Genetic analyses of agronomic traits in Tartary buckwheat (Fagopyrum tataricum (L.) Gaertn.)

Genetic analyses of agronomic traits in Tartary buckwheat (*Fagopyrum tataricum* (L.) Gaertn.)

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The consumption of products made from Tartary buckwheat (*Fagopyrum tataricum* (L.) Gaertn.) has increased in recent years in Japan. Increased consumer demand has led to recognition of the need for early varieties of this crop with high and stable yields. In order to accomplish this, more information is needed on the genetic mechanisms affecting earliness and yield. We conducted genetic analysis of 3 agronomic traits (days to flowering, plant height and total seed weight per plant) to segregate F_2 and F_3 populations derived from a cross between Tartary buckwheat cultivars 'Hokuriku No. 4' and 'Ishisoba'. Broad-sense heritability estimates for days to flowering, plant height and total seed weight were 0.70, 0.62 and 0.75, respectively, in F_3 population. Narrow-sense heritability for total seed weight (0.51) was highest, followed by heritability for days to flowering (0.37), with heritability for plant height (0.26) lowest. Later flowering was associated with increased plant height and higher yields. From the F_4 generation, we identified twelve candidate plants with earlier maturity and reduced plant height compared to 'Hokuriku No. 4', but almost the same total seed weight. These results suggest that hybridization breeding using the single seed descent (SSD) method is an effective approach for improving agronomic characteristics of Tartary buckwheat.

Key Words: Tartary buckwheat, segregating generation, genetic parameter, heritability, genetic correlation, phenotypic correlation, hybridization breeding.

Introduction

Tartary buckwheat (*Fagopyrum. tataricum* (L.) Gaertner) is an annual self-pollinated species. On the other hand, common buckwheat, which is familiar to Japanese food culture, is an outcrossing plant. Tartary buckwheat originated in China and is currently cultivated in China, neighboring countries and other countries of the world (Brunori *et al.* 2006, Lin and Song 2006). In China, Tartary buckwheat has historically been cultivated in areas with harsh environmental conditions (Campbell 2004), such as those found at high elevations on the Loess and Yungui plateaus in the western part of the country. These areas are characterized by a thin soil layer, low temperatures, lower-than-average rainfall, minimal agricultural infrastructure and low crop yields (Lin *et al.* 2006). Recently, the cultivation of Tartary buckwheat has been receiving increased attention in Japan, China, South Korea, Europe, the United States and other countries, where it is recognized as having health-promoting and nutraceutical properties (Joshi 2005, Kreft *et al.* 2003, Wang and Campbell 2007).

In Japan, Tartary buckwheat is considered a functional food that is used for the production of noodles ('sobakiri') and tea ('soba cha'). The annual consumption of products produced from Tartary buckwheat has increased and the demand for this grain is expected to grow several-fold in the coming years (Honda *et al*. 2006). At the present time, most of the Tartary buckwheat consumed in Japan is imported from China. Due to concerns about domestic food security and rising market prices, increased domestic production of Tartary buckwheat has been suggested by both consumers and farmers (Honda *et al.* 2010).

Cultivation of Tartary buckwheat in Japan has relied heavily upon varieties introduced from China, Nepal and Russia (Minami 2004); however, recently, ten varieties of Tartary buckwheat were released and are now cultivated in Japan. For example, cultivar 'Hokkai T No. 8' was developed from 'Rotundatum*'* (abbreviation of *F. rotundatum*– syn. *F. tatarticum*) at the National Agricultural Research Center for the Hokkaido Region in Memuro. The parental genetic material was obtained from the N. I. Vavilov All-Russian Research Institute of Plant Industry (Honda *et al.* 2010). 'Rotundatum' is noted for its resistance to lodging. Cultivar 'Hokuriku No. 4' was developed on the main island of Japan (Ito 2004); it is shorter, with earlier flowering time, and has larger grains than 'Hokkai T No. 8'. 'Hokuriku No. 4' was developed via individual selection utilizing genetic resources obtained from Nepal.

The ten varieties so far released in Japan were bred from imported local varieties or genetic resources via individual plant selection (MAFF 2010). Although presently cultivated

in Japan, these cultivars are not well adapted to the various local growing environments of the districts and are prone to problems associated with lodging due to excessive plant height, frost damage due to late maturity, and low yield. Although attempts to improve these materials via plant selection continue, the genetic base of these cultivars is relatively narrow. Hence, it is not expected that traditional selection methods may result in lines with the desired characteristics. Thus, Japanese plant breeders are challenged with the task of developing new varieties adapted to the diverse environmental conditions within the country.

Hybridization breeding is a very popular method for the improvement of self-pollinating crop plants and can serve to broaden their genetic base. In order to successfully utilize this approach, data are required on the heritability of and correlations between the traits that are to be improved or altered. A typical experimental approach would involve the following: (1) determining the relative importance of genetic effects of the loci for the traits to be improved, (2) determining which selection method(s) would be most efficient for the transfer of these traits and (3) predicting the gain to be expected from the selection process (Poehlman and Sleper 1995). This information can be obtained from populations derived from crosses between appropriate parental lines by examining the segregation patterns and estimating genetic parameters and the relationships among traits.

In this study, we examined heritability and estimated phenotypic and genetic correlations for three traits (days to flowering, plant height, and total seed weight) of F_2 and F_3 populations derived from a cross of the Tartary buckwheat cultivars 'Hokuriku No. 4' and 'Ishisoba'. In addition, we identified superior individuals in the F_4 generation.

Materials and Methods

Plant materials

Cultivars 'Hokuriku No. 4' and 'Ishisoba' were selected as parents for segregating generation analysis; the suitability of these cultivars as parents was demonstrated in a previous study (Li *et al*. 2011). The higher yielding 'Hokuriku No. 4' was developed at Hokuriku Agricultural Station (Ito 2004). This cultivar contains many dominant alleles for several agronomic traits, such as plant height and total seed weight (Li *et al*. 2011). The local variety 'Ishisoba' was originally acquired from Sakhalin (Honda *et al*. 2004). 'Ishisoba' matures earlier, is shorter and contains many recessive alleles for several agronomic traits, such as plant height and total seed weight (Li *et al*. 2011).

The procedures for preparing the segregating populations that were utilized in our experiment are presented in Fig. 1. The initial hybridization of 'Hokuriku No. 4' × 'Ishisoba' was performed in 2005. In 2006, 367 F_2 seeds were produced from a single F_1 plant. One hundred and forty F_2 individuals (Fig. 1A) were utilized to estimate heritability. Of the remaining F_2 seeds, 140 individuals (Fig. 1B) were selected and an F_3 generation was produced from them by single seed descent (SSD) in 2007.

The F_3 population (Fig. 1C) was composed of 140 F_3 individuals that were selected from each F_3 line. To estimate the mode of inheritance, we used 140 F_2 (Fig. 1A) and 140 F_3 (Fig. 1C) individuals.

In addition, one plant in each F_3 line (Fig. 1D) was grown to maturity and F_4 seeds were produced from them in 2009. To investigate the possibility of the occurrence of superior individuals, in 2010 we used the F_4 population (Fig. 1E),
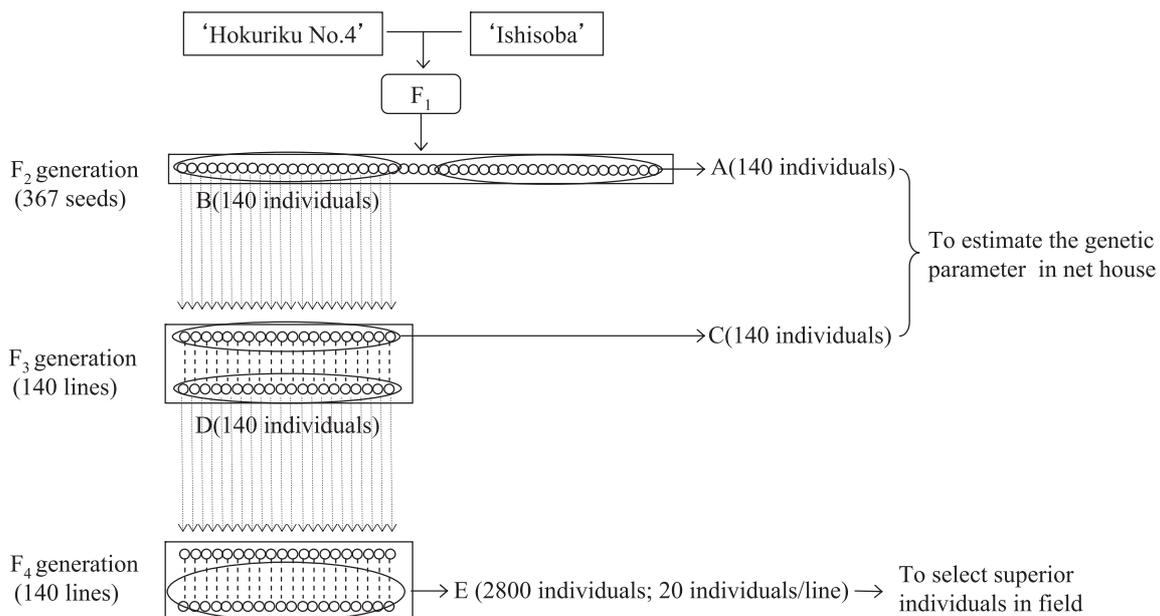

Fig. 1. Procedures for the preparation of the segregating populations used in this study. Squared areas represent each population and circles represent individuals used in the experiment.

which consisted of 140 lines, each of which was composed of 20 individuals.

Plant cultivation

The 140 individual F_2 (Fig. 1A) and F_3 (Fig. 1C) plants and 25 plants of each parent, were grown in a net house at the Agriculture and Forestry Research Center, University of Tsukuba (Ibaraki, Japan). Seeds were sown on August 13, 2010 in 24 cm diameter vinyl pots filled with a standard potting mix (Tsuchitaro, Sumitomo Forestry Co., Ltd.). Each pot contained a single plant.

The 2800 individual plants derived from the 140 F_4 lines and 20 plants of each parent, were grown in the field at the same location as mentioned previously. Seeds were sown on August 11, 2010. The plot size was $1.35 \, \text{m}^2$ for each line. The distance between rows in each plot was 25 cm; the distance between individual plants within plots was 20 cm. Nitrogen, phosphorus and potassium fertilizer was applied prior to planting at a rate of 4, 2 and 2 kg/ha, respectively.

Phenotypic measurements

The three traits evaluated for their heritability were days to flowering, plant height and total seed weight per plant. In the present study, total seed weight per plant is considered a yield trait. When we evaluated candidate individuals in the F_4 generation, both the number of seeds per plant and the 1000 seed weight were measured in order to determine whether the high-yielding selections produced heavier individual seeds or a larger number of seeds. Days to flowering were determined as the number of days from sowing to the date of the first flowering of each plant. Plants were harvested when 70 to 80% of the total seeds per plant were mature. Plant height was measured at harvest time. The 1000 seed weight, number of seeds per plant and total seed weight per plant were measured two weeks after harvesting and drying.

In the F_4 generation, plants with total seed weight per plant heavier, and flowering period earlier than 'Hokuriku No. 4' and plant height 100 cm or less (Li *et al.* 1999) were selected.

Data analysis
Tests of significance between parents, and between F_2 population and F_3 population distribution, for each trait

The t-test was performed to test the significance of differences between parents, and the F-test to test for similarities between the F_2 and F_3 distributions of the three traits. JMP 5.0.1 software was utilized for these tests (SAS Institute Inc., Cary, NC, USA).

Estimation of genetic parameters

We estimated the genetic parameters and heritability from the within-generation variances of each trait. According to Mather and Jinks (1971), within-generation variances are composed of an additive variance component (A), a dominance variance component (D) and an environmental variance component (E) and the phenotypic variance (V_P) of

the F_2 generation is expressed as follows:

$$V_P(F_2) = 1/2A + 1/4D + E_1,$$

and that of the F_3 as follows:

$$V_P(F_3) = 3/4A + 3/16D + E_1.$$

The number of individuals of each parent was different. Hence, we defined E_1 as follows (National Agricultural Research Center 1995):

$$E_1 = (S_1 + S_2)/(n_1 + n_2 - 2),$$

where S_1 and S_2 are the sums of squares, and n_1 and n_2 are the numbers of plants, of each respective parent. The broad-sense ($h_B^2[F_t]$) and narrow-sense ($h_N^2[F_t]$) heritability estimates were defined as follows:

$$h_B^2[F_t] = \frac{(1 - (1/2)^{t-1})A + (1/2)^{t-1}(1 - (1/2)^{t-1})D}{(1 - (1/2)^{t-1})A + (1/2)^{t-1}(1 - (1/2)^{t-1})D + E_1}$$

and

$$h_N^2[F_t] = \frac{(1 - (1/2)^{t-1})A}{(1 - (1/2)^{t-1})A + (1/2)^{t-1}(1 - (1/2)^{t-1})D + E_1}$$

where t is the generation. We also calculated the 95% confidence intervals for broad-sense heritability in each generation with the following formulas (Hashiguchi 1955):

$$\bar{\rho} = 1 - \frac{1}{F_{n_1}^{n_2}(0.025)}(1 - \hat{h}^2)$$

$$\underline{\rho} = 1 - F_{n_2}^{n_1}(0.025)(1 - \hat{h}^2)$$

where $\bar{\rho}$ and $\underline{\rho}$ are the upper and lower limits of the 95% confidence intervals, respectively and n_1 and n_2 are the sample numbers in the segregating and non-segregating generations, respectively. Furthermore, using the additive variances, we determined true-sense heritability—which is independent of generation—defined as follows (Ukai, 2002):

$$h_{true}^2 = \frac{A}{A + E_1}.$$

Estimation of phenotypic and genetic correlation coefficients

In the F_3 population, phenotypic correlations (r_p) and genetic correlations (r_G) among traits were estimated as follows (Ukai 2002):

$$\gamma_P = \frac{\text{Cov}(Y_A, Y_B)}{\sqrt{\text{Var}(Y_A) \times \text{Var}(Y_B)}},$$

and

$$\gamma_G = \frac{\text{Cov}(Y_A, Y_B) - \text{Cov}(e_A, e_B)}{\sqrt{(\text{Var}(Y_A) - \text{Var}(e_A)) \times (\text{Var}(Y_B) - \text{Var}(e_B))}},$$

where Y_A and Y_B are the phenotypic variances of traits A and B, respectively and e_A and e_B are the environmental variances of traits A and B, respectively.

Results

Distributions of parents, F_2 and F_3 generations for each agronomic trait

The differences between parents and the F_2 and F_3 generations were significant ($P < 0.01$) for the observed values of all three traits (Fig. 2). In both F_2 and F_3 generations, the three traits showed similar continuous distribution patterns with a single peak. In general, the patterns show that these are quantitative traits. Moreover, the observed values for days to flowering (A) and plant height (B) of F_2 and F_3 individuals were distributed between those observed for the parental lines. Transgressive segregation was observed for total seed weight (C) in both the F_2 and F_3 generations where it exceeded that of the parental line 'Hokuriku No. 4'.

Genetic parameters of each agronomic trait

For all three traits examined, dominance variance exceeded additive variance, and the average degrees of dominance were greater than 1.0 (Table 1). Broad-sense heritability of days to flowering, plant height and total seed weight were 0.69, 0.63 and 0.73 in the F_2 generation and 0.70, 0.62 and 0.75, in the F_3 generation, respectively. Confidence intervals for both generations were similar. Narrow-sense heritability for the three traits in the F_3 generation was higher than in the F_2 generation. Narrow-sense heritability for total seed weight (0.51) was highest, followed by the heritability for days to flowering (0.37), with heritability for plant height (0.26) lowest in F_3 population. True-sense heritability ranged from 0.48 (plant height) to 0.73 (total seed weight).

Phenotypic and genetic correlation among agronomic traits

The coefficients of genetic correlation for all three traits were higher than their corresponding coefficients of phenotypic correlation (Table 2). Days to flowering were phenotypically and genetically correlated with plant height ($r = 0.356, 0.621$), but were not significantly correlated with total seed weight. Plant height was phenotypically and genetically correlated with total seed weight ($r = 0.546, 0.800$).

Appearance of candidate individuals

Individuals could not be found that met all requirements for selection, so 12 F_4 individuals were identified with total seed weight within the standard deviation for 'Hokuriku
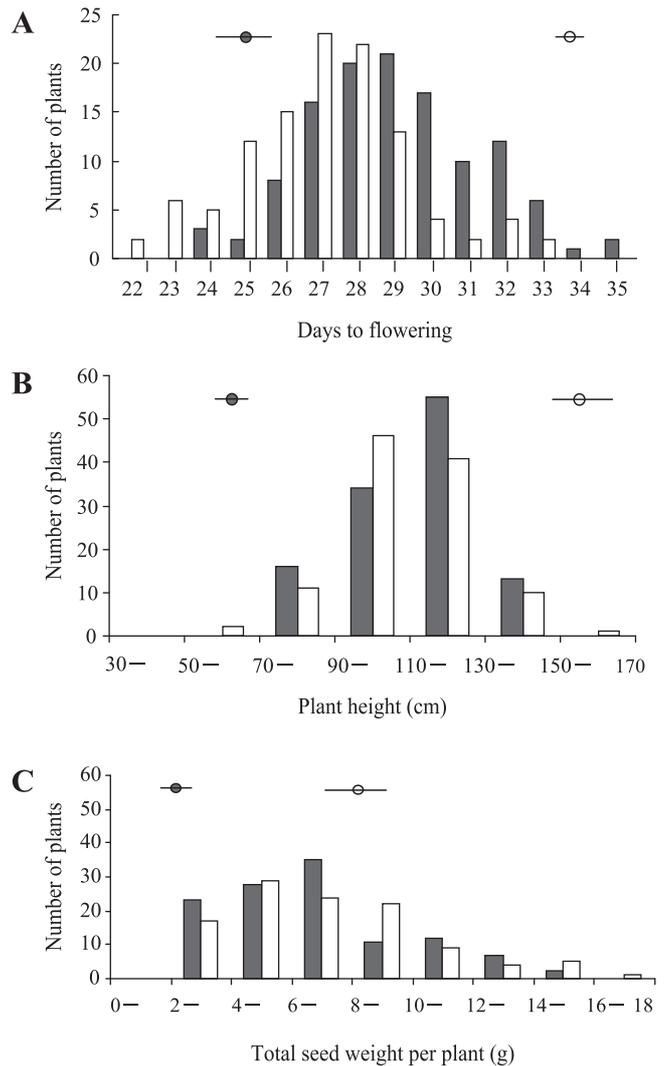
Fig. 2. Distributions of F_2 and F_3 generations for (A) days to flowering, (B) plant height and (C) total seed weight. Solid and open circles are the means of the parents 'Ishisoba' and 'Hokuriku No. 4', respectively. Solid and open histograms indicate the values of F_2 and F_3, respectively.

No. 4' (27~52 g), with earlier flowering time than the mean of 'Hokuriku No. 4' (38 days) and with plant height lower than 100 cm (Table 3). When the 12 individuals (bold diamonds in Fig. 3A, 3B) were compared with the mean of

Table 1. Genetic parameters of three agronomic traits

Traits	Additive variance (A)	Dominance variance (D)	Average degree of dominanace ($\sqrt{D/A}$)	Environ- mental variance (E)	Broad sense heritability (95% confidence interval)		Narrow sense heritability		True sense heritability (A/(A + E))
					F_2	F_3	F_2	F_3	
Days to flowering	2.66	9.17	1.86	1.62	0.69 (0.48–0.81)	0.70 (0.49–0.81)	0.25	0.37	0.62
Plant height	93.69	528.36	2.37	103.29	0.63 (0.39–0.77)	0.62 (0.36–0.76)	0.17	0.26	0.48
Total seed weight per plant	6.98	12.98	1.36	2.54	0.73 (0.54–0.83)	0.75 (0.58–0.84)	0.38	0.51	0.73

Table 2. Phenotypic and genetic correlation among three agronomic traits

Traits	Days to flowering	Plant height	Total seed weight per plant
Days to flowering	—	0.621	0.240
Plant height	**0.356**	—	0.800
Total seed weight per plant	0.131	**0.546**	—

Below the diagonal: phenotypic correlation; Above the diagonal: genetic correlation; Bold font: significant at 1% level.

Table 3. Agronomic traits measured in 12 candidate individuals selected from F_4 population and a parental line ('Hokuriku No. 4')

Plant number	Days to flowering (day)	Plant height (cm)	Total seed weight per plant (g)	Number of seeds per plant	1000 seed weight (g)
18–8	31	74	30	1,795	16.8
18–15	34	92	28	1,571	18.0
21–10	33	93	29	1,294	22.2
25–6	30	96	34	1,889	17.9
27–14	32	93	30	1,826	16.3
70–12	29	91	31	1,452	21.5
73–3	32	89	28	1,171	23.9
73–6	32	82	28	1,224	22.9
75–1	26	94	40	1,883	21.5
81–4	25	76	29	1,610	17.9
86–8	32	90	33	1,916	17.3
94–15	29	96	32	1,582	20.2
u	38	126	40	1,920	20.5
$u - \sigma$	36	106	27	1,358	19.4
$u + \sigma$	40	146	52	2,482	21.6

u and σ are the mean and standard deviation for Hokuriku No. 4, respectively.

Fig. 3. Relationships (A) between total seed weight and days to flowering and (B) between yield and plant height in F_4 generation. Solid and open circles are the means of 'Ishisoba' and 'Hokuriku No. 4', respectively. Vertical bars with horizontal dashed lines indicate standard deviations of total seed weight of 'Hokuriku No. 4'. Each point represents an individual plant in the F_4 population. Bold diamonds indicate the 12 candidate individuals.

'Hokuriku No. 4', they showed flowering time 4 to 13 days earlier, plant height 59 to 76% and total seed weight 70 to 100%.

Discussion

Heritability of agronomic traits

In the present study, broad-sense heritability was around ~0.7 for the three traits examined (Table 1). The results indicate that all traits examined were affected by environmental factors to a comparable degree. Previously, Li *et al.* (2011) reported that all of the 8 traits examined in analyses of a 6 parent diallel cross of Tartary buckwheat had high broad-sense heritability ranging from 0.87 to 0.98. These differences in heritability estimates may come from the estimation methods adopted for environmental variances. They estimated the environmental variance $E1$ based on the means of six parental lines with two replications while, in the present study, we estimated $E1$ from the distributions of two parental line populations according to the procedure described by the National Agricultural Research Center (1995).

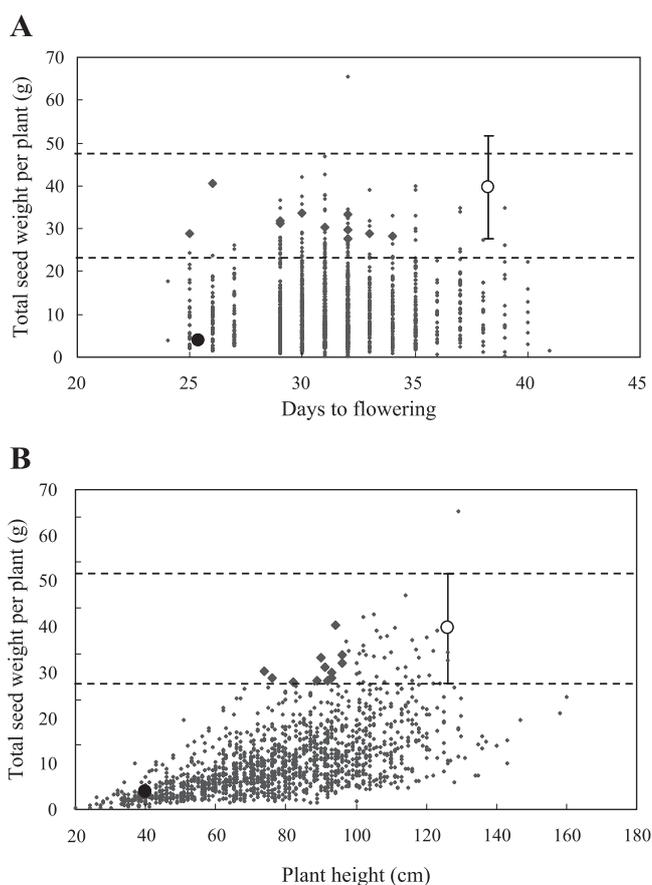Unlike broad-sense heritability, narrow-sense heritability differed among the traits. Total seed weight showed the highest narrow-sense heritability, followed by days to flowering and plant height was lowest in both F_2 and F_3. The lowest narrow-sense heritability for plant height was attributed to the large dominance variance (528.36) associated with this trait. True-sense heritability defined by Ukai (2002), which is independent of the generation in which the heritability is measured, was also lowest for plant height among the three traits.

In lentils, narrow-sense heritability estimates for plant height and days to flowering were 0.65 and 0.31, respectively, in F_2 population (Tullu *et al.* 2008). In chickpeas, narrow-sense heritability estimates of plant height and days to flowering were 0.65 and 0.46, respectively, in F_2 population (Anbessa *et al.* 2006). Narrow-sense heritability of plant height and days to flowering in Tartary buckwheat were lower than in these crops, suggesting that plant height and days to flowering should be selected in advanced generations in Tartary buckwheat.

In rice, broad-sense and narrow-sense heritability

estimates of total seed weight were 0.79 and 0.37, respectively, in F_2 generation (Ahmadikhan 2010). In cowpeas, those values were 0.80 and 0.28, respectively, in F_3 generation (Padi 2007). In comparison with these crops, broad-sense heritability of total seed weight in Tartary buckwheat was lower, but its narrow-sense heritability was larger. This suggested that the additive effect for total seed weight was large in Tartary buckwheat, and it indicated that more rapid fixation of alleles for this trait was possible.

Broad-sense heritability of the three traits was nearly equal between F_2 and F_3; however, as the generations advanced, narrow-sense heritability increased. These results are natural, since the contribution of dominance variance in narrow-sense heritability decreases with the generation.

Correlation between traits

In gramineous crop plants, taller stature is usually associated with higher yield. Our data also indicated significant positive phenotypic and genetic correlations between plant height and total seed weight. In previous studies, Arshad *et al.* (2004), Khan *et al.* (1989) and Malik *et al.* (1987) reported significant positive correlations of grain yield with plant height. In the history of wheat improvement, this positive correlation has hindered breeding efforts in simultaneous selecting of short-strawness and high yield (Law *et al.* 1978). Similarly, the data presented here suggest that breeding for short stature in combination with high yield in Tartary buckwheat may be difficult. It is well known that utilization of the semi-dwarf growth characteristic of 'Norin 10' greatly increased production efficiency in wheat (Vogel *et al.* 1963). The detection or mutagenic induction of semi-dwarfing genes in Tartary buckwheat, if possible, could potentially facilitate the improvement of this crop in a similar manner.

Concerning the use of hybridization breeding for the improvement of Tartary buckwheat

In the present study, the generations were advanced using SSD until F_4, in which selection of promising lines was carried out. Days to flowering, plant height and total seed weight were effectively selected for in the F_4 generation. We obtained 12 candidate individuals in the F_4 generation with total seed weight values comparable to that of 'Hokuriku No. 4', but with days to flowering earlier than 'Hokuriku No. 4' and plant height less than 100 cm (Fig. 3 and Table 3). Of particular note was line Number 75-1 (Table 3), which was 26 days earlier in flowering, shorter in plant height by 94 cm and had nearly equal total seed weight (40 g) to 'Hokuriku No. 4'.

In addition, in their study of lentils, Haddad and Muehlbauer (1981) reported that the genetic variances of plant height, days to maturity and yield in the F_4 generation were significantly higher with SSD than with bulking methods. The results obtained using the F_4 generation would not differ greatly from the results obtained using the F_5 generation, as 87.5% of all loci are expected to be fixed by F_4.

In conclusion, our results indicate that hybridization breeding using the SSD method can be effective for the improvement of yield in Tartary buckwheat. This approach would be especially valuable when combined with QTL analysis.

Acknowledgments

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