Invited Review

Current status and prospects of common buckwheat breeding in Japan

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In this review, the current status and prospects of common buckwheat (*Fagopyrum esculentum* Moench.) breeding in Japan are summarized. The varieties that have been registered in Japan so far are introduced with details regarding their breeding source populations and breeding methods. Because the main breeding method used for common buckwheat is mass selection, the merits and demerits of this method are explored from the perspective of heritability. Although there are many breeding objectives in common buckwheat, high yield and yield stability are discussed here. Regarding the potential of common buckwheat breeding in the future, the prospects of effective exploitation of self-fertility and selection based on genomic information are examined.

Key Words: common buckwheat breeding, breeding methods, yield, yield stability, genomic selection.

Introduction

Common buckwheat (*Fagopyrum esculentum* Moench, $2n = 16$) is an outcrossing pseudocereal crop. According to FAOSTAT (2019), the world buckwheat production in 2017 was approximately 3,827,000 tons. Russia and China were the largest producers, collectively accounting for ca. 78% of global production that year. Japan ranked tenth in total production. Recently, approximately 130,000 and 34,400 tons of common buckwheat are annually consumed and produced, respectively, in Japan. Although domestic production comprises only 0.8% of the global production in 2017, because common buckwheat is a traditional food in Japan, its consumption never declines. The current situation is that most of its supply relies upon imports from overseas. Although demand for domestic buckwheat is high, the most serious challenge associated with common buckwheat production is low yield. The yield of common buckwheat per unit area common buckwheat is approximately 50 kg/10 a, which is relatively low and represents 14% and 8% of the yields for wheat and rice, respectively, in Japan (FAOSTAT 2019). Considering the approximate number of seeds that could be obtained from an individual crop, 200–300 grains can be obtained from wheat, 1000 grains from rice, and only 40–50 grains from common buckwheat. In Japan, in wheat cultivation, approximately 10 kg/10 a of seeds are sown, with the yield being approximately 40-fold. However, in common buckwheat cultivation, the yield is

approximately 50 kg following the sowing of 4 kg/10 a of seeds, which represents an approximate 10-fold increase. A reason why common buckwheat cannot be used as a major crop is its low yield capacity. Conversely, the growth period of common buckwheat is relatively short; flowering begins approximately 20 days after sowing, and individuals attain maturity in approximately 60–70 days after sowing. The short growth period of common buckwheat implies that it serves as a salvage crop during starvation not only in Japan but also globally, or as a pioneering crop for securing food at the beginning of reclamation, and in lands with short cultivation periods such as high latitudes and highlands. Therefore, it plays a major role in food security and production.

Currently, in Japan, the number of farmers leaving due to the lack of successor is increasing, and economic reasons are also on the rise, and there is a tendency for abandoned farmland to expand. Common buckwheat is one of the field crops that could be cultivated more efficiently, and it is a regional specialty crop that supports regional economic activities. To expand the production of common buckwheat, it is essential to improve the agronomic traits such as yield stability and yield. In addition, high-quality production or high value-added activities would substantially promote the spread of common buckwheat production.

Recently, Katsube-Tanaka (2016) conducted a detailed review of Japanese common buckwheat production, consumption, and genetic resources in common buckwheat. Motonishi *et al.* (2018) also commented on current Japanese buckwheat production. In this paper they introduced several Japanese famous varieties. Motonishi *et al.* (2018) focused on the variety ‘Botansoba’, which is a very famous variety, especially in the northern region, and a genetic

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resource useful for subsequent breeding. Of course, this knowledge was invaluable, but the current review provides a more comprehensive description of the current status of common buckwheat breeding, its associated challenges, and future breeding directions.

Historical perspective of common buckwheat breeding

Common buckwheat breeding has been under the Ministry of Agriculture, Forestry, and Fisheries and breeding activities in each prefecture were initiated from around 1990. In addition, the history of common buckwheat breeding by a public organization in Japan spans only approximately 30 years. Common buckwheat is a crop whose breeding has not advanced despite a history of cultivation and its significance with regard to food supply in Japan.

In **Table 1**, the varieties bred before the enactment of the Plant Variety Protection and Seed Act (PVPSA) in 1978 and those registered after the PVPSA are summarized. Japan joined the International Union for the Protection of New Varieties of Plants (UPOV) in 1982, and following the revision of the UPOV Convention in 1991, the PVPSA was radically revised in 1998.

Among the varieties registered in Japan, ‘Mogamiwase’, selected from the local varieties at the Yamagata Prefectural Agricultural Experiment Station in 1919, is the oldest one. The origin of this line was a line grown in 1919 by a pure line selection method from a local variety at the experiment station Mogami site. Thereafter, in 1987 pure line selection was performed again because of deterioration in characteristics due to contamination, and it was selected as the recommended variety of the prefecture (Iwate Prefecture 1989). Simultaneously, in 1918, at the Aomori Agricultural Experiment Station, ‘Hashikamiwase’ was selected from the local varieties in Hashikami village (Aomori Agr. Exp. Stn. 1959). The Japanese word “wase” in the variety name indicates early maturing and/or flowering. ‘Tochigi 1 gou (Wagatsumazairai)’ was selected from local variety in Wagatsuma county in Tochigi Prefecture at the Tochigi Agricultural Experiment Station in 1924 (Tochigi Agr. Exp. Stn. 1969). ‘Botansoba’ was selected at the Hokkaido Agricultural Experiment Station in 1930 and was the most cultivated variety in Hokkaido for nearly 70 years until ‘Kitawasesoba’, a registered variety, was released in 1990. ‘Soba Shinano 1 gou’, which was bred from the local varieties in Fukushima Prefecture at the Nagano Prefectural Agricultural Experiment Station in 1944, is a widely grown variety to date. This variety is the same variety name as ‘Shinano No. 1’ or ‘Shinano 1’, which has been described in several studies such as Matsui *et al.* (2004), Motonishi *et al.* (2018), Takeshima *et al.* (2019), etc. Subsequently, in 1982, ‘Miyazaki-ootsubu’, a tetraploid variety developed at Miyazaki University, became the first variety to be registered under PVPSA, and 34 varieties have been registered as varieties to date.

Regarding the breeding of registered varieties, 20 of the 34 varieties have been bred using local varieties, old varieties, and registered varieties as the source populations. Because the selection method often used is mass selection or pedigree selection, some aspects of these methods remain unclear; however, these methods are essentially based on maternal selection, and many cases potentially combine mass and pedigree selection. Similar to the case of ‘Kaidawase’, undesirable individuals are removed for several generations, and there are some cases wherein such varieties are registered as varieties bred using mass selection. In many cases, approximately 1000 individuals are cultivated from a source population, from which hundreds of desirable individuals are selected to form the next generation for improvement. Alternatively, selection is repeated to select up to several individuals from hundreds of individuals; then, the individual lines are developed, and pedigree selection is performed.

Next, pedigree selection is performed based on comparisons with the check or comparative cultivar. There are cases wherein each line is isolated and maintained during pedigree selection and cases wherein crossing between lines is not controlled, and excellent individuals within a line are adopted for the following generation line.

The source populations of eight varieties among all registered varieties are populations of mating progeny that are employed in expanding variation or introducing desirable traits through mating between varieties or lines. Then, breeding is performed using mass selection and/or pedigree breeding to select multiple individuals and advance generation. The source population of ‘Natsumi’ is not a biparental progeny but is a group in which several summer varieties are mixed and then mated randomly. In addition, four of the registered varieties, namely Miyazaki-ootsubu, Sinshu-oosaba (4baitai), Dewakaori and Hokkai No. 3 are bred using mass selection from populations in which tetraploids have been induced by treating local varieties with colchicine; however, as a result, in ‘Dewakaori’ (**Table 1**), several diploid individuals have been selected. In addition, mutation breeding has been attempted, and three varieties, ‘Ganma no irodori’, ‘Cobalt no chikara’ and ‘Ruchiking’, have been bred. This method represents mass selection from irradiated individuals. The basic form of selection for any variety described above is maternal selection.

Table 2 lists the three most cultivated varieties in the major domestic cultivation areas over the last 10 years. In Hokkaido, ‘Kitawasesoba’, registered in 1990, is the most cultivated variety; however, ‘Botansoba’, registered in 1930, is still cultivated. In Yamagata Prefecture, ‘Dewakaori’ has been the most cultivated variety over the last few years; however, ‘Hashikamiwase’ and ‘Mogamiwase’, which were registered about 100 years ago, are still cultivated. In Nagano Prefecture, ‘Soba Shinano 1 gou’, registered 75 years ago, and ‘Shinano-Natsusoba’, registered 40 years ago, are still cultivated. In general, the main reason for the slow replacement of buckwheat varieties is not

Table 1. Common buckwheat cultivars in Japan

Variety name	Applicant	Breeding site	Year of registration	Ecotype Ploidy	Notable traits ^c	Breeding methods	Breeding source Population	Literature
Before PVPSA^a								
Mogamiwase	Yamagata Prefecture	Yamagata Agricultural Experiment Station	1987 Adopted as an excellent variety	Intermediate late summer 2×	High yield	Pedigree selection started in 1919 and reselection in 1987,	Unnamed local variety in Yamagata Prefecture	Hayashi (2011), Abe (2004a)
Hashikamiwase	Aomori Prefecture	Aomori Agricultural Experiment Station	1918 Adapted as a recommended cultivar	Intermediate summer 2×	Wide range of indications for sowing period High yield	Pedigree selection started in 1914	Local variety in Sannohe-Gun, Hashikami-village, Aomori Prefecture	Aomori Agr. Exp. St. (1959) Hayashi (2011), Yanagino (2004)
Tochigi 1 gou (Kamitsugazairai)	Tochigi Prefecture	Tochigi Agricultural Experiment Station	1924 Release as a cultivar	Late summer 2×	—	Pedigree selection started in 1919	Local variety in Kamitsuga-gun in Tochigi Prefecture	Tochigi Agri. Exp. Stn (1969) Hayashi (2011), Yuzawa (2004)
Botansoba	Hokkaido Prefecture	Hokkaido Agricultural Experiment Station	1930 Adopted as an excellent variety	Summer 2×	Large seed size	Mass selection	Local variety distributed from Date-mura agricultural committee, Hokkaido	Honda (2004)
Soba Shinano 1 gou	Nagano Prefecture	Nagano Agricultural Experiment Station, Kikyogahara site	1944 Adapted as a recommended cultivar	Intermediate 2×	Wide range of indications for sowing period	Pedigree selection	Unnamed local variety in Fukushima Prefecture	Hayashi (2011), Murayama (2004)
Iwatowase	Iwate Prefecture	Iwate Agricultural Experiment Station	1990 Adapted as a recommended cultivar	Intermediate 2×	Suitable plant type for machine cultivation	Pedigree selection started in 1975	Local variety 'Sotoyama zairai' in Tamayama-mura, Iwate Prefecture	Iwate Prefecture (1989) Hayashi (2011), Sakuyama (2004a)
Iwatanakate	Iwate Prefecture	Iwate Agricultural Experiment Station	1990 Adapted as a recommended cultivar	Intermediate 2×	Yield stability High quality	Pedigree selection started in 1978	Local variety 'Ninohe zairai' in Iwate Prefecture	Iwate Prefecture (1989) Hayashi (2011), Sakuyama (2004b)
Shinano-Natsusoba	Nagano Prefecture	Nagano Chushin Agricultural Experiment Station	1979 Adapted as a recommended cultivar	Summer 2×	High yield Short plant height	Mass selection	Local Variety in Kijimadaira-mura, Nagano Prefecture	Nishimaki <i>et al.</i> (1983)
After PVPSA								
Miyazaki-oosuba	Nagatomo Takashi	Miyazaki University, Miyazaki Agricultural Experiment Station	1982	Late summer 4×	Heavy seed weight	Mass selection	Individuals from colchicine-induced tetraploid from local variety 'Miyazaki zairai'	Nagatomo <i>et al.</i> (1982)
Sinshu-oosaba (4baitai)	Ujihara Akio	Shinshu University, Nagano Prefecture	1985	Intermediate late summer 4×	Heavy seed weight	Pedigree selection	Individuals from colchicine-induced tetraploid from variety 'Shinano 1 gou'	Ujihara <i>et al.</i> (1977)
Hitaichakisoba	Ibaraki Prefecture	Ibaraki Agricultural Experiment Station	1987	Intermediate late summer 2×	High quality High yield	Mass and pedigree selection	Local variety 'Kanasago zairai' in Ibaraki Prefecture	Nakagawa <i>et al.</i> (1985)
Kitawasesoba	NARO ^b	Hokkaido Agricultural Experiment Station	1990	Summer 2×	Early mature High yield	Mass and pedigree selection	variety 'Botansoba'	Inuyama <i>et al.</i> (1994)
Takanerubi	Takano Co. and Ujihara Akio	Shinshu University, Takano Co., Nagano Prefecture	1993	Late summer 2×	Red flower, Landscape plants	Pedigree selection	Unnamed local variety in Nepal	Hayashi (2011), MAFF (2019)
Kitayuki	NARO	Hokkaido Agricultural Experiment Station	1993	Summer 2×	Downy mildew resistance	Mass and pedigree selection	Local variety in Tsubetsu, Hokkaido	Honda <i>et al.</i> (1994) Hayashi (2011), MAFF (2019)
Shineired	Nagata Eiichi	Nagano Prefecture	1996	Intermediate late summer 2×	Red flower, Landscape plants	Pedigree selection	Unnamed imported variety	Hayashi (2011), MAFF (2019)
Greatorubi	Takano Co. and Ujihara Akio	Shinshu University, Nagano Prefecture	1998	Late summer 2×	Red pericarp	Pedigree selection	Variety 'Shinsyu-oosoba'	Hayashi (2011), MAFF (2019)

Table 1. (continued)

Variety name	Applicant	Breeding site	Year of registration	Ecotype Ploidy	Notable traits ^c	Breeding methods	Breeding source Population	Literature
Shimadasukaret	Tomono agurika Co.	Shizuoka Prefecture	1999	Intermediate 2×	Red pericarp	Pedigree selection	Unnamed local variety	Hayashi (2011), MAFF (2019)
Dewakaori	Yamagata Prefecture	Yamagata Prefecture Agricultural Experiment Station	1999	Intermediate late summer 2×	Heavy seed weight	Mass selection	Individuals from colchicine-treated diploid from variety 'Mogamiwase'	Yamagata Agr. Exp. Stn. (1996) Abe (2004b)
Sun Rutin	Takano Co. and Ujihara Akio	Shimshu University, Nagano Prefecture Agricultural Experiment Station	2002	Intermediate summer 2×	High rutin content	Pedigree selection	Variety 'Botansoba'	Hayashi (2011), MAFF (2019) Minami <i>et al.</i> (2000) Minami (2004)
Horominori	Horokanai-cho, Hokkaido	Horokanai-cho Agriculture Research Center	2004	Summer 2×	Determinate type	Pedigree selection	Variety 'Kitawasesoba'	Wagatsuma (2004) MAFF (2019)
Hokkai No. 3	NARO	Hokkaido Agricultural Experiment Station	2005	Summer 4×	Heavy seed weight	Pedigree selection	Individuals from colchicine-induced tetraploid from variety 'Botansoba'	Hayashi (2011), MAFF (2019)
Kitanomashu	NARO	Hokkaido Agricultural Experiment Station	2005	Summer 2×	Determinate type	Mass selection	Mutants in variety 'Kitawasesoba'	Honda <i>et al.</i> (2009)
Toyomusume	NARO	Hokuriku Agricultural Experiment Station in Niigata Prefecture	2007	Intermediate late summer 2×	High rutin content High yield	Mass and pedigree selection, each selected line was isolated propagation	Local variety 'Kuzuu zairai' in Tochigi Prefecture	Ito <i>et al.</i> (2006)
Kaidawase	Nagano Prefecture	Nagano Chushin Agricultural Experiment Station	2009	Intermediate late summer 2×	Early flowering period Heavy seed weight	Mass selection: eliminate undesirable individuals during five generations in isolated filed	Local variety in Kaide-village, Nagano Prefecture	Murayama <i>et al.</i> (2000)
Buckwheat 'Norin-PL1'	NARO	Kyushu Okinawa Agricultural Research Center	2009	Intermediate summer 2×	Self-fertilization, non-shattering	Interspecific crossing and pedigree method	Progeny of a cross between variety 'Botansoba' and <i>Fagopyrum homotriplicum</i>	Matsui <i>et al.</i> (2008)
Aizunokaori	Fukushima Prefecture	Fukushima Agricultural Experiment Station, Aizu site	2009	Intermediate late summer 2×	High appearance quality, High yield, High rutin content	Pedigree selection	Local variety in Shimogou-machi, Fukushima Prefecture	Hayashi (2011), MAFF (2019)
Natsumi	NARO	Hokuriku Agricultural Experiment Station in Niigata Prefecture	2010	Summer 2×	High rutin content	Mass and pedigree selection	Progeny of a cross among varieties, Foreign variety 'Tempest', variety 'Kitawasesoba', 'Shinano-natsusoba' and local variety 'Natsusoba'	NARO (2006) Hayashi (2011), MAFF (2019)
Harunoibuki	NARO	Kyushu Okinawa Agricultural Research Center	2010	Intermediate summer 2×	Preharvest sprouting resistance, early spring cultivation in Kyushu region	Mass selection	Variety 'Hashikamiwase'	Hara <i>et al.</i> (2012)
Sachiizumi	NARO	Kyushu Okinawa Agricultural Research Center	2010	Intermediate late summer 2×	Early mature type compare to local variety 'Kanoya zairai' which is major variety in South Kyushu area	Mass selection	Progeny of a cross local variety 'Ashimura zairai3' in Asahimura, Niigata Prefecture and local variety 'SOBA' in Tsushima, Kyushu	Matsui <i>et al.</i> (2013)
Miyazakiwase-kaori	Miyazaki Prefecture	Miyazaki Agricultural Research Institute	2010	Intermediate late summer 2×	Early mature compare to original local variety 'Kanoya zairai'	Pedigree selection	Early mature compare to original local variety 'Kanoya zairai'	Hayashi (2011), MAFF (2019)
Tachiakane	Nagano Prefecture	Nagano Vegetable and Ornamental Crop Experimental Station	2010	Intermediate late summer 2×	Red pericarp Lodging tolerance	Mass and pedigree selection	Local variety 'Usudamachi zairai' in Nagano Prefecture	Mariyama <i>et al.</i> (2010)
Reranokaori	NARO	Hokkaido Agricultural Experiment Station	2010	Summer 2×	Good flouring character	Mass and pedigree selection	Genetic resource 'Tanno-Huushinai' in Hokkaido	Morishita <i>et al.</i> (2013)

Table 1. (continued)

Variety name	Applicant	Breeding site	Year of registration	Ecotype Ploidy	Notable traits ^c	Breeding methods	Breeding source Population	Literature
Hietsu No. 1	Ishida Isoroku (Personal)	Gifu Prefecture	2012	Late summer 2×	Short seed length Late mature	Mass selection	Progeny between local variety 'HidaMiyagawa zairai' in Gifu Prefecture and local variety 'Echizen zairai' in Fukui Prefecture	MAFF (2019)
Takanerubi2011	Takano Co.	Takano Co., Nagano Prefecture	2013	Late summer 2×	Red flower, Landscape plants	Pedigree selection	Variety 'Takane rubi'	MAFF (2019)
Ganna no irodori	NARO	Institute of Radiation Breeding, Ibaraki Prefecture	2013	Intermediate 2×	High rutin content, Antioxidant ability	Mutation breeding, Pedigree selection	Individuals from cultivar 'Botansoba' irradiated gamma rays repeatedly	Morishita <i>et al.</i> (2019) MAFF (2019)
Cobalt no chikara	NARO	Institute of Radiation Breeding, Ibaraki Prefecture	2013	Intermediate 2×	High catechin content, Antioxidant ability	Mutation breeding, Pedigree selection	Individuals from cultivar 'Botansoba' irradiated gamma rays repeatedly	Morishita <i>et al.</i> (2019) MAFF (2019)
Ruchiking	NARO	Institute of Radiation Breeding, Ibaraki Prefecture	2013	Intermediate 2×	High rutin content	Mutation breeding, Pedigree selection	Individuals from cultivar 'Botansoba' irradiated gamma rays repeatedly	Morishita <i>et al.</i> (2019) MAFF (2019)
Izumonomai	Shimane Prefecture	Shimane Agricultural Technology Center	2014	Intermediate 2×	High yield	Pedigree selection	Progeny of a cross between 'Botansoba' and local variety 'Yokota zairai' in Shimane Prefecture	Hashimoto and Takahashi (2015)
Akiakane	Shinshu University, Takano Co.	Takano Co., Nagano Prefecture	2014	Late summer 2×	Red flower, Landscape plants	Mass selection	Progeny of a cross between semidwarf line bred from variety 'Shinano 1 gou' and Dark red line selected from variety 'Takane rubi'	Sasaki <i>et al.</i> (2012)
Nijiyutaka	NARO	Tohoku Agricultural Experiment Station, Iwate	2014	Intermediate late summer 2×	High lodging resistance	Mass and pedigree selection	Progeny of a cross between local variety 'Kuzuu zairai' in Tochigi Prefecture and local variety 'Togakushi zairai' in Nagano Prefecture	Yui <i>et al.</i> (2012)
Nagano S No. 8	Nagano Prefecture	Nagano Vegetable and Ornamental Crop Experimental Station	2014	Intermediate late summer 2×	Deep Green Seed	Mass and pedigree selection	Progeny of a cross between breeding line 'Kanto 1 gou' and variety 'Shinano 1 gou'	Mariyama <i>et al.</i> (2014)
Kitamitsuki	NARO	National Agricultural Research Center for Hokkaido Region	2019	Summer 2×	High yield, High rutin content	Maternal selection (Mass selection)	Progeny of a cross between local variety 'Tanno 43' and variety 'Kitawasesoba'	MAFF (2019)

^a PVPSA: The Plant Variety Protection and Seed Act.^b NARO: National Agriculture and Food Research Organization.^c These traits listed in this column were selected by the author as notable traits and do not necessarily represent all important traits.

Table 2. Present situation of buckwheat cultivation in Japan

Region	Hokkaido			Yamagata Prefecture			Nagano Prefecture		
	Total cultivation area of each prefecture in 2016 (ha)								
	21,500			5,100			4,130		
Order Yeat	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
2007	Kitawasesoba	Botansoba	－	Mogamiwase	Dewakaori	Hashikamiwase	Soba Sinano 1 gou	Shinanonatsusoba	Local varieties
2011	Kitawasesoba	Botansoba	－	Mogamiwase	Dewakaori	Hashikamiwase	Soba Sinano 1 gou	Shinanonatsusoba	Local varieties
2016	Kitawasesoba	Botansoba	Reranokaori	Dewakaori	Mogamiwase	Hashikamiwase	Soba Sinano 1 gou	Shinanonatsusoba	Ngano S8
Area (ha)	19,000	877	840	2,259	2,213	36	2,979	438	121
Percentage (%) in each region	88	4	4	44	43	1	72	11	3

Tokusansyubyo 9 (2010), 19 (2015), 28 (2019).

clear, but it is difficult to actively update new varieties in various parts of Japan. However, establishing a seed supply system is indispensable for breeding of varieties, but the supply of seeds is not sufficient in general buckwheat cultivation, which is why general buckwheat varieties are not being renewed. In addition, novel variety would be more attractive to farmers and consumers if they have better qualities, e.g., stable exhibition of a two-fold increase in yield compared with that by conventional varieties.

Common buckwheat breeding methods

The selection of common buckwheat is delayed compared with that in the breeding of other major crops. In general, common buckwheat is characterized by complete outcrossing owing to heteromorphic self-incompatibility (Campbell 1997), which is under the control of the S-locus (Lewis and Jones 1992). Similar to that in breeding programs for other cross-pollinated species, mass selection for population improvement is performed conventionally wherein the lack of control over pollen and inbreeding depression hinder efficient genetic improvement (Acquaah 2009).

A key advantage of mass selection is that the procedure is simple; therefore, it can manipulate a large number of individuals. In addition, because one cycle represents one generation, the period until desirable lines are acquired could be shortened. Conversely, a demerit of mass selection is that selection works only for maternal genes by the targeting of open-pollinated populations, and there is no selection of pollen parents. In addition, selection has been conducted on an individual basis based on phenotypic characteristics only; therefore, the method is susceptible to the influence of the environment. According to Yano *et al.* (2002), the inability to evaluate single plants minimizes the efficiency of mass selection and indicates that error control for yield could be beneficial when selection is performed only over a few cycles (generations). However, population size is a critical factor when selection is performed in more cycles for optimal exploration of the genetic potential of a target population in cross-fertilizing cereal crops such as common buckwheat. However, to the best of our knowledge, no field study has explored the effect of individual selection and population size at the time of population

selection in common buckwheat breeding in Japan to date. In the case of mass selection, selection efficiency decreases when traits with low heritability and genotype–environment interaction traits are selected.

Few studies have explored differences in the heritability of various common buckwheat traits; however, there are reports on the heritability of agronomic traits (Kitabayashi *et al.* 1995, Ohsawa *et al.* 1995, Rana and Sharma 2000). Relevant data are summarized in Table 3. Ohsawa *et al.* (1995) demonstrated that although seed weight is genetically stable and selection efficiency is high as well as plant height and flowering period are genetically stable traits, it is necessary to select traits while taking into account the influence of annual variation. In addition, the heritability of seed yield per unit area is lower than in other traits, and the difference across years is considerable. The abovementioned results are almost consistent with the findings reported by Rana and Sharma (2000). Regarding plant components such as rutin or proteins, Kitabayashi *et al.* (1995) reported that the heritability of rutin content in seed is 0.590, which is not high compared with that of other agronomic traits. Considering the heritability of yield, the heritability of the number of seeds per individual is low in common buckwheat, which highlights the challenge of selecting phenotypes based on individuals that are considerably influenced by the environment. Such perspectives further support the effectiveness of selection based on genotypes as discussed later.

Based on the information mentioned above, it is evident that breeding targets associated with yield face considerable challenges, which is not the case for the breeding of individuals for qualitative traits such as in red flower and red skin. Although improvements in flowering time and maturation time have occurred in various areas, such selection activities were expected. Conversely, although the yield per unit is somewhat superior to that in cases of other varieties in various areas, there is no case of considerably high yield or substantially high stability.

Efforts to achieve stable and high yield

Some of the important breeding objectives in common buckwheat breeding include stable yield, superior seed

Table 3. Heritability and its confidence interval by variety comparison of agronomic traits in common buckwheat

	Seed yield		Plant height		Flowering period		1000 seeds weight	
Year	1993	1995	1993	1995	1993	1995	1993	1995
Heritability	0.540	0.846	0.861	0.906	0.808	0.951	0.932	0.991
95% confidence interval								
Lower limit	0.153	0.624	0.654	0.753	0.550	0.866	0.817	0.974
Upper limit	0.840	0.955	0.960	0.973	0.943	0.987	0.981	0.998
modified Ohsawa <i>et al.</i> (1995)								
	Seed weight/plant		Plant height		Flowering period		100 seed weight	
Heritability	0.792		0.729		0.574		0.491	
modified Rana and Sharma (2000)								
	Seed weight/plant				Days to flowering		1000 seed weight	
Heritability	0.070				0.750		0.380	
modified Kitabayashi <i>et al.</i> (1995).								

quality, control ecotype, lodging resistance, determinate growth habit, low shattering, flood resistance, rutin content, low allergenic protein content, good aroma, and pre-harvest sprouting resistance (Ohsawa 2011). The improvement of each trait is progressing gradually, and varieties with lodging resistance, namely ‘Tachiakane’ (Maruyama *et al.* 2010) and ‘Nijiyutaka’ (Yui *et al.* 2012) and pre-harvesting sprouting resistance, namely ‘Harunoibuki’ (Hara *et al.* 2012) have been developed (Table 1). However, currently, limited progress has been made in the improvement of yield stability. Yield stability refers to grown varieties that exhibit minimal variation in terms of yield following changes in macro environments, e.g., location, year, and cultivation conditions. Within a macro environment, it is particularly difficult to forecast annual fluctuations. The so-called “yield instability” in common buckwheat is also often presented based on annual fluctuations.

Generally, high yields are expected in a good crop year. However, yield does not drastically decrease even in a poor crop year. Although it is acknowledged widely that common buckwheat yield is unstable, the factors influencing common buckwheat yield stability have not been explored adequately. Therefore, it is essential to clarify the factors influencing common buckwheat yield including physiological and genetic factors, which could facilitate the achievement of stable, high yield in common buckwheat. In recent years, few studies have explored such factors, and it is necessary to re-examine which individual traits are appropriate breeding targets. In addition, in crops, in general, varieties with high yield stability are considered adaptable. Inter-regional Liaison tests are also required because low inter-regional variation is critical for yield stability. In addition, genotype selection based on inter-regional variation data should be considered.

Considering the yields of common buckwheat globally (FAOSTAT 2019), China has an average yield of 83 kg/10 a in 5 years, whereas France has an average yield of 366 kg/10 a in 5 years, Ukraine records 108 kg/10 a and the United

States records 105 kg/10 a, with a unit yield 1.5–7 times the unit yield in Japan. In Japan, it may not be possible to maximize the potential yield of common buckwheat. However, is it possible to demonstrate the potential maximum yield of common buckwheat in Japan? It is necessary to clarify the factors limiting the yield of common buckwheat in Japan including physiological and genetic factors.

Future directions in common buckwheat breeding

Nakayama (1975) reported that the reasons for the lack of progress in common buckwheat breeding are the (1) inability to breed genetically fixed populations due to incompatibility, (2) need to simultaneously consider multiple environmental factors due to complex ecotypes, and (3) instability of flowering and maturing due to environmental influences.

Because common buckwheat is an outcrossing crop, it is commonly argued that its genetic analysis is difficult. In fact, genetic analysis methods for self-pollinating crops are generally unavailable for analysis of outcrossing plant. However, understanding the genotype composition of a population and observing the degrees of improvement in a population require an understanding of the fitness of the population in nature, and advancements in knowledge and techniques in population genetics and statistical genetics could be exploited more effectively to facilitate the breeding of outcrossing crops. Such activities require large numbers of genetic markers, which are also essential in common buckwheat breeding. If molecular markers could be used to elucidate the simultaneous transition of multiple loci, including linkage blocks, it would be possible to reveal the trends in the whole genome, which would be the basis for population improvement in outcrossing crops.

For the genetic analysis of diverse common buckwheat traits, in addition to the method of using genomic information, the conversion of outcrossing common buckwheat lines into self-fertile lines could be considered. Matsui

et al. (2008) actually bred a self-fertile common buckwheat line, 'Buckwheat Norin PL-1'. Farmers cannot use this line directly because its low yield, but a method has been developed to use such individuals as parents to promote self-fertilization in common buckwheat. The production of large numbers of inbred individuals would generate a useful population that would act as a genetic resource for common buckwheat breeding in the future. In addition, it would be possible to reveal genetic variations in such allogeneic plant populations. Although self-fertility confers some advantages in genetic analysis, considering that the description of common buckwheat has developed over the years as an outcrossing species while maintaining heterogeneity, it may be necessary to clarify the benefits of heterogeneity. It may be possible to determine the active role played by heterogeneity in common buckwheat population, which could reveal its potential adaptability to diverse environments.

Effectiveness of genomics-based breeding

In outcrossing crops such as common buckwheat, a key challenge is the fixing of quantitative traits such as yield and secondary metabolite amounts, which are under the control of multiple genes/quantitative trait loci (QTLs), in addition to requiring an enormous amount of time to breed a variety with excellent traits. As described above, common buckwheat breeding in Japan has been promoted by mass selection in which excellent individuals are selected from local varieties for many generations; however, the breeding efficiency is poor compared with that in other self-pollinated crops. In particular, because common buckwheat is heterogamous and its seed is the product when selection is performed by evaluating the quantity (yield) and quality of the seed, individuals have already been pollinated with pollen from other individuals. In addition, even if a superior individual is selected, the pollen parents are not selected; therefore, the selection efficiency is low. In the future, hybrid breeding would be an indispensable strategy for the improvement of traits, which would facilitate the exploitation of a wider range of genetic resources. Similarly, the development and deployment of novel technologies for selecting excellent individuals from mixed populations with high accuracy would be indispensable.

Over the recent years, the application of genomic selection (GS), a novel selection method that attempts to achieve genetic improvement of quantitative traits based on DNA markers distributed over a genome-wide range, has been promoted. The method has begun to record great results in the improvement of breeding efficiency. The key advantage of GS is that, unlike conventional marker assisted selection, it is suitable for the improvement of quantitative traits governed by multiple QTLs. In addition, because it is not necessary to evaluate characteristics at the time of selection in the course of GS, e.g., in the case of a crop, the breeding period can be substantially shortened by conducting selection using GS while promoting generation in environments

such as a greenhouse, which represents an additional advantage. GS is a breeding method that takes advantage of the association between genome-wide DNA markers and QTLs involved in quantitative traits (linkage disequilibrium); however, its application in crops is only at the initial stages. This is due to the need for the application of genome-wide markers in GS. In common buckwheat breeding, for which adequate genome information has not been accumulated to date, the accumulation of genome information has not progressed due to small research force, and the application of GS is considered difficult. However, in recent years, advances in the efficiency of technologies and cost reduction in genome analysis technologies have made it possible to apply GS to crops with minimal genomic information.

GS in common buckwheat could enhance selection efficiency and shorten the breeding period. Because it is possible to select an individual before it blooms in GS, it is possible to crossbreed only superior individuals and to select pollen parents, so that the selection efficiency would be enhanced compared with that in the case of phenotypic selection in which pollen parents are unselected such as in common buckwheat. In addition, the selection of common buckwheat based on GS while promoting production in greenhouses enables selection 3–4 times annually and shortens the number of years required for breeding. In the future, even in crops such as common buckwheat for which research has been limited and genomic information is unavailable, the introduction of novel technologies such as GS would facilitate the production of lines with high regional adaptability, yield (needs of farmers), and functionality (needs of consumers) within a relatively short period of time.

Yabe *et al.* (2018) performed an experimental GS breeding in common buckwheat to confirm that GS is useful for population selection in populations. They demonstrated that GS could increase common buckwheat yield per individual by 1.44-fold within 3 years. Considering the low heritability of yield per plant in common buckwheat, the result of GS is groundbreaking. Higher yields could be achieved by determining the genotypic compositions of selected populations and by making more markers available. A recently published draft sequence of the common buckwheat genome (Yasui *et al.* 2016) has made it possible to apply such methods. In addition, the availability of such information facilitates the identification of agronomically useful genes that have been revealed in other plant species from the common buckwheat genome (Matsui *et al.* 2018, Yasui *et al.* 2016). Such rapid advancements in genomic technologies will certainly enhance genomics-based breeding in common buckwheat in the near future.

Conclusion

Over the 8 years since I first explored the prospects of common buckwheat breeding (Ohsawa 2011), many varieties of

common buckwheat have been developed and applied in cultivation regionally. Despite the low number of researchers involved, the progress achieved deserves recognition. Common buckwheat is an indispensable crop for the Japanese; therefore, it cannot be considered a minor crop. However, because the expansion of common buckwheat production is expected in future, studies focusing on “stable, high yield” are required, which could be achieved through the accumulation of basic knowledge and improvements in genomics-based breeding methods.

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