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ESEACH ARTICLE

Genetic analysis of agronomic traits of inter-subspecific cross populations of Tartary buckwheat

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Abstract

To provide a good basis for breeding new varieties, two different Tartary buckwheat (*Fagopyrum tataricum* Gaertn. 2n = 16) lines belonging to different sub-species with large differences in plant height were crossed. The progeny was analyzed for the genetic pattern of each agronomic trait and correlation analysis between traits. In terms of their coefficients of variation, the node numbers on the main stem and the weights per thousand kernels were small, while the number/weight of seeds per plant was large, indicating that the former character is more stable while the latter has greater potential for improvement. The average degrees of the dominance of plant height, number of main stem nodes, and number/weight of seeds per plant were greater than 1, indicating that dominant effects mainly controlled these traits. The heritability of the thousand kernel weight was greater than for the other traits, indicating that this trait is suitable for single plant selection in early generations. Correlation analysis of each agronomic trait revealed that plant height significantly and positively correlated with all other traits in the F_3 population, indicating the difficulty of selecting strains with dwarf stature and high-yield traits. Nevertheless, 13 strains with dwarf stems and high yields were screened in the F_5 population. The present study showed that the thousand kernel weight can be improved by single plant selection, while other traits need to be considered together to achieve optimal selection when endeavoring to breed dwarf, high-yield Tartary buckwheat.

Keywords: Tartary buckwheat, breeding, dwarf, high-yield, genetics.

Introduction

Tartary buckwheat (*Fagopyrum tataricum* Gaertn. 2n = 16) is an annual self-pollinated herb of the genus *Fagopyrum* in the Polygonaceae family. It is a short-day plant with good cold tolerance and is widely grown in some high-altitude areas of Eurasia. It is a major food crop in southwest China, as well as a cash crop and famine food (Lin 2013). Buckwheat has attracted considerable interest amongst the global scientific community due to its nutritional and pharmaceutical properties. It is a low input crop whose cultivation has persisted through centuries of civilization in almost every country where cereals were cultivated (Chrungoo and Chettry 2021). Seeds of buckwheat are a rich source of high biological value protein with a balanced amino acid composition, antioxidant and anti- cancer effects, rich in dietary fiber, minerals and flavonoids such as rutin, which is known for its antioxidant, vasoprotective, antihypertensive, and cardioprotective properties (Krkoskova and Mrazova 2005; Alamprese et al. 2007; Gimenz-Bastida and Zielinski 2015; Ganeshpurkar and Saluja 2017). Therefore, Tartary buckwheat is often added as a nutritional supplement or used as part of a medicated diet to improve health (Jiang et al. 2012). In-depth studies of Tartary buckwheat have gradually confirmed its unique nutritional, health care, and medicinal benefits, and Tartary buckwheat products are

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becoming increasingly more popular and in greater demand among consumers (Feng et al. 2005). Therefore, the current task is to increase the efficiency and economic benefits of Tartary buckwheat production by variety improvement and to expand the scale of production to meet the needs of consumers.

Tartary buckwheat is a pseudo-cereal crop, so its low yield is a fundamental problem that severely restricts the expansion of its production around the world (Lu 1994). Over the years, many researchers have dedicated their efforts to improving the production capacity of Tartary buckwheat and have bred many new varieties with high yields (Zhang et al. 2016; Wang et al. 2017). However, these varieties are prone to lodging, which affects plant agronomic traits as well as seed quality in severe cases, with yield reductions of more than 50% (Xiang et al. 2014; Wang et al. 2015).

Some studies have shown that lodging is the main cause of yield reduction in Tartary buckwheat, but not much research has been conducted on lodging. Many factors, and especially external factors such as wind and rain, growing conditions and cultivation practices, can trigger or aggravate lodging (Zhou et al. 2009). Internal factors, such as excessive plant height, are also important factors that predispose the plant to collapse (Gao et al. 2012; Luo et al. 2012). In cereal breeding, improved yields have been achieved by the introduction of dwarf varieties, such as the numerous semi-dwarf rice varieties that have been bred since the insertion of the semi-dwarf gene *sd1* into rice in 1960 (Hedden 2003). At present, dwarf breeding has become an important breeding objective, and the contribution of dwarf and semi-dwarf varieties to yield has been confirmed by numerous scientific and production practices (Daoura et al. 2014; Wang et al. 2015; Yang et al. 2015). In buckwheat, Canadian researchers have produced inbred common buckwheat lines that are resistant to loading, but research has not focused on the lodging tolerance of these lines or on specific breeding programs to improve loading tolerance (Hayashi et al. 2009). In Tartary buckwheat, no research programs have yet reported genetic analysis of dwarf-related traits or studies of loading by crossing populations and breeding dwarf varieties.

Plant height is believed to be significantly positively correlated with lodging; therefore, reducing plant height is the most effective way to improve resistance to lodging, and the breeding of dwarf varieties is viewed as the most economical and effective way to solve the lodging problem of Tartary buckwheat (Zhang 2006). However, dwarf traits in buckwheat are quantitative in nature and their expression is controlled by both genotype and environment; therefore, direct identification of the relevant genes is difficult, as is improvement using traditional breeding methods (Lin 2013). This problem could be addressed by genetic analysis aimed at obtaining genetic markers linked to the dwarf gene for molecular marker-assisted breeding, as this can reduce the size of the breeding population and improve breeding efficiency (Gupta et al. 2008). The aim of the present study was to lay a good foundation for the genetic study of Tartary buckwheat agronomic traits, especially dwarf traits, using the cross-population of two Tartary buckwheat varieties belonging to different sub-species that show large differences in plant height and other traits to determine the inheritance pattern of agronomic traits and correlation conduct analyses between them. Dwarf and high-yielding individuals were screened in the cross progeny, and the findings have important implications for solving the Tartary buckwheat lodging problem and improving production efficiency.

Materials and methods

Plant materials

The female parent, 'Yunqiao No. 1' (*F. tartaricum* ssp. *tataricum*), is a variety created by 60Co γ-irradiation and selected and bred using a systematic breeding program from local Tartary buckwheat cultivated in Qujing city in Yunnan Province of China by Biotechnology and Germplasm Resources Research Institute, Yunnan Provincial Academy of Agricultural Sciences, China (Fig. 1). This variety has a wide range of adaptations and an average yield of 2219 kg/hm^2 or more, so it is planted throughout China (Wang et al. 2014). However, when planted in the spring and summer, 'Yunqiao No. 1' usually grows too tall and becomes prone to lodging, making it difficult to exploit the high yield potential of this variety. The male parent YZ56 is a dwarf wild Tartary buckwheat (*F. tartaricum* ssp. *Potanini batalin*) found in Yunnan Province, China (Fig. 1). This variety has a very short main stem and is resistant to lodging, but because of its low yield and the presence of seed thorns, it cannot be used in production.

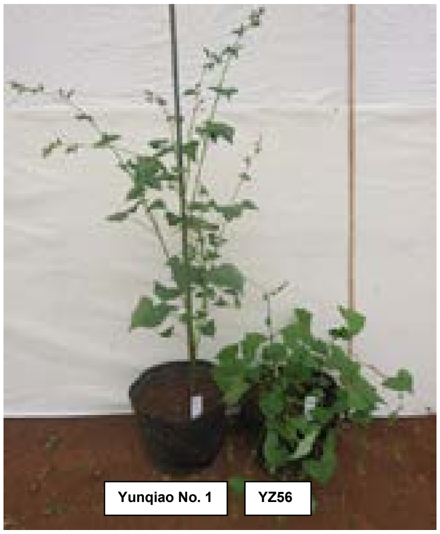

Fig. 1. Parent used in this study. Left: Yunqiao No. 1; Right: YZ56

Experimental method

Field trails were carried out on the farm of Baicheng Academy of Agricultural Sciences, Baicheng city, Jilin Province, P.R. of China (122°47′E Longitude, 45°37′N Latitude, 143.65m Altitude). The 236 seeds of the F_2 generation obtained by the crossing of Yunqiao No. 1 and YZ56 were sown in September 2019, along with 10 seeds of each parent. The seeds were planted outdoors in pots and moved to a greenhouse in early October. The F_3 generation was obtained by selfing. In June 2020, 236 strains of the F_3 generation, along with 10 seeds from each parent, were planted in pots for agronomic trait measurement, and the F_4 generation was obtained by selfing. In March 2021, the F_5 generation was obtained by selfing in a greenhouse using the single seed descent method. At the end of June of the same year, 50 seeds from each strain of the 236 F_5strains were randomly selected and planted in the field. Five of those plants were randomly selected for agronomic trait measurement when the seeds were mature.

Phenotypic measurements

Phenotypic measurements were performed on the F_2 and F_3 populations. When 70 to 80% of the seeds had matured, the agronomic traits, including the plant height (PH), node number of the main stem (NN), number of primary branches (NPB), number of secondary branches (NSB), and stem diameter (SD), were investigated for each individual. Each plant was then harvested individually, and the number of seeds per plant (NS), seed weight per plant (SW), and thousand kernel weight (TKW)were measured after 2 weeks of air-drying.

Data analysis

Analysis of the expression values of the agronomic characters of the parents and the F_2 and F_3 populations was done. Variance analysis and correlation analysis were performed using JMP version 9.0.2 (SAS Institute, Cary, NC, USA).

Estimation of genetic parameters

The genetic parameters and heritability were estimated from the within-generation variances of each trait (Ukai 2002). The variance of the F_2 and F_3 populations can be composed of an additive variance (A), a dominant variance (D), and an environmental variance (E). E is defined as follows (Yamamoto et al. 1996):

$$E = \frac{S_1 + S_2}{n_1 + n_2 - 2},$$

where S_1 and S_2 are the sums of squares of Yunqiao No. 1 and YZ56, and n_1 and n_2 are the numbers of plants of Yunqiao No. 1 and YZ56. The E was E_1 for the F_2 generation and E_2 for the F_3 generation. The phenotypic variance (V_p) of the F_2 generation was calculated as follows:

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

and that of the F_3 as follows:

$$V_p(F_3) = 3/4\,A + 3/16\,D + E_2,$$

A and D were found using $V_p(F_2)$ and $V_p(F_3)$, and then A and D were used to calculate the broad-sense ($h^2_B[Ft]$), narrow-sense$h^2_N[Ft]$, and true-sense (h^2_{true}) heritability (Ukai 2002):

$$h^2_B[Ft] = \frac{[1-(1/2)^{t-1}]A + (1/2)^{t-1}[1-(1/2)^{t-1}]D}{[1-(1/2)^{t-1}]A + (1/2)^{t-1}[1-(1/2)^{t-1}]D + E},$$

$$h^2_N[Ft] = \frac{[1-(1/2)^{t-1}]A}{[1-(1/2)^{t-1}]A + (1/2)^{t-1}[1-(1/2)^{t-1}]D + E},$$

$$h^2_{true} = \frac{A}{A+E},$$

where *t* is the generation.

Results and discussion

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

The phenotypic values of the agronomic traits of the parents and the F_2 and F_3 populations are summarized in Table 1. The mean values of PH, NN, NPB, NSB, and TKW were smaller for the F_2 population than for the F_3 population, while the mean values of SD, NS, and SW were larger than for the F_3 population. For the F_3 population, the means for all traits, except NN, NPB, and NSB, were smaller than the means of the female parent. The means of almost all the traits were greater than the means of the male parent, except for NPB, NS, and SW in the F_2 population and NPB and NSB in the F_3 population. The super parental segregation for all agronomic traits showed in the F_2 and F_3 populations suggests a cumulative effect of some genes in Yunqiao No. 1 and YZ56. This result confirmed the possibility of selecting strains with better traits than both parents in the progeny obtained from mating the two parents for use in the breeding dwarf and high-yield varieties. Super parental segregation of hybrid progeny is a common phenomenon in studies of different crops, and this was again verified in this study on Tartary buckwheat (Liang et al. 2014; Xu et al. 2015; Zhu et al. 2022).

The coefficient of variation is a specific expression of the genetic variation of a trait, and a higher coefficient of variation indicates a greater potential for improvement of the trait (Alizadeh et al. 2015). In this study, the coefficient of variation of almost all the traits were smaller in the F_2 population than in the F_3 population, except for PH and NSB. Apart from NS and SW, where the coefficient of variation was greater than 50%, the coefficients of variation for all traits ranged from 10 to 40% (Table 1), indicating that

Table 1. Phenotypic values of agronomic traits in parents and F_2 and F_3 populations

Traits	Generation	Population			Yunqiao No. 1 (♀)	YZ56 (♂)
		Range of variation	Average value	CV(%)		
PH/cm	F_2	35 ~ 150	80.90	25.76	143.00	43.40
	F_3	44 ~ 153	100.52	22.71	105.43	50.25
NN	F_2	9 ~ 18	13.46	12.74	17.50	10.20
	F_3	12 ~ 27	19.34	15.58	14.86	14.25
NPB	F_2	2 ~ 7	4.51	20.18	5.70	5.20
	F_3	1 ~ 11	4.92	35.18	4.00	5.50
NSB	F_2	2 ~ 13	5.71	33.68	8.10	5.70
	F_3	0 ~ 22	9.31	33.48	3.57	11.00
SD/mm	F_2	2.05 ~ 6.18	3.78	20.79	4.30	3.69
	F_3	1.51 ~ 6.15	3.54	23.76	3.83	2.77
NS	F_2	19 ~ 687	184.80	62.81	464.70	226.10
	F_3	22 ~ 642	161.12	76.60	302.71	69.50
SW/g	F_2	0.27 ~ 16.79	3.77	71.88	10.30	4.27
	F_3	0.26 ~ 13.98	2.97	82.89	6.07	1.04
TKW/g	F_2	12.4 ~ 26.0	19.71	12.38	22.25	19.10
	F_3	13.85 ~ 27.27	19.94	14.15	22.58	17.19

CV = Coefficient of variation

few candidates would be available for the selection of dwarf strains in the progeny. The coefficients of variation for NN and TKW were relatively small, at less than 20%, indicating that they were more stable than the other traits. The coefficient of variation for PH was slightly above 20%, indicating that few candidates would be available for the selection of dwarf strains in the progeny. Improvement of PH traits is a major objective of current Tartary buckwheat breeding, and expanding the plant numbers in candidate populations is necessary when the coefficient of variation is not high.

Genetic parameters of each agronomic trait

As shown in Table 2, the additive variance of the NPB, NSB, SD, and TKW was greater than the dominant variance, and the mean dominance was less than 1. Conversely, the dominant variance of PH, NN, NS, and SW was greater than the additive variance, and the mean dominance was greater than 1. These values are consistent with the results obtained from different Tartary buckwheat combinations, indicating that these traits are susceptible to environmental factors and require selection in later generations (Li et al. 2012; Li et al. 2020). The broad-sense heritability of the eight agronomic traits ranged from 0.62 to 0.86 in the F_2 population and from 0.64 to 0.89 in the F_3 population. Among these values, PH was the lowest, at 0.62 and 0.64 in the F_2 and F_3 populations, respectively, while TKW was the highest, at 0.86 and 0.89 in the F_2 and F_3 populations, respectively. TKW showed greater additive variance than the dominant variance in this study, as well as a greater broad-sense, narrow-sense, and true-sense heritability than the other traits, which is consistent with the results of Li et al. (2019), indicating that this trait can be improved by single plant selection in the early generations.

In terms of narrow-sense heritability, the eight agronomic traits ranged from 0.41 to 0.65 in the F_2 population and from 0.51 to 0.77 in the F_3 population. Among them, NN was the lowest, at 0.41 and 0.51 in the F_2 and F_3 populations, respectively, while TKW was the highest, at 0.65 and 0.77 in the F_2 and F_3 populations, respectively. In terms of true-sense heritability, the eight agronomic traits ranged from 0.64 to 0.85, with PH the lowest, at 0.64, and TKW the highest, at 0.85. It can be concluded that, the narrow-sense heritability of each agronomic trait in the present study increased gradually from the F_2 generation to the F_3 generation, reaching a maximum true-sense heritability at the F_5 generation, indicating that selection for the traits was most effective at later generations.

Phenotypic correlations among agronomic traits in the F_3 population

Correlations between various agronomic traits and yield have been reported in many crops (Zeng et al. 2019; Balcha et al. 2020; Li et al. 2022), and understanding the correlation between traits can provide a scientific basis for breeding.

Table 2. Genetic parameters of agronomic traits

Traits	Additive variance (A)	Dominance variance (D)	Average degree of dominance	Broad-sense heritability		Narrow-sense heritability		True-sense heritability
			($\sqrt{D/A}$)	F_2	F_3	F_2	F_3	
PH	172.11	208.22	1.10	0.62	0.64	0.49	0.59	0.64
NN	2.23	3.74	1.29	0.69	0.72	0.41	0.51	0.71
NPB	3.45	2.97	0.93	0.65	0.70	0.55	0.58	0.72
NSB	18.31	1.43	0.28	0.67	0.75	0.50	0.53	0.69
SD	1.77	0.53	0.55	0.63	0.70	0.54	0.65	0.75
NS	3387.94	5139.09	1.23	0.72	0.75	0.57	0.64	0.74
SW	13.85	27.29	1.40	0.79	0.81	0.48	0.54	0.79
TKW	7.80	4.90	0.79	0.86	0.89	0.65	0.77	0.85

Table 3. Phenotypic correlations among agronomic traits in the F3 population

Traits	PH	NN	NPB	NSB	SD	NS	SW	TKW
PH	—							
NN	0.756***	—						
NPB	0.348***	0.343***	—					
NSB	0.292**	0.336**	0.295**	—				
SD	0.655***	0.622***	0.498***	0.556***	—			
NS	0.699***	0.710***	0.425***	0.613***	0.797***	—		
SW	0.696***	0.694***	0.421***	0.575***	0.780***	0.983***	—	
TKW	0.311**	0.245**	0.084	-0.114	0.164*	0.241**	0.332***	—

Table 4. Phenotypic values of agronomic traits of superior strains

Strain No.	PH/cm	NN	NPB	NSB	SD/mm	NS	SW/g	TKW/g
1	138.32	25.84	9.16	28.83	5.77	983.31	19.52	22.42
10	164.17	27.53	6.24	16.77	6.38	881.52	17.41	21.54
15	122.51	22.39	7.67	25.47	5.25	606.12	11.80	21.20
17	135.28	25.86	9.53	23.31	5.84	720.54	14.80	25.48
21	129.37	23.56	8.25	24.59	5.33	877.39	15.74	21.24
24	128.63	23.37	9.71	26.93	5.30	666.28	11.81	21.10
42	154.54	22.81	9.19	21.17	5.83	769.21	13.31	19.66
44	147.18	24.19	11.20	33.65	5.90	954.34	19.63	22.46
65	167.34	27.26	8.41	25.22	6.07	1019.58	19.07	21.52
78	130.95	21.18	9.33	37.43	5.98	721.16	13.49	19.14
79	139.62	20.73	6.59	17.29	7.15	989.77	22.37	23.02
83	131.31	22.48	6.66	20.60	6.93	958.61	20.15	22.04
99	153.52	26.61	11.21	21.84	5.42	542.24	11.19	23.50
Yunqiao No. 1 (♀)	179.12	25.36	6.18	6.15	5.57	454.26	10.40	21.45
YZ56 (♂)	55.18	15.27	6.32	13.35	3.15	103.34	1.60	18.39

Bold font: Most promisingstrains

Table 3 shows that most traits were significantly or very significantly correlated with each other, and only the correlation between TKW and NPB/NSB was not statistically significant. In terms of the degree of correlation, positive correlations existed between most traits, with negative correlations found only between TKW and NSB. The highest correlation coefficient was found between NS and SW, while the lowest was found between NPB and TKW. The correlation coefficients of TKW with all other traits were at low levels, while NS/SW had moderate or higher correlation levels with all other traits except NPB and TKW. These results indicated the difficulty of selecting low PH and high SW varieties.

Selection of superior strain

Among the F_5 population, strains with lower pH and greater yield-related traits than Yunqiao No. 1 were selected as candidate parents for future breeding. Although the previous results indicate that selecting varieties with both lower PH and high SW is difficult, we selected 13 superior strains with shorter PH and more SW than the parent strains among the 236 F_5 strains (Table 4).

The PH of these strains ranged from 128.63 to 167.34 cm, with an average of 141.75 cm, which was 37.37 cm shorter than Yunqiao No. 1. Their NS ranged from 542.24 to 1019.58, with an average of 822.31, which was 368.05 greater than Yunqiao No. 1. For other traits, the selected strains had higher SW, with a mean of 16.18 g, which was 5.78 g higher than Yunqiao No. 1; they also had higher SD, with a mean of 5.93 mm, which was 0.36 mm higher than Yunqiao No. 1. Among the strains, those numbered 1, 79, and 83, which ranged in PH from 39.5 to 47.81 cm and were shorter than Yunqiao No. 1, had NS all above 900 and SW around 20 g, indicating short-stemmed and high-yielding characteristics. Based on these results, these three strains, with dwarf stems but high yields, were considered the most promising ones obtained in this experiment. Therefore, in cases where PH is highly correlated with other traits, single plant selection at a later generation can select individuals that meet the requirements for both PH and other traits. This method is also suitable for improving traits that are highly correlated with other traits. The three most promising strains selected in this study, with their combination of dwarf and high-yielding characteristics, may be an important material for future Tartary buckwheat breeding.

Authors' contribution

Conceptualization of research (CL, J, RKC, CR); Designing of the experiments (CL, J, HW, CW, CR); Contribution of experimental materials (CL); Execution of field/lab experiments and data collection (CL, J, JT, MS, LG, LW); Analysis of data and interpretation (CL, J, RC, CR); Preparation of the manuscript (CL, RC).

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