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Article

Genetic parameters and response to selection in the PANDOLY.PABG wheat population

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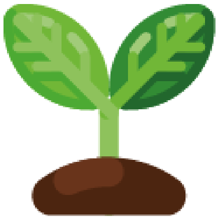
Abstract

Genetic breeding in autogamous species has been carried out through recurrent selection methods that imply reduced variability and long periods between selection cycles. To determine genetic variability, heritability, and response to selection, we estimated the genetic parameters of 14 recurrent selection cycles in the male-sterile wheat population PANDOLY.PABG, which carries the dominant male-sterile mutant gene ‘Oly’. During the 2016-2017 winter cycle in Chapingo and Santa Lucía, Texcoco, Mexico, 100 plants per cycle were labeled and the following variables were recorded: days to flowering, days to physiological maturity, grain filling rate, plant height, biological yield per plant, grain yield per plant, harvest index, weight of 100 seeds, number of spikes per plant, and number of spikelets per spike. The selection cycles were evaluated in three environments in a completely randomized design. The response to selection was negative for days to flowering, days to physiological maturity, biological yield per plant, number of spikes per plant, and number of spikelets per spike; the variability decreased in days to flowering, days to physiological maturity, plant height, biological yield per plant, number of spikes per plant, W100S; and the variables of grain yield per plant, harvest index, and weight of 100 seeds presented high values of h^2 and σ^2A; the latter are considered important variables to achieve greater gains in subsequent selection cycles. The above changes are the result of 14 recurrent selection cycles and it was confirmed that, with the PANDOLY population, there are advantages when compared to the traditional method to achieve genetic advances in a recurrent selection cycle per crop cycle.

Keywords:

Triticum aestivum L., dominant mutant, heritability, male sterility.



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Introduction

Wheat (*Triticum aestivum* L.) is one of the main crops in the world; 770 million tonnes were harvested in 2021 (FAOSTAT, 2023) and it is estimated that a 1% annual increase in yield is required to meet global demand in the future (FAO, 2021). To this end, it is important to use breeding methods that increase genetic gain and use available resources efficiently (Tadesse *et al*., 2019).

Speeding up selection cycles can be an effective way to increase gene gain; however, it is the least used (Cobb *et al*., 2019). As selection cycles are increased, it is desirable that gains in traits of interest are obtained without reducing variability and heritability; the estimation of genetic parameters in segregating populations provides information on variability and heritability, allowing strategies to be designed to achieve further advances (Melendres-Martínez *et al*., 2018).

Genetic breeding by recurrent selection differs in autogamous and allogamous species since, for the former, it implies reduced variability and a long time between selection and recombination cycles, while in allogamous species, there are high levels of variation in each cycle and reduced time between them (Villaseñor-Mir *et al*., 2002b). Based on the above, the opportunity for recombination in each selection cycle puts autogamous species at a disadvantage compared to allogamous ones.

In Mexico, to obtain uniform wheat lines originating from crosses and selection in segregant populations, it takes about four years when two crop cycles are advanced per year (Figueroa-López *et al*., 2010; Solís-Moya *et al*., 2019), time needed to cover a recurrent selection cycle; in contrast, the use of male sterility-facilitated recurrent selection (MSFRS) requires one sowing cycle per recurrent selection cycle, as reported by Villaseñor-Mir *et al*. (2018) in the generation of the Valles F2015 variety.

In Mexico, there are studies on wheat that have used the MSFRS to evaluate genetic progress in grain yield; research reports that a recurrent selection cycle was carried out in a sowing cycle; Villaseñor-Mir *et al*. (2002a), when they controlled both parents and after three selection cycles, report gains of 4.09% per cycle; Solís-Moya *et al*. (2002), after five selection cycles, report genetic advances of 1.88% per cycle and Díaz-Ceniceros *et al*. (2020), after 14 selection cycles, report gains of 3.58% per cycle.

For their part, Villaseñor-Mir *et al*. (2002b) indicate that MSFRS is a rapid technique for improving a genetic basis and is suitable for selecting quantitative traits and for conserving genetic variability. Although the use of androsterility can be applied in wheat, it is desirable that the source of androsterility is not linked to deleterious effects, that it is preferably attributed to a single dominant gene and that its incorporation into elite germplasm is effective (Villaseñor-Mir *et al*., 2014).

In the wheat genetic breeding program at INIFAP-CEVAMEX, a dominant androsterile mutant called ‘Oly’ is used (Villaseñor-Mir *et al*., 2014), which has been incorporated into 68 elite genotypes and has allowed the formation of various populations (Villaseñor-Mir *et al*., 2015).

The present study aimed to estimate the genetic parameters of morphophysiological traits and their phenotypic relationship with the advancement in yield after 14 cycles of recurrent selection of the PANDOLY.PABG population, where it was hypothesized that MFRS applied to this population is a strategy that allows selection while conserving genetic variability.

Materials and methods

The Androsterile Dominant Population ‘Oly’ with Broad Genetic Base (PANDOLY. PABG) is a recombinant population that integrated 20 parents of the wheat program of the Valle de México Experimental Field (CEVAMEX, for its acronym in Spanish) of the National Institute of Forestry, Agricultural and Livestock Research (INIFAP, for its acronym in Spanish), which was subject to population improvement through recurrent selection where the mass selection method with control of females was used.

The original cycle (C_0) was formed with seed of the balanced compound F_2, as described by Solís-Moya *et al*. (2002); the population size was 10 000 plants and during flowering, the androsterile plants (female plants) that were left to free mating were marked, 5% of the best recombinant plants were harvested in mass, thus generating 14 cycles of recurrent selection (Díaz-Ceniceros *et al*., 2020).

Of the 14 recurrent selection cycles (C_1 to C_{14}) that were applied in the PANDOLY.PABG population, remnant seed of fertile plants from the original cycle (C_0) and from the even cycles C_2 to C_{14} was used to form three trials; the first in the 2016-2017 autumn-winter cycle in Chapingo, Texcoco, Mexico under irrigated conditions, the second in the 2017 spring-summer cycle in Chapingo, Texcoco, Mexico, and the third in this same cycle in Santa Lucía, Texcoco, Mexico, the latter two in rainfed conditions.

The experimental unit consisted of four rows of 8 m in length, with a distance between rows of 0.3 m and a density of 10 plants per linear meter. Fertilization was broadcast applied at sowing, at a dose of 80N-40P-00K. Narrow-leaved weeds were opportunely controlled with Topik® 240EC (300 ml ha^{-1}) and broadleaf weeds with Esteron® 47M (750 ml ha^{-1}); in the booting stage, Folicur® (500 ml ha^{-1}) was applied for the control of *Puccinia striiformis* f. sp. *tritici* W.

In flowering, 100 plants with full competence were labeled and used to record the following variables: days to flowering (DF), days from sowing until 50% of the spikes were exposed; plant height (PH, cm), from the soil surface to the apex of the spike; days to maturity (DM), days from sowing until 50% of the peduncle turned yellow; number of spikes per plant (NSP), number of spikelets per spike (NSS), grain yield per plant (GYP, g), weight of 100 seeds (W100S, g), grain filling rate (GFIR, g day^{-1}), GFIR= GYP/(DM-DF), biological yield per plant (BYP, g), and harvest index (HI)= GYP/BYP.

The estimation of the components of genetic variance was based on the Design of Maternal Half-Sibling Families (Sahagún-Castellanos, 2000). Combined analysis of variance was performed, in which the factors were environments (replications), cycles and plants within cycles; the latter were distributed in each environment based on a completely random design handled as a series of experiments, where the environment was considered as a replication; the statistical package of SAS 9.4 (2014) was applied based on the model: $Y_{ijk}= \mu + A_i + C_j + P/C_k + E_{ij} + W_{ijk}$.

Where: Y_{ijk}= response variable; μ= mean; A_i= effect of the i-th environment; C_j= effect of the j-th cycle; P/C_k= effect of the k-th plant within the cycle; E_{ij}= inter-plot error corresponding to the j-th cycle and the i-th environment and W_{ijk}= intra-plot error corresponding to the observation of plant k in the cycle j of the environment. The population mean square was taken as the phenotypic variance that was used to analyze genetic variability across selection cycles (Table 1).

Table 1. Analysis of variance that considers environments such as replications, cycles, and plants within a cycle (P/C_{0-14}).

SV	DF	MS	E(MS)
Environments	(a-1)	…	…
Cycles	(c-1)	M1	$\sigma^2 W/n+ \sigma^2BE+a\sigma^2BG$
P/C_0	(n-1)	M2	σ^2WG
P/C_2	(n-1)	M3	σ^2WG
P/C_4	(n-1)	M4	σ^2WG
P/C_6	(n-1)	M5	σ^2WG
P/C_8	(n-1)	M6	σ^2WG
P/C_{10}	(n-1)	M7	σ^2WG
P/C_{12}	(n-1)	M8	σ^2WG
P/C_{14}	(n-1)	M9	σ^2WG
*Eintra	(a-1)(n-1)	M10	$\sigma^2WG+n\sigma^2WE$
Einter	Dif.	M11	$\sigma^2W/n+ \sigma^2BE$
Total	acn-1	…	…

SV= sources of variation; DF= degrees of freedom; MS= mean squares (M_{1-11}); E(MS)= expectations of mean squares; Eintra= intra-plot; Einter= inter-plot error; a= 3; c= 8; n= 100; *= average of individual analyses for each trait.

The phenotypic variance (σ^2F) is composed of the genetic variance between cycles (σ^2BG), the environmental variance between cycles (σ^2BE), the genetic variance within cycles (σ^2WG), and the environmental variance within cycles (σ^2WE) (Márquez-Sánchez, 1985) and was represented with the model $\sigma^2F= \sigma^2BG+ \sigma^2BE+ \sigma^2WG+ \sigma^2WE$. The total genetic variance (σ^2GT) is the sum of $\sigma^2BG+ \sigma^2WG$ (Márquez-Sánchez, 1988). Where= $\sigma^2BG= [(M_1 - M_{11})/a]$ and $\sigma^2WG= M_{(2\text{-}9)} - [(M_{(2\text{-}9)} - M_{10})/n]$ for each selection cycle.

The genetic parameters calculated were: a) additive variance (σ^2A); b) dominance variance (σ^2D); c) coefficient of additive genetic variation (CVA)= $\sigma A/\mu$ (where σA is the standard deviation and μ is the mean of the trait); d) average degree of dominance (ADD)= $(2\ \sigma^2D/\ \sigma^2A)^{1/2}$; e) narrow-sense heritability (h^2)= $\sigma^2A/\ \sigma^2F$; f) response to selection r(RS)= $(bi/\ X_{C0})*100$. Where= bi is the simple linear regression coefficient of the mean of each trait divided by the number of cycles; X_{C0} is the average of each trait in C_0 (Benítez-Riquelme, 2001).

The evaluation was carried out in populations equivalent to an F3 generation due the level of homozygosity (Villaseñor-Mir *et al*., 2018); therefore, the corresponding proportions are 1/2 of σ^2A and 1/16 of σ^2D of the σ^2BG; likewise, they are 1/4 of σ^2A and 1/8 of σ^2D of the σ^2WG for this generation (Márquez-Sánchez, 1988).

Results and discussion

For the sources of variation environments (A) and cycles (C), there were highly significant differences for all traits (Table 2). The σ^2F originates from the σ^2G plus the environmental variance, both between and within cycles. For this reason, and due to the broad genetic base of the study population, the coefficients of variation were high for GFIR, PH, GYP, BYP, HI and NSP.

Table 2. Mean squares of the analysis of variance in eight cycles representing 14 cycles of recurrent selection in the PANDOLY.PABG wheat population. Chapingo and Santa Lucia, Mexico, cycles AW/2016-2017 and SS/2017.

SV	DFr	DF	DM	GFIR	PH	GYP
Environments	2	78 875.83**	69715.17**	0.48**	34 780.34**	2 023.3**
Cycles	7	150.53**	170.04**	0.14**	3 350.37**	379.1**
Einter	2 399	18.68	23.6	0.03	267.82	80.1
CV (%)		6	4	55	21	56
SV	DFr	BYP	HI	W100S	NSP	NSS
Environments	2	3 392.65**	0.45**	119.92**	4 354.46**	846.73**
Cycles	7	7 175.05**	0.16**	3.37**	60.65**	29.81**
Einter	2 399	516.4	0.0087	0.398	22.39	4.23
CV (%)		63	29	16	42	12

SV= sources of variation; DFr= degrees of freedom; DF= days to flowering; DM= days to physiological maturity; GFIR= grain filling rate; PH= plant height; GYP= grain yield per plant; BYP= biomass per plant; HI= harvest index; W100S= weight of 100 seeds; NSP= number of spikes per plant; NSS= number of spikelets per spike; Einter= inter-plot error; CV (%)= coefficient of variation; **= highly significant.

The main objective of the INIFAP-CEVAMEX rainfed wheat genetic breeding program is to generate lines with yield potential, drought tolerant, disease resistance, and industrial quality (Villaseñor-Mir, 2015). A typical wheat breeding cycle can take more than 12 years for crossing, self-fertilization, testing, and selection. Broadly speaking, the recurrent selection process is a cycle consisting of four sequential activities: 1) hybridization to recombine breeding materials; 2) generation of new individuals that are plants, families, or lines; 3) evaluation of individuals; 4) selection of the best individuals as parents (Rutkoski *et al*., 2022).

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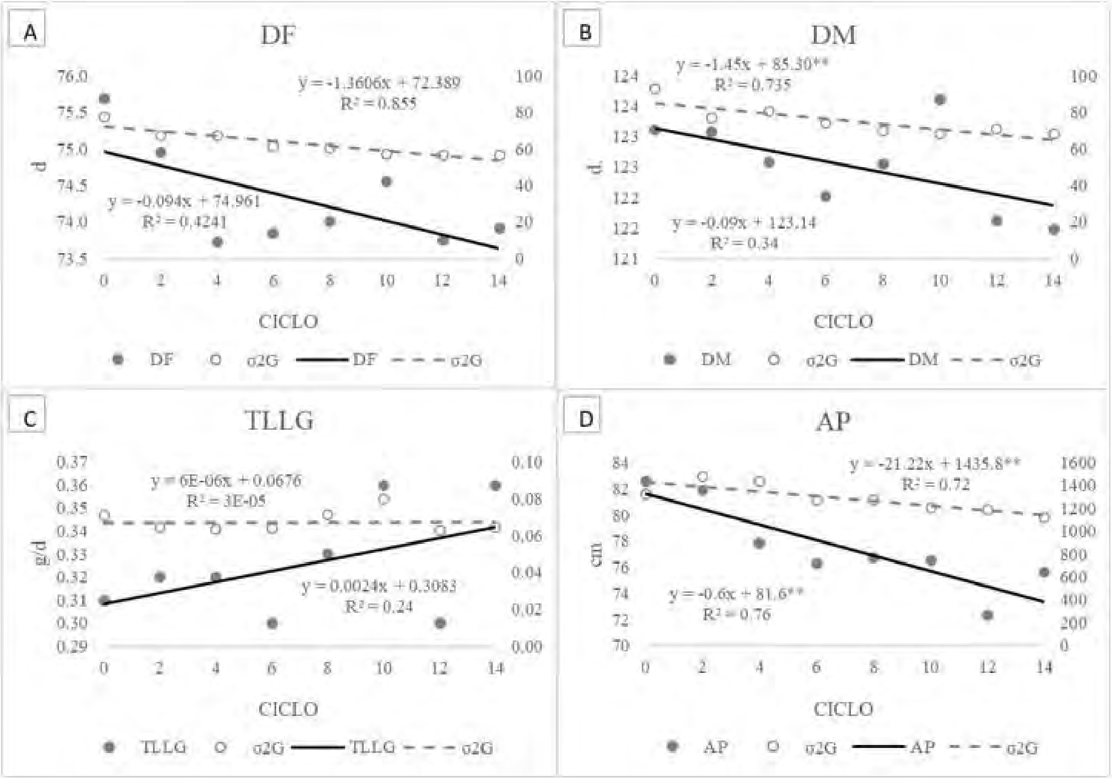
The genetic gain per year is affected by the length of the reproduction cycle, so that shorter reproduction cycles lead to faster genetic gains; in Mexico, two generations can be obtained per year, which reduces the time between one cycle and another by 50%. On the other hand, the reproductive biology of wheat acts as a limiting factor to shorten the cycles of recurrent selection and it has been observed that male sterility greatly facilitates crossing between individuals (Rutkoski *et al*., 2022).

Authors such as Huang and Deng (1988) proposed the use of the Taigu genetic male sterility gene, *Ms2*, to facilitate recurrent selection based on open pollination in wheat; likewise, Marais *et al*. (2000) used a *Ms3* gene (dominant androsterile gene) to establish a base population of recurrent selection. Liu *et al*. (2007) established a base population of recurrent selection using cytoplasmic androsterility type D^2. In Mexico, Villaseñor-Mir *et al*. (1996); Solís-Moya *et al*. (2002) used a recessive androsterility gene to form populations to apply recurrent visual mass selection.

In 2014, Villaseñor-Mir *et al*. (2014) reported the generation of the dominant androsterile gene 'Oly', which allowed the formation of the PANDOLY population. The selection of individual plants with desirable characteristics and with the control of the female parent allowed the response by cycle in the PANDOLY.PABG population for DF, DM, and PH presented a significant negative linear relationship, which was reflected in the decrease of 1.32 days to anthesis, 1.26 days to physiological maturity, and 8.45 cm in height after 14 cycles of selection (Figure 1A, 1B and 1D); Olmedo-Arcega *et al*. (1995) also report a decrease per cycle of -0.22 (bi) for days to flowering when evaluating three cycles of recurrent selection.

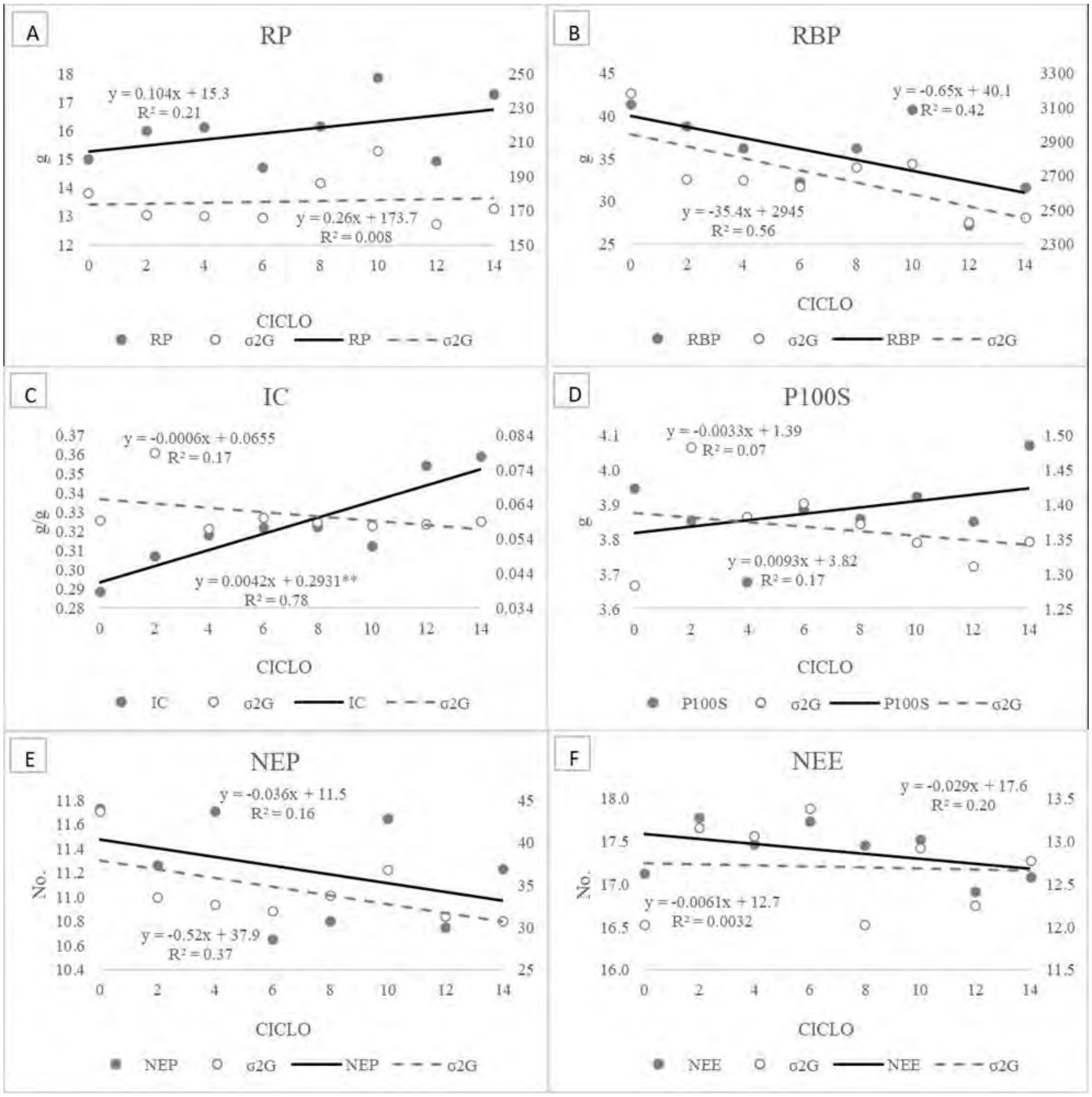
Figure 1. Response to selection (solid line) and genetic variance (σ^2G) (dotted line) through selection cycles for days to flowering (DF), days to physiological maturity (DM), grain filling rate (TLLG= GFIR) and plant height (PH).



Earliness is one of the virtues sought in the lines for rainfed conditions, which is why the selection was aimed at generating lines with a short life cycle, but without affecting the grain filling rate. The grain filling rate is the grain yield divided by the period in days from flowering to physiological maturity of the plant. In this study, since the grain filling period was not affected throughout the recurrent selection process, GFIR presented a positive linear relationship with grain increase of 2.4 mg d^{-1} per plant, which indicates that 33.6 mg d^{-1} more was accumulated in C_{14} than in C_0 and with the advantage that genetic variability was maintained (Figure 1C), unlike DF, DM, and PH, where the latter decreased (Figure 1).

The HI shows a positive and significant response, with an advance per cycle of 0.042 (bi), Figure 2C, which was explained by the decrease in BYP and increase in GYP, Figure 2A, 2B, and 2D. The NSP and the NSS present a negative linear relationship and are interpreted as the reduction of 0.5 spikelets and 0.4 spikelets per plant throughout the recurrent selection process (Figure 2E and 2F), indicating that these variables have changed little and that they would have a positive effect if taken as selection criteria, which would allow for more grains per spike or longer spike length, traits that are correlated with yield (Sowmya *et al*., 2017; Tanveer *et al*., 2018).

Figure 2.Response to selection (solid line) and genetic variance (σ^2G) (dashed line) through cycles for grain yield per plant (GYP), biological yield per plant (BYP), harvest index (HI), weight of 100 seeds (W100S), number of spikes per plant (NSP) and number of spikelets per spike (NSS).



Response to selection (RS) indicates the predicted genetic gain for a particular trait under selection cycles and measures the level of stability under selection (Lamara *et al*., 2022). The RS by year and total is shown in (Table 3), for the variables DF, DM, GFIR, PH, GYP, BYP, HI, W100S, NSP, and NSS. The response to the selection was negative for DF, DM, PH, BYP, NSP and NSS, and it was positive for the rest of the variables.

Table 3.Linear regression coefficient (bi) of the meaning of each variable over the number of selection cycles, the response to selection in percentage per year (RS year^{-1}) and after 14 recurrent selection cycles (RS-T).

Variable	bi	RS year^{-1}	RS-T
DF	-0.094	-0.25	-1.74
DM	-0.09	-0.15	-1.02
GFIR	0.0024	1.55	10.84
PH	-0.6	-1.45	-10.18
GYP	0.104	1.39	9.7
BYP	-0.65	-3.14	-21.98
HI	0.0042	2.91	20.4
W100S	0.0093	0.47	3.3
NSP	-0.036	-0.61	-4.3
NSS	-0.029	-0.34	-2.37

DF= days to flowering; DM= days to maturity; GFIR= grain filling rate; PH= plant height; GYP= grain yield per plant; BYP= biological yield per plant; HI= harvest index; W100S= weight of 100 seeds; NSP= number of spikes per plant; NSS= number of spikelets per spike.

The study of heritability and genetic parameters in populations under genetic improvement facilitates the identification of the best strategy to be taken during the selection process, since it allows us to know the population. The estimation of genetic parameters such as the mean for each cycle, additive variance (σ^2A), dominance variance (σ^2D), coefficient of additive genetic variation (CVA), average degree of dominance (ADD) and narrow-sense heritability (h^2) of 10 traits of interest for the genetic breeding program are shown in Table 4.

Table 4. Estimates of additive variance (σ^2A), dominance variance (σ^2D), additive variability coefficient (CVA), and narrow-sense heritability (h^2) for the variables evaluated.

PP	X	σ^2A	σ^2D	CVA	ADD	h^2	X	σ^2A	σ^2D	CVA	ADD	h^2
				DF						DM		
P/C_0	75.7	30.3	6.9	0.07	0.68	0.32	123.1	35.3	8.5	0.05	0.69	0.3
P/C_2	75	27.8	5.6	0.07	0.64	0.32	123.1	31.5	6.6	0.05	0.65	0.31
P/C_4	73.7	27.7	5.6	0.07	0.64	0.32	122.6	32.3	7	0.05	0.66	0.31
P/C_6	73.8	26.3	4.9	0.07	0.61	0.33	122	30.7	6.2	0.05	0.64	0.31
P/C_8	74	26	4.8	0.07	0.61	0.33	122.6	29.6	5.7	0.04	0.62	0.32
P/C_{10}	74.6	25.3	4.4	0.07	0.59	0.33	123.6	29.3	5.5	0.04	0.61	0.32
P/C_{12}	73.8	25.1	4.3	0.07	0.59	0.33	121.6	29.9	5.8	0.04	0.62	0.32
P/C_{14}	73.9	25.1	4.3	0.07	0.59	0.33	121.5	29.2	5.5	0.04	0.61	0.32
			GFIR						PH			
P/C_0	0.32	0.03	0.01	0.52	0.7	0.26	82.6	587.7	101.2	0.29	0.59	0.37
P/C_2	0.33	0.03	0.01	0.48	0.68	0.26	81.9	627	120.9	0.31	0.62	0.36
P/C_4	0.33	0.02	0.01	0.48	0.67	0.26	77.9	615	114.9	0.32	0.61	0.36
P/C_6	0.3	0.03	0.01	0.52	0.68	0.26	76.3	575	94.8	0.31	0.57	0.37
P/C_8	0.33	0.03	0.01	0.5	0.7	0.26	76.8	574.9	94.8	0.31	0.57	0.37

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PP	X	σ^2A	σ^2D	CVA	ADD	h^2	X	σ^2A	σ^2D	CVA	ADD	h^2
			DF						**DM**			
P/C_{10}	0.36	0.03	0.01	0.47	0.73	0.26	76.5	559.2	86.9	0.31	0.56	0.38
P/C_{12}	0.31	0.02	0.01	0.51	0.67	0.26	72.3	553.1	83.9	0.33	0.55	0.38
P/C_{14}	0.36	0.03	0.01	0.44	0.68	0.26	75.6	537.2	76	0.31	0.53	0.39
			GYP						BYP			
P/C_0	15	70	16.3	0.56	0.68	0.27	41.4	1350	258.9	0.89	0.62	0.37
P/C_2	16	66.8	14.7	0.51	0.66	0.27	38.8	1225	196.2	0.9	0.57	0.38
P/C_4	16.1	66.6	14.6	0.51	0.66	0.27	36.2	1223	195.5	0.97	0.57	0.38
P/C_6	14.7	66.3	14.5	0.55	0.66	0.27	32.2	1214	190.9	1.08	0.56	0.38
P/C_8	16.1	71.5	17	0.52	0.69	0.27	36.3	1242	204.9	0.97	0.57	0.38
P/C_{10}	17.9	76.1	19.4	0.49	0.71	0.27	40.7	1248	207.8	0.87	0.58	0.38
P/C_{12}	15	65.5	14.1	0.54	0.66	0.27	27.2	1162	165	1.25	0.53	0.39
P/C_{14}	17.3	67.7	15.2	0.48	0.67	0.27	31.6	1168	167.9	1.08	0.54	0.39
			HI						W100S			
P/C_0	0.29	0.03	0	0.58	0.55	0.41	3.94	0.57	0.1	0.19	0.59	0.34
P/C_2	0.31	0.03	0.01	0.59	0.63	0.37	3.85	0.62	0.12	0.2	0.63	0.33
P/C_4	0.32	0.03	0	0.52	0.53	0.42	3.68	0.59	0.11	0.21	0.61	0.33
P/C_6	0.32	0.03	0	0.52	0.55	0.41	3.88	0.6	0.11	0.2	0.61	0.33
P/C_8	0.32	0.03	0	0.52	0.54	0.41	3.86	0.59	0.11	0.2	0.61	0.33
P/C_{10}	0.31	0.03	0	0.53	0.53	0.41	3.92	0.58	0.11	0.2	0.6	0.34
P/C_{12}	0.35	0.03	0	0.47	0.54	0.41	3.85	0.58	0.1	0.2	0.59	0.34
P/C_{14}	0.36	0.03	0	0.47	0.54	0.41	4.06	0.58	0.11	0.19	0.6	0.34
			NSP						NSS			
P/C_0	11.7	14.1	4.7	0.32	0.81	0.21	17.1	5.1	0.97	0.13	0.61	0.32
P/C_2	11.3	11.6	3.4	0.3	0.77	0.21	17.8	5.4	1.11	0.13	0.64	0.31
P/C_4	11.7	11.4	3.3	0.29	0.76	0.21	17.5	5.4	1.1	0.13	0.64	0.31
P/C_6	10.7	11.2	3.2	0.31	0.76	0.21	17.7	5.5	1.14	0.13	0.64	0.31
P/C_8	10.8	11.6	3.4	0.32	0.77	0.21	17.5	5.1	0.97	0.13	0.61	0.32
P/C_{10}	11.7	12.4	3.8	0.3	0.78	0.21	17.5	5.4	1.08	0.13	0.64	0.31
P/C_{12}	10.8	11	3.1	0.31	0.75	0.21	16.9	5.2	1	0.13	0.62	0.32
P/C_{14}	11.2	10.9	3	0.29	0.75	0.2	17.1	5.3	1.06	0.14	0.63	0.31

PP= population parameter; X= mean; P/C_{0-14}= plants within the cycle.

According to the results of the average GYP by selection cycle, C_{14} plants produce 15.33% more grain than C_0 plants. Conversely, but for BYP, C_0 plants produce 31.01% more biomass than C_{14} cycle plants (Table 4). This is due to the fact that during the 14 selection cycles, recombinant plants of shorter height were selected, which allowed the allele frequency of low-sized genes to increase throughout the cycles.

It is expected that the highest value of σ^2A is found in C_0 because it is the initial cycle where the total number of parents were recombined, but this was not the case for PH (C_2), GYP (C_{10}), HI (C_2), W100S (C_2), and NSS (C_6); the same happens with σ^2D (Table 4), since it is expected that populations subjected to a breeding process will decrease their variability. The σ^2A in C_2 increased in NSS, PH, W100S, and HI of 5.9, 6.7, 8.8, and 17.8%, respectively, and in subsequent cycles, it began to decrease, except for NSS, which increased and decreased throughout the cycles.

For the rest of the traits, C_0 has the highest σ^2A and then there is a decrease. High CVA values in GFIR, PH, GYP, BYP, HI, W100S, and NSP indicated the existence of greater additive genetic variability, so they would be useful traits for the genetic breeding program. The average degree of dominance or type of gene action (ADD) for all traits, throughout the 14 cycles of recurrent selection, is less than one (Table 4). These results indicate that it is a partial dominance gene effect for all traits.

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Heritability is important for predicting the response to selection in a population. The estimated values of h^2 ranged from 0.2 to 0.41, the lowest corresponding to NSP and the highest to HI (Table 4). According to the classification used by Lamara *et al*. (2022), heritability is classified as low (0 to 0.3), moderate (>0.3 to 0.6), and high (>0.6). For this study, the traits NSP (0.21), GFIR (0.26), and GYP (0.27) showed low heritability, while DM (0.31), NSS (0.31), DF (0.33), W100S (0.33), PH (0.37), BYP (0.38), and HI (0.41) presented moderate heritability; Hassan *et al*. (2013); Saeed and Khalil (2017) report similar results in wheat.

For DF and DM, the values are lower than those reported by Magda and El-Rahman (2013); Laala *et al*. (2017). The HI had a favorable response to the selection and values of 0.37 to 0.41 h^2 were estimated, which agree with those reported by Ataei *et al*. (2017). When there are high values of h^2 and σ^2A, as is the case with GYP, HI, and W100S, gains are expected in subsequent selection cycles (Benítez-Riquelme, 2001).

All the changes described in the population parameters are the result of the recurrent selection that was applied for 14 years in the PANDOLY population. The population has a great advantage over the traditional method due to the reduction of the time to carry out a breeding cycle and the possibility of recombination among all individuals.

Conclusions

The variance components indicated that the additive variance was greater than the dominance variance in all traits. In general, the coefficients of additive variability were maintained throughout the recurrent selection cycles for each variable, as was heritability. The average degree of dominance was less than one for all the traits evaluated, which indicates the presence of partial dominance. Estimates of narrow-sense heritability were generally moderate. The greatest response to the selection was for the HI and is explained by the reduction in the BYP and the increase in the GYP. The results of heritability, coefficient of additive variation, genetic variance and response to selection indicate that the GYP, HI, and W100S are the basis for the following recurrent selection cycles.

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