crop for human nutrition and prospects of effective exploitation genomic information of common and Tartary buckwheat for genome assisted breeding.

Keywords Pseudocereals · Buckwheat · Genome-wide association study · Marker-assisted selection · Genomic selection · Genotyping by sequencing

Introduction

Food Security-A Complex Issue

Food insecurity is a problem with multiple manifestations. Multiple contributory factors such as social norms, individual behaviour, quantity and quality of food produced as well as its availability make it a problem which requires comprehensive approaches. Food and Agriculture Organization (FAO) has defined food security as a state when "all people, at all times, have physical and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life". Individuals/households were classified as "food insecure" when they are "unable to acquire nutritionally adequate, safe, and culturally appropriate food in a socially acceptable way". Sustainable utilization of limited natural resources for maximizing food production has always remained a serious challenge for achieving the United Nations Sustainable Development Goals (SDGs) of "zero hunger" and "good health". Over the past five decades, one of the greatest achievements of mankind has been the maintenance of pace of food production with demand. However, despite the advances made towards achieving the millennium goal of "Zero hunger", globally over 820 million people are still facing food insecurity and at least 2 billion are facing nutritional insecurity [1]. While population growth is a major factor which determines the gap between demand and supply of food crops, consumer preferences for different types of food, including their nutritional quality, has added to the complexities of food security. FAO has identified "population gap" and "nutrition gap" as

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the two major lacunae which would constrain the achievement of "Zero hunger" status by 2050. According to FAO estimates, a 30 percent increase in global population by 2050 would require 60–70 percent increase in food production [1]. Since wheat, rice and maize grown seem to be near to 80 percent of their yield potential, reliance on these crops alone would not be sufficient to bridge the gap between demand and supply. Achieving a status of "Zero hunger" therefore necessitates a substantial increase in diversity of agricultural basket in the coming decades. This would also require incorporation of socially inclusive, economically productive and environmentally sustainable food systems into agricultural portfolio. Even though much has been written over the years about the need for new crops and many candidate crops have been proposed for incorporation into agricultural portfolio, no comprehensive strategy for their domestication has been proposed till date. In addition to various technical aspects, introduction of new crops into agro-ecosystems has economic as well as social facets where tradeoffs are inescapable. It is thus essential to have a defined strategy that reduces the time required to bring a new crop to full commercialization by prioritizing plants with fortuitous pre-adaptations for sustained gains in yield and marketability. Given the vast repository of such crops, how can those with sufficient potential to justify investing the very limited resources available for their improvement be identified? International Network of Food Data Systems (INFOODS) has drawn a list of candidate crops available in different parts of the globe [2]. Inspite of potential advantages, several factors hinder their widespread incorporation into food systems. These factors, which range from agronomical, such as yield potential, quality traits, to social such as consumer acceptability, have stark similarities regardless of the crop in question. Since many of these crops are cultivated in marginal systems, they do not benefit from high-input agriculture, which is customary for cultivation of major staples. Thus, our knowledge of the yield and quality of these crops comes largely from low-input systems, thereby limiting our ability to gauge their potential under high-input agricultural systems. While these crops continue to be maintained by socio-cultural preferences, they remain inadequately characterized. Although a number of such "area specific species" can be identified on the basis of an assessment of their availability, acceptance and present status, a question that needs answer is: Do these crops have the traits that would favour domestication? DeHaan et al. [3] have suggested (a) phenotype, (b) grain morphology (c) availability of genetic resources and ease of breeding, (d) ease of harvest, (e) yield and quality attributes (f) product value and cultural acceptability, as some of the primary criteria for evaluation of a species under consideration for domestication. While no candidate crop would meet all the criteria, the best candidates would have some fortuitous pre-adaptations or biological considerations.

Beyond the Cereal Box

Although wheat, rice, and maize, together contribute more than 50% of the global calorie intake, they are deficient in several micronutrients including essential amino acids, vitamins and minerals [4]. Consequently, exclusive dependence on these crops contributes significantly towards hidden hunger. On the other hand, some nutritionally-dense crops, which have been historically a part of the staple diets across several cultures, have percolated into small niches in the global food system. Based on a survey of regionally available genetic resources, FAO has identified 39 "nutrition-sensitive" and "climate-resilient" crops from South and South East Asia as "Future Smart Foods". These include eight species of grain crops (common buckwheat, Tartary buckwheat, foxtail millet, proso millet, sorghum, grain amaranth, quinoa), six species of roots and tubers (taro, swamp taro, purple yam, fancy yam, elephants foot yam, and sweet potato), 9 species of pulses (grasspea, fababean, cowpea, mungbean, blackbean, ricebean, lentil, horsebean, and soybean), 9 species of fruits and vegetables (drumstick, chayote, fenugreek, snake gourd, pumpkin, roselle, Indian gooseberry, jackfruit and wood apple), and five species of nuts, seeds and spices (linseed, walnut, Nepali butter tree, perilla and Nepali pepper). Quinoa (*Chenopodium quinoa*), common buckwheat (*Fagopyrum esculentum*), Tartary buckwheat (*Fagopyrum tataricum*), pearl millet (*Pennisetum glaucum*), finger millet (*Eleusine coracana*), proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*), are currently a part of the agricultural portfolio under subsistence farming in some regions of the world. These crops do not require high agricultural inputs and can be inter-cropped or rotated with other staple crops. Since these crops are adapted to marginal conditions, they can make production systems more sustainable and climate resilient. While high nutritional value, palatability and cooking qualities were important factors in greater acceptability of quinoa as a food crop, extensive research efforts aimed at (i) development of a core collection, (ii) quality trait assessment (iii) process development for value addition and (iv) creation of supportive policy framework, accelerated its evolution as a commercially important food crop.

Although the genus *Fagopyrum* has 30 species [5], only two species viz. *Fagopyrum esculentum* (common buckwheat) and *Fagopyrum tataricum* (Tartary buckwheat) are cultivated (Fig. 1). Buckwheat has been grown for centuries for its grains as well as foliage. However, it got neglected during the XXI century because of greater focus on developing high yielding varieties of rice, wheat and maize during the Green Revolution. Nonetheless, it is recognized as a potential super food because of its

Fig. 1 Phenotypic variations in the two cultivated species of buckwheat viz. *Fagopyrum esculentum*, *F. tataricum*, and the wild perennial species viz. *F. cymosum*

nutraceutical properties (Table 1) and potential for use in preparation of functional foods [6, 7]. Buckwheat is rich in nutrients and its grains contain 100–125 mg g^{-1} of protein, 650−750 mg g^{-1} of starch, 20−25 mg g^{-1} of fat and 20−25 mg g^{-1} of minerals [7]. The low proportion of prolamins and absence of α-gliadin, which is a key factor for gluten-free nature of buckwheat grain protein, makes buckwheat a healthy alternative to gluten-containing grains in diets of patients with gluten-related disorder, such as celiac disease, non-celiac gluten sensitivity, wheat allergies, and dermatitis herpetiformis. The amino acid composition of buckwheat grain protein matches the WHO recommended values for nutritionally rich proteins [8]. The major grain protein in buckwheat is a 13S globulin which contains 5.9% lysine and 2.3% methionine [8–12]. Compared to other plant proteins, buckwheat 13S globulin has significantly higher ratios of lysine to arginine and methionine to arginine [8]. Such rare plant proteins are widely recognized for their cholesterol-lowering effects in blood [13]. The buckwheat protein has been assigned an amino acid score 100 [14], which is the highest among plant proteins. Buckwheat grains also contain higher amount of vitamin B_1 (thiamine), B_2 (riboflavin), B_3 (niacin and niacinamide) and B_6 [15]. The major flavonoids in buckwheat grains are rutin, quercetin, orientin, homoorientin, vitexin and isovitexin [16–19]. Therapeutic actions of rutin include modulation of hypercholesterolemia, prevention of oxidative damage in aortic endothelial cells by lowering nitrotyrosine immune-reactivity, anti-platelet aggregation, prevention of cognitive impairments like Alzheimer's disease by ameliorating oxidative stress and prevention of splenocyte apoptosis [20, 21]. Rutin is also

Table 1 Nutritional composition of buckwheat in comparison to major cereals, tuber crops and pulses (nd: not detected)

Crop→	Pseudocereals			Tuber crops			Cereal grains						Pulses					
Nutrients ↓	Buck-wheat [30, 31]	Quinoa [30, 31]	Amaranth [31, 32]	Sweet Potato [30]	Potato [31, 33]	Cassava [31, 34]	Wheat [35]	Maize [31, 36]	Milled Rice [37]	Brown Rice [36, 38]	Barley [31]	Sorghum [31, 38]	Chickpea [34]	Kidney Bean [39]	Lentil [31]	Soyabean [31]	Green Gram [31]	Pea [31]
Proximate composition (100 g fresh weight^{-1})																		
Energy (kcal)	355.000	354.000	346.000	86.000	95.000	160.000	344.000	366.000	345.000	362.000	352.000	329.000	1201.000	1245.000	1349.000	1597.000	1363.000	1269.000
Crude protein (g)	5.700-14.200	14.100	14.500	1.600	2.630	1.360	11.800	9.400	6.800	7.500	9.900	10.600	17.100	22.900	25.100	43.200	24.000	72.000
Total carbohydrates (g)	72.900	57.160	63.000	20.120	21.400	38.100	71.200	63.600	78.200	76.200	77.700	72.100	60.900	60.600	59.000	20.900	56.700	15.900
Total fiber (g)	17.800	7.000	12.500	3.000	2.300	1.800	12.200	7.300	4.100	3.600	15.600	6.700	3.900	4.800	0.700	3.700	4.100	4.000
Fat (g)	7.400	4.700	2.500	4.700	0.130	0.280	2.730	4.700	3.600	2.400	2.300	nd	5.110	1.770	0.750	19.420	1.140	1.890
Minerals and trace elements (mg 100 g fresh weight^{-1})																		
Ca	110.000	54.000	162.000	30.000	18.000	16.000	30.000	48.300	10.000	33.000	29.000	13.000	202.000	260.000	69.000	240.00	124.000	20.000
Fe	4.000	5.270	10.000	0.610	1.070	0.270	3.500	4.800	0.700	1.800	2.500	3.360	4.600	5.100	7.580	10.400	4.400	1.500
Mg	390.000	227.000	138.000	25.000	30.000	21.000	138.000	107.900	64.000	143.000	79.000	165.000	169.000	184.000	80.000	238.000	127.000	34.000
P	330.000	527.000	455.000	47.000	71.000	27.000	298.000	210.000	160.000	264.000	221.000	222.000	312.000	410.000	293.000	690.000	326.000	139.000
Mn	3.400	nd	2.300	0.258	0.228	0.384	2.290	1.000	0.510	nd	nd	0.780	0.740	1.600	1.040	2.350	2.470	nd
Zn	0.800	3.570	2.700	0.300	0.350	0.340	2.700	2.210	1.300	2.020	2.100	1.700	2.900	4.500	2.800	4.400	3.000	nd
K	450.000	649.000	284.000	337.000	550.000	2710	376.000	324.800	nd	nd	nd	nd	nd	nd	629.000	nd	843.000	79.000
Na	11.000	7.000	6.000	55.000	14.000	14.000	17.100	35.000	nd	4.000	2.100	1.700	nd	nd	40.100	nd	28.000	7.800
Cu	0.515	0.192	0.149	0.151	0.107	0.100	0.452	1.300	nd	nd	nd	nd	1.180	1.450	1.870	1.380	0.390	0.230
Essential amino acids (% of total protein)																		
Lys	5.900	5.400	5.190	0.066	0.137	0.044	2.300	2.700	3.900	4.100	3.500	2.700	440.000	460.000	440.000	400.000	460.000	400.000
Met	3.700	2.200	2.170	0.029	0.041	0.011	1.200	1.900	1.700	2.400	2.200	1.000	80.000	60.000	50.000	80.000	80.000	60.000
Trp	1.400	1.200	1.310	0.031	0.027	0.019	2.400	0.500	1.300	1.400	1.500	1.000	50.000	60.000	60.000	80.000	60.000	60.000
Leu	6.700	5.900	5.150	0.092	0.125	0.039	6.300	12.400	8.100	8.600	6.600	14.200	580.000	470.000	470.000	480.000	510.000	380.000
Vitamins (mg 100 g fresh weight^{-1})																		
Vitamin B1(Thiamine)	3.300	0.520	0.500	0.078	0.067	0.087	0.470	0.320	0.410	0.590	0.120	0.330	0.300	0.882	0.450	0.730	0.470	0.250
Vitamin B2 (Riboflavin)	10.600	0.310	0.200	0.061	0.048	0.048	0.090	0.100	0.020	0.070	0.050	0.130	0.150	0.186	0.200	0.390	0.270	0.010
Vitamin B3 (Niacin)	18.000	1.600	5.500	0.557	1.350	0.854	3.700	1.900	1.900	4.000	2.700	3.400	2.900	2.489	2.600	3.200	2.100	0.800
Total Folate	0.042	0.054	0.022	0.011	0.026	0.027	0.057	0.003	0.020	0.0450	0.020	nd	0.186	0.121	0.036	0.100	0.140	nd
Carotenoids (μg 100 g fresh weight^{-1})																		
Lutein	220.000	53.000	3.600–4.400	nd	19.000	nd	1.230–23.930	0.036–0.109	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Zeaxanthin	nd	nd	trace-0.300	nd	nd	nd	1.440–32.400	0.014–0.037	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
β-carotene	1.050	3.000	nd	8510.000	6.000	8.000	2.000	171.000	nd	nd	7.000	nd	nd	157.000	2.000	1.000	128.000	nd
Flavonoids (μg 100 g fresh weight^{-1})																		
Quercetin	7.000	68.000	60.000	10.000	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.420	1.410	nd	nd
Rutin	808.400	6.150	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd

known to have cardio-protective, anti-inflammation, cytoprotective and anti-diabetic properties [22, 23]. Rutin has also been reported to inhibit transcription of more than 20 genes coding for critical pro-inflammatory factors including TNF-α, IL-1 and IL-8 [24]. The bitter taste of dough made from buckwheat flour is, however, due to the presence quercetin, which is a hydrolysis product of rutin due to rutinosidase activity [25]. Bai et al. [26] have demonstrated the role of lectins, present in grains of Tartary buckwheat, in reducing the proliferation of spontaneous and induced tumours. Besides the high protein and flavonoid content, buckwheat grains also contain higher level of zinc, copper, and manganese than other cereals [27, 28]. Buckwheat grains are also a rich source of dietary fiber which regulates postprandial blood glucose level and increases insulin sensitivity [29].

A major constraint in large scale incorporation of such nutraceutical crops in the agricultural portfolio is the inability of researchers and policy framework administrators to address all the issues along the value chain. FAO [2] has highlighted the fact that while potential future smart crops, such as buckwheat and millets, contribute only a small portion to the food basket at the national levels, their contribution towards nutritional security at local household levels in small and marginal farming communities in rural areas is quite high. However, over the last two decades there has been a slow but consistent decrease in the global area under buckwheat cultivation [1]. Limited investments in research and development of processes for post harvest processing including value addition have hampered any large scale incorporation of buckwheat into the agricultural portfolio as a smart crop.

Domestication Events in Buckwheat

Inspite of the long history of its cultivation, buckwheat has a limited history of domestication. Even though *F. tataricum* has relatively higher rate of seed set, its seeds have a strongly adhering hull and its flour is bitter in taste because of the presence of quercetin. Wu et al. [40] have shown three evolutionary transitions viz. (i) reduction in flower size, (ii) decrease in number of pollen grains *per* flower and (iii) herkogamy, in the genus *Fagopyrum*. On the other hand, Zhang et al. [41] have identified 150 sweeps across 3415 putative genes, covering 8% (39 Mb) of the assembled genome, between the Himalayan wild and Chinese south-western landraces of Tartary buckwheat. They also identified 156 sweeps across 3,006 putative genes, covering 8.5% (41 Mb) of the assembled genome, between the Himalayan wild and landraces of Tartary buckwheat from north and central China, Korea, Central Asia and Asian Russia, Europe, and North America. On the basis of F_{ST} values and comparison of genetic diversity ($\pi_{wild}/\pi_{landrace}$) amongst populations, they reported four unique selective sweeps in south-western and 8 unique selective sweeps in Northern landraces. Zhang et al. [41] suggested the occurrence of two independent domestication events, driven by human intervention, in south-western and northern China, which resulted in diverse characteristics of present day Tartary buckwheat. Zhang et al. [41] also identified eight unique GWAS signals for various agronomic traits such as plant height, time taken to maturity, grain weight, grain shape, grain width, pericarp colour, and grain yield in south-western and Northern landraces of Tartary buckwheat. One such signal represented a protein kinase gene *FtPinG0505903200*, which showed strong correlation with plant height. Zhang et al. [41] could not detect other well-characterized domestication genes of crops such as *sh4* for seed shattering in rice [42], *tga1* for naked grains in maize [43], PROG1 for tiller angle in rice [44] in the genetically selective sweeps during buckwheat domestication. These observations support the concept that the domestication process in buckwheat is still at a relatively very early stage.

Breeding Strategies in Buckwheat

Similar to breeding programs in other cross-pollinated species, conventional approaches towards improvement of common buckwheat have been hindered by lack of pollen control, inbreeding depression and difficulties in evaluating single plants [45]. Thus, compared to wheat, rice or maize, conventional breeding in common buckwheat could make only limited progress. As a strategy to overcome breeding barriers in common buckwheat, development of self-pollinating buckwheat by inter-specific hybridization between *F. esculentum* and *F. tataricum* and between common buckwheat and its wild homomorphic relative, *Fagopyrum homotropicum*, has always been considered as an important step. Similarly, breeding for *F. tataricum*, traditionally known as ‘bitter buckwheat’, having non-adhering hulls and low rutinosidase activity has always remained a priority area for enhancing its domestication. Availability of heterotic pools, represented by at least two populations with strong agronomic adaptability, while being genetically distant enough to exhibit strong heterosis, is one of the essential requirements of hybrid breeding. The extensive collection of buckwheat germplasm from different regions of globe could provide valuable gene pool for isolation of genetically divergent heterotic pools in buckwheat. Another essential requirement of large scale hybrid development programs is the availability of an efficient crossing technique. Mukasa [46] was able to produce cross hybrids in common buckwheat using homozygous homostyle (S^hS^h) and pin (ss) lines as pollen and seed parents, respectively. The resulting homostylous self-compatible (S^hs) F_1 hybrids showed 10–15% advantage in grain yield over the open pollinated common buckwheat.

These results suggest that heterosis breeding can be used to increase seed yield in common buckwheat. A major disadvantage of this method, however, is the lengthy cycle of successive selfing generations to produce homozygous inbreds. Double haploid technology, however, allows accelerated recovery of absolute homozygous lines. With the availability of optimized growth conditions for stable induction and regeneration of gynogenic haploids [47, 48], double haploid technology might become available for inbred development and hybrid breeding in buckwheat.

Attempts to improve the existing varieties of buckwheat by introgression of agronomically useful traits have their origin in crosses between *F. esculentum* and *F. tataricum* [49]. Despite successful crosses, most of the inter-specific hybrids were sterile [50–52]. A major success in developing inter-specific hybrids in buckwheat came with a cross between *Fagopyrum esculentum* and *Fagopyrum homotropicum* [53–56], which paved the way for successful introgression of the self-compatibility trait of *F. homotropicum* into common buckwheat. Matsui et al. [56] developed "Norin-PL1″, a breeding line of common buckwheat, by crossing *F. esculentum* cv. Botansoba and *F. homotropicum*, followed by recurrent backcrossing of F_1 hybrid with *F. esculentum.* Woo et al. [57], however, reported better cross-compatibility when thrum-type common buckwheat was used as the female parent rather than the pin-type. The resulting F_1 plants were partially fertile, late maturing and intermediate between the parents in floral morphology and plant height. The progeny segregated into heterostylic and homostylic types in equal numbers, indicating that homostyly is controlled by a single dominant gene. Backcrossing of thrum-type F_1 hybrids with *F. esculentum* and advancing of homostylic F_1 hybrids to F_2 and F_3 generations together with the BC_1F_1 for the analysis of stylar genes, revealed that genes coding for heterostyly and homostyly were controlled by a multiple allelic "S" locus. Woo et al. [57] suggested that the pin/thrum complex in *F. esculentum* was controlled by a single genetic locus "S" having two alleles"S" and "s". While the "Ss" genotype had thrum-type flowers, the "ss" genotype had pin-type flowers. Subsequently, inter-specific hybrids were also developed between *F. cymosum* and *F. esculentum* as well as *F. esculentum* and *F. tataricum* [58]. Matsui et al. [59] investigated the inheritance of brittle pedicels using 2 self-compatible lines (01AMU2, which has brittle pedicels and KSC2, which has non-brittle pedicels) produced by an inter-specific cross between *Fagopyrum esculentum* cv Botansoba (non-brittle) and *F. homotropicum* (brittle). While the F_1 plants derived from crosses between Botansoba and 01AMU2 as well as Botansoba and KSC2, had brittle pedicels, the F_2 population of Botansoba x 01AMU2 showed segregation of brittle and non brittle pedicels in the ratio of 3:1. On the basis of this ratio, Matsui et al. [59] inferred that the non-brittle pedicel trait in *F. esculentum* cv. Botansoba was controlled by a single recessive gene (*sht*1). On the other hand, the F_2 population of Botansoba x KSC2, showed segregation of brittle and non-brittle pedicels in the ratio of 9:7, thereby indicating that the non-brittle pedicel trait in KSC2 was controlled by a different recessive gene (*sht*2). Matsui et al. [60] developed 5 AFLP markers, which were linked to the *sht1* locus, and converted two of them into STS markers for MAS of plants with non-brittle pedicels.

Genomics Assisted Breeding in Buckwheat

Improvement of yield, palatability and development of self-compatible lines are important objectives in buckwheat breeding. While QTL mapping, genome-wide association studies (GWAS), and genomic selection (GS), have been effectively used for genome assisted breeding of crops during the last few decades [61–63], application of these tools in minor crops is yet to gain momentum because of paucity of information on their genome. Yabe and Iwata [64] were able to score only 220 hits for mining data on application of QTL mining in 12 minor crops such as *Triticum spelta, Triticum turgidum, Triticum monococcum, Sorghum bicolor, Chenopodium quinoa, Amaranthus cordatus, Fagopyrum esculentum, Fagopyrum tataricum, Salvia hispanica, Avena sativa, Secale cereale* and *Eragrostis tef.* Even amongst these, most of the hits were scored for sorghum. While AFLP markers have not yet been converted to single locus markers in *Fagopyrum esculentum*, SSR marker based amplification of specific gene loci has proved to be difficult in this species, because of the high level of genetic diversity between cultivars. Hara et al. [65] were the first to map QTLs controlling photoperiod in a segregating F_4 population of common buckwheat derived from a cross between two autogamous lines, 02AL113 (Kyukei SC2)LH.self and C0408-0RP. The linkage map revealed three putative genes (*FeCCA1*, *FeELF3* and *FeCOL3*) for photoperiod-sensitivity in common buckwheat. However, availability of high-throughput genotyping system is necessary to fully utilize genomic selection as a tool in buckwheat breeding, because a large number of genome-wide markers need to be genotyped for all the plants in a breeding population. Yabe et al. [66] used an array-based genotyping system to construct a high-density linkage map, composed of 8,884 markers spanning 756 loci converging into eight linkage groups, in *Fagopyrum esculentum*. They also linked four QTLs to length of the main stem. Yabe et al. [67] have demonstrated the importance of both breeding cycle acceleration and frequent model updating in GS breeding, the latter of which may be a unique requirement for GS breeding in allogamous crop populations with low linkage disequilibrium.

The emergence of genomic information on buckwheat [68, 69] has paved the way for development of breeding pipelines, which can integrate the emerging "omics", phenotyping, and genome editing technologies for desirable traits. The last decade has also witnessed transcriptome-based gene expression profiling for characterization of candidate genes which regulate various agronomic traits, such as heterostyly, seed size, yield, flavonoid biosynthesis, nutritional quality and abiotic stress tolerance in buckwheat [68, 70–72]. Exploring the draft genome as a reference sequence for GBS mapping, Yasui et al. [68] reported that the *"S*-allele region", specific to common buckwheat with short-styled flower, comprised of 332 scaffolds encompassing 5.4 Mbp. Their results revealed several sites and two *S*-allele-specific genes, *S-ELF3* and *SSG2*, which specifically mapped in short-styled plants but not in long-styled plants. While several GBS pipelines are available to characterize single genotypes, they do not have much application in crops like common buckwheat, which exist as genetically heterogeneous, open-pollinating populations. Nay et al. [73] have described a GBS pipeline which, rather than reporting the state of bi-allelic single nucleotide polymorphisms (SNPs), resolves allele frequencies within populations on a genome-wide scale. The genome-wide allele frequency fingerprints (GWAFFs) provide an excellent opportunity to associate allele frequencies to phenotypic traits and quality parameters, which are most reliably described on population level. Genic-SSR markers, developed from the transcriptome of common and Tartary buckwheat by Shi et al. [74], can be used to construct linkage maps and marker-assisted selection in the two cultivated species. Shi et al. [74] have reported the presence of 2454 genic-SSRs from 2326 transcripts with a frequency of one SSR *per* 1.17 kb. Amongst the randomly chosen 150 SSR markers, 36 markers showed polymorphism in 24 accessions of common buckwheat. Out of these, 141 SSRs (94.0%) were transferable to Tartary buckwheat. In order to identify important loci for buckwheat breeding, Penin et al. [75] utilized long-read technology for the assembly of buckwheat genome and generated a high-resolution expression atlas for 46 organs and developmental stages of common buckwheat. Their study revealed a threefold larger size of common buckwheat genome than that of Tartary buckwheat. The difference in genome size was ascribed to "transposon burst" in common buckwheat that occurred 0.5–1 Mya. Recently, Zhang et al. [76] have generated a comprehensive database on genomic variations on Tartary buckwheat germplasm by high-throughput sequencing of Tartary and rice-Tartary buckwheat and F2 population of the cross between Tartary and rice-Tartary buckwheat. Based on Bulked Segregant Analysis, they identified a genetic locus housing 45 SNPs/indels and 36 genes, which controlled easy de-hulling trait in rice-Tartary buckwheat. In this context, introducing the concept of pan-genomics to study buckwheat diversity would expedite molecular breeding in this crop. While pan-genomic studies may be in their infancy in non-model crops, with the release of genome assembly mapping of common buckwheat using *de novo* MAGICTM (NR Gene, Israel) (https://www.nrgene.com/nrgeneassembles-buckwheat-genome/), global scientific community can anticipate the development of buckwheat genomic resources via pan-genomics approach. Metabolomics, proteome mapping, and ionomics interventions is another component that has been explored to develop a roadmap for trait improvement in buckwheat. Metabolome profiling of dehulling-recalcitrant and easy-dehulling varieties of buckwheat has revealed the role of lignin to cellulose ratio in the hull in determining the ease of grain dehulling [77]. This study could provide a major direction to breeding program for identification/development of varieties with better dehulling ability.

Future Directions in Breeding Buckwheat as a Strategic Crop

With a growing interest in healthy lifestyle, buckwheat has started to receive global attention as a component of functional foods. However, cultivation of buckwheat is limited by several unfavourable traits such as indeterminate growth habit, unstable yields, high rate of flower abortion, palatability and poor shelf life of grains. Further, genetic variation available in buckwheat gene pool has remained by and large poorly characterized for agronomic traits. This necessitates systematic analysis of the available genetic diversity for economic traits through development of core collections and their multi-locational evaluation. Because of high amylose content, buckwheat flour has poor dough making qualities. Screening of genotypes in their haploid phase for alleles for low amylose content would open a new direction for isolation of low amylose genotypes of buckwheat. In comparison to common buckwheat, Tartary buckwheat has higher and more stable yield attributes due to low-seed abortion, homomorphic self-compatibility and frost tolerance. However, Tartary buckwheat has not received much favour for cultivation because of the tightly adhering hull. While rutin is present mainly in the embryos, flavonol-3-glucosidase, the rutin-degrading enzyme, is localized only in the testa. Since rutin and rutin-degrading enzyme are spatially separated from each other in the grains, it is possible to avoid enzymatic degradation of rutin by using flour from dehulled grains for making dough. Breeding for *F. tataricum* with non-adhering hulls and low rutinosidase activity would be crucial for enhancing cultivation of Tartary buckwheat. With an improved understanding of agronomically important genes in buckwheat genome, combinatorial approach of speed breeding with CRISPR/Cas9 genome editing and GWAS would accelerate its domestication. Application of Next-Gen artificial intelligence for integration of multi-omics datasets would enable accurate prediction of phenotypes from diverse sets of buckwheat genotypes under different environmental conditions. The pre-ambient prediction

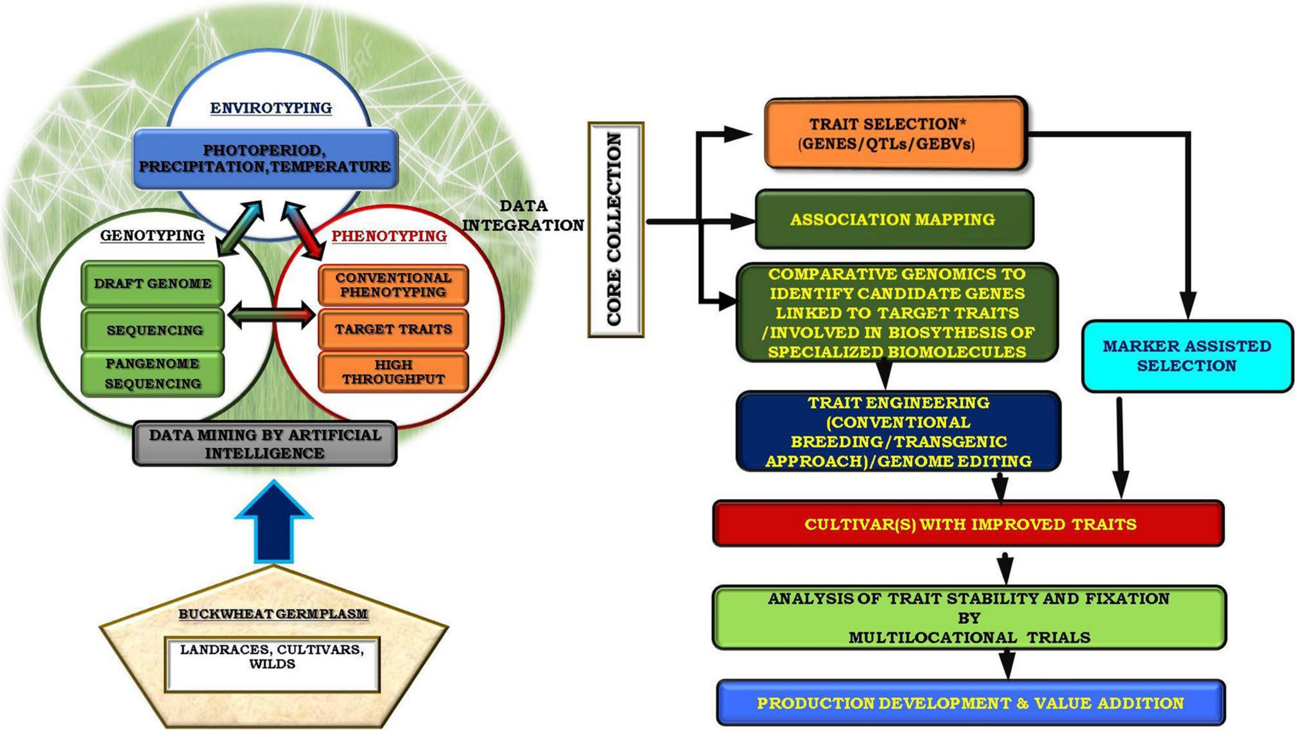

Fig. 2 Schematic representation of an integrated genomics driven breeding approach for achieving trait based genetic gains in common and Tartary buckwheat. *Determinate growth habit, low rutinosidase activity, loose hulled grains, low amylose/amylopectin ratio of starch, self-compatibility

data generated using Next-Gen AI, when interfaced with data generated for diverse buckwheat germplasms using pan-genomic approach, would enable buckwheat breeders to rapidly identify better genotypes. This approach can also be important in identification of optimum combination of genes for a given location. A flowchart for harnessing the potential of buckwheat as a strategic crop for human nutrition is given in Fig. 2.

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Declarations

Conflict of Interest The authors declare that they have no competing conflicts of interest.

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