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YELLOW PEARL POPCORN IS A VIABLE ALTERNATIVE TO IMPROVE MEXICAN POPCORN VARIETIES

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ABSTRACT

The deacclimatization of introduced maize varieties or races (*Zea mays* L.) limits their use. The effects of deacclimatization on the ability to produce pollen from introduced varieties are unknown. Therefore, the purpose of this study was to determine if the weather conditions in the High Valleys of central Mexico limit the ability to produce pollen from the North American Yellow Pearl Popcorn race for use as a male parent in popcorn breeding. Eight genotypes, including two from the Corn Belt of the United States, were evaluated in two sites. The morphological characteristics of tassel, pollen grain, ear, and viability were registered. Additionally, intervarietal and plant-to-plant crossing were used to observe the effect of pollen on the characteristics of the ears. Differences were found in the number of branches of the tassel, pollen grain diameter, ear diameter, and viability. There were no differences in ear characteristics between the types of crosses used. It was concluded that the climate conditions of the high valleys of central Mexico do affect the morphological characteristics of the race studied but do not limit their ability to produce pollen. Therefore, North American Yellow Pearl Popcorn race can be used as a pollen donor in the breeding of local popcorn varieties.

Keywords: introduced variety, deacclimatization, breeding, intervarietal cross.

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INTRODUCTION

Plant breeding uses a variety of methodologies to produce improved varieties, including recurrent selection and hybridization with either local or exotic varieties. Exotic varieties are introduced to incorporate desirable characteristics into improved or native varieties. The disadvantage of the latter procedure is that the introduced varieties can undergo deacclimatization, which may cause problems with the reproductive ability of the introduced variety (Santiago-López *et al*., 2020; López-Morales *et al*., 2021).

Diverse studies have been conducted, including the introduction of an exotic variety to incorporate desired characteristics. Ramírez-Díaz *et al*. (2007) proposed a breeding method to introduce genes from exotic varieties into native varieties through crosses. They concluded that this method is more efficient than other methods like reciprocal selection or conventional backcross. According to Gómez-Espejo *et al*. (2015), introducing exotic varieties from warm to temperate climates can promote the development of varieties with alleles of interest for the Mexican High Valleys region. Velasco-García *et al*. (2020) suggest using the variability of native and exotic varieties in the High Valleys of Mexico in maize breeding programs to increase heterosis. In turn, Santiago-López *et al*. (2020) mentioned that the use of adapted tropical germplasm as a source of variation for the maize of the High Valleys is feasible.

In the High Valleys of Mexico, Palomero Toluqueño is the popcorn race with the greatest popping volume, although breeding developed on this variety is limited (Bautista-Ramírez *et al*., 2020). Research on this race has focused on conservation, management, and use Gámez-Vázquez *et al.* (2014) highlight a focus on tortilla production, and propose an standardization of popping methods (de la O-Olán *et al.*, 2018; Trejo-Pastor *et al.*, 2023), yield, and expansion ability (Bautista-Ramírez *et al.*, 2020), as well as conditions and factors of its distribution (Bautista-Ramírez *et al.*, 2018). Bautista-Ramírez *et al*. (2020) found an average grain expansion volume of 2.73 cm^3 g^{-1} in 47 accessions of the Palomero Toluqueño race held at the National Institute of Forestry, Agricultural and Livestock Research (INIFAP) germplasm bank. However, the Yellow Pearl North American popcorn race has a much greater ability for popping than the Mexican variety, with expansion volumes of 40 cm^3 g^{-1} (Santacruz-Varela *et al*., 2004). Thus, the North American Yellow Pearl Popcorn race could be introduced into Mexican popcorn breeding programs to boost Palomero Toluqueño expansion.

Although numerous studies have been conducted to investigate the effects of introducing an exotic variety in order to incorporate desirable characteristics, there has been little research on this topic for popcorn. The extent to which the environment of the High Valleys in central Mexico can influence the morphological characteristics of the tassel, pollen grain, and ear, as well as whether these can have a negative influence on pollen production, is unknown, and thus whether or not it can be effective when introduced in breeding programs of Mexican popcorn programs is unclear. As a result, the goal of this research was to determine to what extent the environmental conditions of Mexican High Valleys influence the development of plants and pollen production in the North American Yellow Pearl popcorn race, allowing it to participate, at least as a male parent, in local popcorn breeding programs.

MATERIALS AND METHODS

Study locations

In the 2022 spring-summer season, two experiments were established: one in San Salvador Atenco and the other in Montecillo, Texcoco, both in the State of Mexico, Mexico, at an altitude of 2250 m with a mean annual temperature of 15 °C and a mean annual rainfall of 645 mm.

Genetic material

The plant material consisted of eight genotypes: two populations corresponding to advanced generations of hybrids of the North American Yellow Pearl Popcorn (NAYPP; Jack Superior and Iowa Pop 12), a variety of the Palomero Toluqueño race (Criollo Plaza), a synthetic variety derived from the cross between Palomero Toluqueño and the North American Yellow Pearl, a variety of the Chalqueño, Cacahuacintle, and Cónico races, which are native to the High Valleys, and a population of teosinte (*Zea mays* ssp. *mexicana*) of the Chalco race, which only participated in the viability and pollen morphology studies.

Phenotypic characterization in the field

A completely randomized experimental design with six repetitions was used in both locations. The experimental unit consisted of two rows (5 m long and spaced by 0.8 m). Each row contained 11 plants, resulting in a total of 44 plants per experimental plot.

The following phenological and morphological variables were evaluated: 1) Days to male flowering (DMF), determined by counting the number of days from planting until 50 % of the plants in each experimental plot exhibited anthesis; 2) Peduncle length (PL, cm), measured with a measuring tape from the last internode to the beginning of the tassel ramifications; 3) Length of the ramified part of the tassel (LRAP, cm), measured from the tassel (LMA, cm), measured from the end of the branches to the tip of the tassel; and 5) Number of primary branches (NB), determined by counting the primary branches present on the tassel.

In addition, five ears formed by open pollination, representative of each experimental unit, were evaluated for the following ear-related morphological variables: 6) Ear length (EL, cm), measured with a measuring tape from the base to the tip of the ear; 7) Ear diameter (ED, cm), measured at the midpoint of the ear using a caliper; 8) Number of kernel rows per ear (NR); 9) Number of kernels per row (NKR), determined by counting the kernels in two rows per ear and calculating the average; and 10) Shelling factor (SHF), calculated as the ratio of maize grain weight to total sample weight, evaluated by treatment and cross type.

Reproductive ability of the pollen in the field

Intervarietal and plant-to-plant crosses were conducted within each experimental unit using the same experimental setup established for the characterization of the genotypes. Plant-to-plant crosses were performed in row 1, while intervarietal crosses were conducted in row 2. This design aimed to assess potential differences in the effects of pollen from the same genotype (plant-to-plant crosses) compared to pollen from an exotic genotype belonging to the North American Yellow Pearl Popcorn race (intervarietal crosses using Jack Superior as the pollen donor) on ear morphological traits. The evaluated variables included ear length (EL, cm), ear diameter (ED, cm), number of kernel rows (NR), number of kernels per row (NKR), and shelling factor (SHF).

Pollen variables determined in the laboratory

Pollen grain viability was assessed by collecting pollen from 10 plants per treatment. The ears were placed in wax paper bags (No. 12 pollination bags), and after 10 min, the bags were shaken and removed from the tassels. The contents of the individual bags were pooled into a single bag to obtain a representative mixture of pollen grains for each treatment. The pollen was collected in the morning, when air temperatures ranged between 18 and 22 °C (Escobar and Pardey, 2020).

The impurities were removed from the pollen using a sieve (No. 120). Once it was clean, 0.5 g was weighed using a digital scale (Uline® brand, model H-9884, Pleasant Prairie, WI, USA) and emptied into an Eppendorf tube for microcentrifugation with a capacity of 1 mL, into which 0.5 mL of a 0.5 % 2,3,5-triphenyltetrazolium chloride solution was added. The tubes were wrapped in metal foil to avoid contact with light and then set aside for 4 h (Martins *et al*., 2017). Then, permanent mounts were made on four slides per treatment. Glycerinated gelatin was used, and they were dried for 24 h. The preparations were sealed with clear nail polish and left to dry for 24 h (Martins *et al*., 2017).

Using the AmScope software and microscope with a built-in camera, 10 photographs (40 per treatment) of the pollen grains were taken. The stained, non-stained, and total pollen grains were then counted using the "cell counter" tool in ImageJ. The result was calculated as a percentage of viability using the stained, non-stained, and total grains counted. Using the AmScope "line" tool, the diameter of the pollen grain (μm) was measured from end to end, along with the diameter of the pore (μm) and the thickness of the exine (μm) from the internal part of the last layer of the pollen grain to the external part. These variables were measured in 15 pollen grains from each treatment.

Statistical analysis

All statistical analyses were carried out using SAS/STAT v9.0 (SAS Institute, Cary, NC, USA). A completely randomized block experimental design was used to analyze the variables of days to male flowering and morphological variables of the tassel for genotype characterization. The statistical model was as follows:

$$Y = \mu + Gen + Loc + Gen \ x \ Loc + e$$

where Y is the response variable, μ is the general mean, *Gen* is the effect of the genotypes, *Loc* is the effect of the locations, $Gen \times Loc$ is the effect of the Genotype-Environment interaction, and e is the experimental error.

The morphological variables used to evaluate the crosses underwent an analysis of variance and Tukey means comparison test ($p \leq 0.05$). The following statistical model was used:

$$Y = \mu + Gen + Loc + TC/Gen + Loc \ x \ (TC/Gen) + e$$

where *Y* is the variable of response, *μ* is the general mean, *Gen* is the effect of the genotypes, *Loc* is the effect of the locations, *TC/GEN* is the effect of the cross types within genotypes, *Loc* × *(TC/GEN)* is the effect of the interaction of locations by type of cross within genotypes, and *e* is the experimental error.

In the case of pollen, for the percentage of grain viability, the data were transformed using the arc sine function, given the percentage scale with which the information was obtained. This variable, along with the morphological variables of the pollen grain, was analyzed using a completely randomized experimental design, with analysis of variance and Tukey means comparison ($p \leq 0.05$). The statistical model used was as follows:

$$Y = \mu + Gen + e$$

where *Y* is the response variable, *μ* is the general mean, *Gen* is the effect of the genotypes, and *e* is the experimental error.

RESULTS AND DISCUSSION

Phenotypic characteristics of the genotypes

Significant differences were observed in the variables of days to male flowering, ear length, ear diameter, number of kernel rows, number of kernels per row, and shelling factor between genotypes (Table 1). For the variables corresponding to the morphology of the tassel, there were no statistically significant differences.

Table 1. Analysis of variance, mean squares, and significance of the variables and characteristics of the tassel and the ears in the popcorn maize (*Zea mays* L.) populations evaluated.

Variable	Variation factor						Error	CV (%)
	Gen		*Loc*		*Gen × Loc*			
DMF	172.07	**	581.440	**	228.30	**	48.230	8.57
EL	21.18	**	0.102	ns	3.36	ns	4.224	17.44
ED	9.02	**	3.313	*	1.50	ns	0.853	26.16
NR	157.77	**	0.154	ns	27.35	**	3.800	16.23
NKR	297.46	**	41.005	ns	107.49	**	14.636	18.88
SHF	0.04	**	0.002	ns	0.03	**	0.004	8.22
LS	16.37	ns	77.500	*	11.04	ns	15.180	17.33
LRAP	6.59	ns	169.940	**	15.10	*	5.070	24.14
LMA	26.02	ns	267.580	**	9.86	ns	13.170	13.75
NB	27.52	ns	295.570	**	16.75	ns	12.85	34.51

**: significant at $p \leq 0.01$; *: significant at $p \leq 0.05$; ns: not significant; Loc: location; *Gen × Loc*: Genotype × Location; DMF: days to male flowering; EL: ear length; ED: ear diameter; NR: number of kernel rows; NKR: number of kernels per row; SHF: shelling factor; LS: length of peduncle; LRAP: length of the ramified part of the tassel; LMA: length of main axis; NB: number of branches.

Fonseca *et al.* (2003) mentioned that deacclimatization of a variety can affect the pollen availability and floral synchrony. Uribelarrea *et al.* (2002) also mentioned that pollen production is affected by the delay in planting dates. In this investigation, the North American Yellow Pearl Popcorn (NAYPP) race showed a difference in terms of days to male flowering, resulting in one of the latest, leading to the results supporting the theory, since differences were observed with the group of adapted genotypes (Cónico, Chalqueño, and Cacahuacintle).

No differences were found in three of the four morphological variables of the tassel evaluated among races (Table 2). The Iowa Pop variety, which corresponds to the NAYPP race, was the only one to show a difference in the variable of number of branches (NB). The results indicate that the NAYPP race, despite being an introduced variety, displays similar morphological tassel characteristics to the popcorn races that predominate in the highlands of central Mexico and related native races of this region. Vidal-Martínez *et al.* (2004) highlight that the most important components for production are the total of male flowers, flowers per branch, flowers on the main axis, and the number of branches of the tassel. Fonseca *et al.* (2003) observed that the number of branches also positively affects the production of pollen per tassel. As the number of branches per tassel decreases, so will the production of pollen (Tranel *et al*., 2009). The present work supports this statement since the Jack Superior variety, derived from the NAYPP, as in the controls used, had the highest number of branches

Table 2. Days to male flowering and morphological variables means of the ear and tassel of seven popcorn maize (*Zea mays* L.) genotypes introduced and native to the High Valleys in San Salvador Atenco and Montecillo, Mexico.

Genotype	Race	DMF	EL (cm)	ED (cm)	NR	NKR	SHF	LS (cm)	LRAP (cm)	LMA (cm)	NB (cm)
Jack Superior	PPAN	87 a	11 b	2.5 b	10.65 c	16 d	0.72 c	23 a	9.3 a	9 a	10 a
Iowa Pop	PPAN	80 a	10 c	2.8 b	13.20 b	20 b	0.79 a	23 a	7.8 a	8 a	7 b
Chalqueño	Chalqueño	77 b	13 a	4.2 a	11.51 c	22 a	0.84 a	23 a	9.3 a	9 a	9 a
Criollo Plaza	Palomero Toluqueño	81 a	12 a	3.7 a	15.6 a	24 a	0.83 a	21 a	9.7 a	9 a	12 a
Criollo Plaza × Iowa Pop 12	Palomero Toluqueño × PPAN	77 b	12 a	3.7 a	14.66 a	24 a	0.81 a	23 a	9.8 a	9 a	10 a
Cacahuacintle	Cacahuacintle	79 a	12 a	3.8 a	9.60 d	16 d	0.76 b	22 a	9.1 a	9 a	11 a
Cónico	Cónico	85 a	12 a	3.9 a	8.82 e	18 d	0.83 a	21 a	10 a	10 a	10 a
HSD (0.05)		8	2	0.7	1.6	3	0.05	4	2.7	2	4

Means with the same letter are statistically equal (Tukey, $p \leq 0.05$). HSD: honest significant difference; DMF: days to male flowering; EL: ear length; ED: ear diameter; NR: number of kernel rows; NKR: number of kernels per row; SHF: shelling factor; LS: length of peduncle; LRAP: length of the ramified part of the tassel; LMA: length of main axis; NB: number of branches.

per tassel, implying that it can produce the same amount of pollen. The number of branches conditions the number of anthers produced, which, in turn, conditions the amount of pollen produced.

Velasco-García *et al.* (2020) mentioned that the introduction of exotic varieties without prior adaptation may present greater changes in plant morphology characteristics, such as height, earliness, and morphological changes in the ear. The results support this statement, since differences were observed in all the morphological ear variables evaluated of the NAYPP race compared to the genotypes adapted to the weather conditions of the Mexican highlands (Table 2). Therefore, it can be considered that this North American race differs completely in morphological characteristics from the rest of the genotypes. Schoper *et al.* (1987) mentioned that the grain viability and amount of pollen released limit the production of grains on the ear when the tassels are exposed to heat stress, which occasionally occurs in the spring and summer in the area under study.

Pollen production by location

The differences in days to male flowering and morphological tassel characteristics between locations (Table 3) may indicate a difference in pollen productivity for the varieties studied. Humidity and warm temperatures, combined with a well-distributed rainfall, favor pollen production (Rácz *et al.*, 2006). Another aspect worth considering is the genetic component. Vidal-Martinez *et al*. (2004) consider that phenotypic plasticity plays an important role in the production of pollen in maize. Likewise, Fonseca *et al*. (2003) found that pollen production is conditioned by genotypic and environmental variations.

Table 3. Comparison of means between locations for the variables of days to male flowering, ear morphology, and tassel characteristics evaluated in popcorn maize (*Zea mays* L.) genotypes.

Loc	DMF	EL (cm)	ED (cm)	NR	NKR	SHF	LS (cm)	LRAP (cm)	LMA (cm)	NB (cm)
Atenco	78.40 a	11.75 a	3.39 a	12.04 a	19.76 a	0.79 a	23.4 a	7.90 b	28 a	9 b
Montecillo	83.66 b	11.80 a	3.67 a	11.98 a	20.75 a	0.80 a	21.5 b	11.0 a	25 b	12 a
HSD	3.03	0.62	0.28	0.59	1.16	0.2	1.69	1	1.6	2

Means with the same letter are statistically equal (Tukey, $p \leq 0.05$). HSD: honest significant difference; DMF: days to male flowering; EL: ear length; ED: ear diameter; NR: number of kernel rows; NKR: number of kernels per row; SHF: shelling factor; LS: length of peduncle; LRAP: length of the ramified part of the tassel; LMA: length of main axis; NB: number of branches.

Ear characteristics by location

There no statistical differences in the means of the variables corresponding to the ear characteristics between locations (Table 4).

Table 4. Comparison of means between locations of the ear morphology variables evaluated in popcorn maize (*Zea mays* L.) genotypes.

Location	EL (cm)	ED (cm)	NR	NGH	FDES
Atenco	11.75 a	3.39 a	11.98 a	19.76 a	0.79 a
Montecillo	11.80 a	3.67 a	12.04 a	20.75 a	0.80 a
DMS	0.62	0.28	0.59	1.16	0.02

Means with the same letter are statistically equal (Tukey; $p \leq 0.05$); HSD: honest significant difference; EL: ear length; DM: ear diameter; NR: number of kernel rows; NKR: number of grains per row; SHF: shelling factor.

Effect of pollen origin on ear characteristics (crosses)

The combined analysis of variance across locations for the morphological ear variables (Table 5) showed differences between phenotypes for all morphological variables of the ear.

Table 5. Mean squares and their significance from the combined analysis of variance across locations for ear-related variables in popcorn (*Zea mays* L.) genotypes.

Variable	*Gen*		*Loc*		TC/*Gen*		*Loc*/(*TC*/*Gen*)		CV (%)
EL	21.18	**	0.100	*	6.920	ns	3.36	ns	17.44
ED	9.02	**	3.310	*	1.810	*	1.0	ns	26.16
NR	157.77	**	0.150	ns	12.800	*	14.58	**	16.23
NKR	297.46	**	41.000	ns	30.110	ns	56.78	**	18.88
SHF	0.04	**	0.002	ns	0.004	ns	0.01	**	8.22

**: Significant at $p \leq 0.01$; *: significant at $p \leq 0.05$; ns: not significant; Loc: location; Gen: genotype; TC: type of cross (plant-to-plant and intervarietal cross); EL: ear length; ED: ear diameter; NR: number of kernel rows; NKR: number of kernels per row; SHF: shelling factor.

Diverse studies point out yield as the main adaptation indicator (Gómez-Espejo *et al.,* 2015; Santiago-López *et al.,* 2020; López-Morales *et al.,* 2021). The difference in yield usually determines if an introduced variety adapts and becomes a candidate for breeding programs. In contrast to this study, where variables such as pollen viability were included, the ear characteristics resulting from intervarietal crosses in comparison to those obtained with plant-to-plant crosses act as indicators of the potential of the NAYPP race to produce pollen and act as a male parent under the weather conditions of the central Mexico highlands.

The comparison of means for the morphological ear variables for different maize genotypes (Table 6) showed differences in all variables. The NAYPP race presented a slight reduction in the values of ear length, ear diameter, and number of kernel rows. There were differences in the morphology of the ear of the NAYPP race in comparison to the remaining races, showing that it was negatively affected.

Table 6. Comparison of means of the variables of ears from different popcorn (*Zea mays* L.) genotypes.

Genotype	Race	EL (cm)	ED (cm)	NR	NKR	SHF
Jack Superior	PPAN	11.06 c	2.53 b	10.65 d	15.83 d	0.72 c
Iowa Pop 12	PPAN	10.28 c	2.81 b	13.20 b	20.45 b	0.79 b
Chalqueño	Chalqueño	13.20 a	4.20 a	11.51 c	22.41 b	0.84 a
Criollo Plaza	Palomero Toluqueño	11.51 b	3.70 a	15.60 a	24.16 a	0.83 a
Criollo Plaza × Iowa Pop 12	Palomero Toluqueño × PPAN	11.93 b	3.71 a	14.66 b	24.29 a	0.81 b
Cacahuacintle	Cacahuacintle	12.22 b	3.80 a	9.60 d	16.54 d	0.76 b
Cónico	Cónico	12.25 b	3.93 a	8.82 e	18.08 c	0.83 a
HSD (0.05)		1.77	0.79	1.68	3.3	0.05

Means with the same letters are statistically equal (Tukey; $p \leq 0.05$); HSD: honest significant difference; EL: ear length; ED: ear diameter; NR: number of kernel rows; NKR: number of kernels per row; SHF: shelling factor.

Within the varieties, no differences were observed in the characteristics of the ears from plant-to-plant crosses or intervarietal crosses (Table 7). Criollo Plaza variety statistically displayed the same ear length with both crossing methods when using the Jack Superior genotype as a pollen source. The results show that comparing the means of the types of crossing of the morphological variables indicates that they are equal and that an intervarietal cross leads to the risk of winning or losing 2.51 cm. In the case of ear length, such a difference is not statistically significant. The values of the intervarietal crosses, in comparison with the plant-to-plant crosses, were equal for ear characteristics, indicating that there is a sufficient ability of the pollen of the introduced NAYPP variety to produce normal ears.

In general terms, the NAYPP race displayed different and inferior morphological tassel and ear characteristics to those of the native varieties under the weather conditions of the central Mexican highlands. However, these differences did not limit its ability to produce pollen with characteristics comparable to the Palomero Toluqueño race. Therefore, its use is possible in the breeding programs for local popcorn varieties. The separation between original populations without any adaptation and those selected in the High Valleys has been previously reported (Velasco-García *et al.*, 2020).

Table 7. Comparison of means of the ear variables depending on the type of the crossing method used in popcorn (*Zea mays* L.) genotypes evaluated.

Genotype	Type of cross	EL (cm)	ED (cm)	NR	NKR	SHF
Jack Superior	Plant-to-plant	11.60 a	2.53 a	10 a	16 a	0.72 a
	Intervarietal	11.60 a	2.53 a	10 a	15 a	0.73 a
Iowa Pop 12	Plant-to-plant	9.85 a	2.67 a	12 a	20 a	0.79 a
	Intervarietal	10.71 a	2.95 a	13 a	20 a	0.80 a
Chalqueño	Plant-to-plant	13.12 a	3.94 a	11 a	21 a	0.85 a
	Intervarietal	13.28 a	4.46 a	11 a	23 a	0.83 a
Criollo Plaza	Plant-to-plant	11.77 a	3.66 a	15 a	24 a	0.83 a
	Intervarietal	11.25 a	3.75 a	15 a	24 a	0.83 a
Criollo Plaza × Iowa Pop 12	Plant-to-plant	11.60 a	3.25 a	13 b	22 a	0.80 a
	Intervarietal	12.26 a	4.18 a	16 a	25 a	0.82 a
Cacahuacintle	Plant-to-plant	10.99 a	3.34 a	8 a	14 a	0.73 a
	Intervarietal	13.45 a	4.26 a	10 a	18 a	0.79 a
Cónico	Plant-to-plant	11.87 a	8.50 a	8 a	16 a	0.82 a
	Intervarietal	12.63 a	4.06 a	9 a	19 a	0.83 a
HSD (0.05)		2.51	1.13	2	4	0.08

Means with the same letter are statistically equal (Tukey; $p \leq 0.05$); HSD: honest significant difference; EL: ear length; ED: ear diameter; NR: number of rows; NKR: number of grains per row; SHF: shelling factor.

However, when carrying out intervarietal crosses, the NAYPP pollen had no negative effect on the characteristics of the ears and can therefore be used as a male parent for intervarietal crosses.

The introduction of exotic varieties has not yet been fully studied in popcorn, so more investigations are required to help to determine their potential to be used as parents in breeding programs or as varieties after undergoing an adaptation process through recurrent selection in the new target environment. This would help generate new varieties that help boost production in order to reduce the imports of this grain and the conservation of the Palomero Toluqueño race in Mexico.

Study of pollen grains

The analysis of variance for the variables of viability and morphology of the pollen grain (Table 8) showed highly significant differences in the variables of viability and diameter of the grain (Figure 1). However, for the variables of pore diameter and thickness of exine, significant differences were only observed in the genotype variation factor.

The pollen grain viability is negatively affected by deacclimatization (Fonseca *et al.*, 2003). The results contrast with the above statement, since the viability of the pollen grain from the NAYPP race is different from some genotypes but had the same viability as the group of genotypes adapted to the weather conditions of the High Valleys of Mexico (Table 9).

Table 8. Analysis of variance of the characteristics evaluated in the pollen of maize (*Zea mays* L.) genotypes.

Variable	df	Genotype		Error	CV (%)
VIA	7	333.15	**	55.62	12.32
DPG	14	1457.89	**	55.93	8.30
DP	14	8.23	*	0.81	15.55
EXT	14	0.21	*	0.08	27.77

**: Significant at $p \leq 0.01$; *: significant at $p \leq 0.05$; ns: not significant; df: degrees of freedom; CV: coefficient of variation; VIA: viability; DPG: diameter of the pollen grain; DP: diameter of pore; EXT: exine thickness.

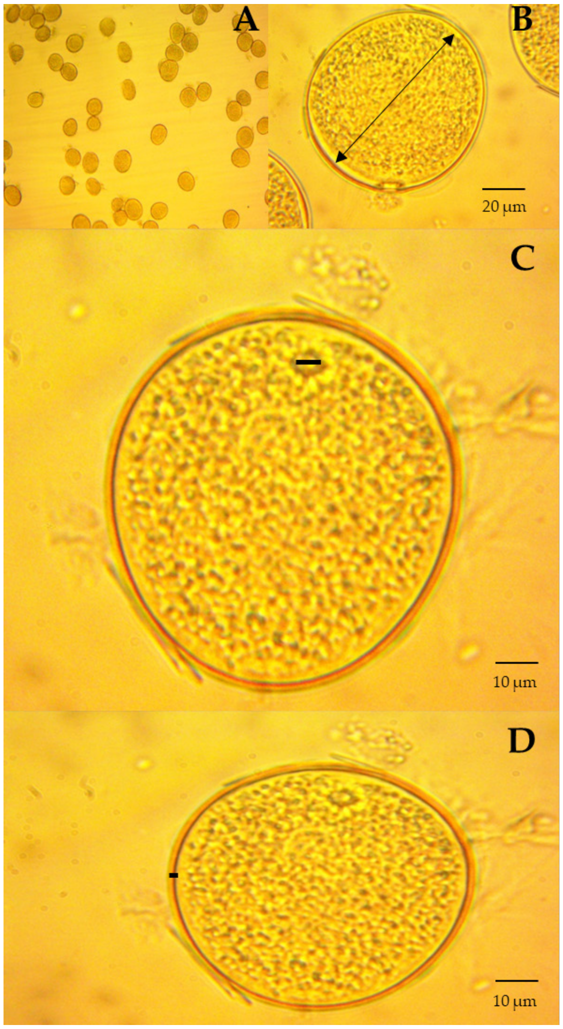

Figure 1. Maize (*Zea mays* L.) pollen grain dimensions. A: pollen grains; B: pollen grain diameter; C: pore diameter; D: exine thickness.

Table 9. Comparison of means for viability and morphology of the pollen grains of maize (*Zea mays* L.) genotypes.

Genotype	Race	VIA	DGP (μm)	PD (μm)	EXT (μm)
Jack Superior	NAYPP	65 a	92 a	5.7 b	1.0 a
Iowa Pop 12	NAYPP	63 a	95 a	5.0 c	1.0 a
Chalqueño	Chalqueño	56 c	92 a	6.4 a	1.0 a
Criollo Plaza	Palomero Toluqueño	59 b	88 b	5.7 b	1.2 a
Criollo Plaza × Iowa Pop 12	Palomero Toluqueño × NAYPP	60 a	90 a	5.6 c	1.0 a
Cacahuacintle	Cacahuacintle	59 b	95 a	6.6 a	1.1 a
Cónico	Cónico	60 a	91 a	5.7 b	1.0 a
Teosinte	Chalco	59 b	67 c	5 d	0.9 b
HSD (0.05)		5	6.2	0.7	0.2

Means with the same letter are statistically equal (Tukey; $p \leq 0.05$); HSD: honest significant difference; VIA: percentage of viability; DPG: diameter of the pollen grain; DP: diameter of pore; EXT: exine thickness; NAYPP: North American Yellow Pearl Popcorn.

Pollen is an important vector in the genetic flow of maize (Luna *et al.,* 2001). The NAYPP race did not differ with three of the genotypes studied (Table 9). Its viability behaved in the same way as the Cónico race and did not show an evolutionary tendency towards the loss or gain of viability of the pollen grain, since the teosinte that represents the basal position in the evolutionary scale has an intermediate pollen viability, with races of higher or lower pollen viability. The pollen grain viability of the North American race was not affected by the weather conditions of the High Valleys of Mexico, possibly as a survival mechanism against the lack of adaptation for grain yield.

Regarding pollen morphology, an increase stands out in the dimensions of the grain diameter, pore diameter, and exine thickness in the planted maize races in comparison to the wild relative. A slight tendency was observed towards the increase in the viability of the pollen as the dimensions of the morphology variables increase, particularly the variable of the pollen grain diameter, since the viability of the pollen is highly conditioned by the temperature and relative humidity of the environment (Kaefer *et al.,* 2016; Razzaq *et al.,* 2019). The size of the pollen grain is related to the amount of water it contains (Aylor, 2003); therefore, the smallest grains are less visible. Teosinte and Criollo Plaza are among the genotypes with the least viability, as well as the smallest size (Table 9).

Results show that pollen grain characteristics depended more on the variety, reflecting previous breeding work. For example, the Jack Superior and Iowa Pop varieties, despite deriving from the same maize race, are different for the pore diameter variable, whereas for the rest of the variables, they were equal. Taking the diameter of the pollen grain (DPG) as a reference, the varieties that showed the most breeding work displayed a greater grain diameter in relation to the oldest maize varieties, such as Palomero Toluqueño (Kato-Yamakake, 2023) or teosinte itself. This was also observed for the diameter of the pore (DP) and exine thickness (EXT), where teosinte displayed the lowest values. It is possible that the smallest diameter of the grain is caused by a tolerance to desiccation (Table 10), since, at flowering, the pollen grains are larger when they undergo intense stress due to desiccation (Ejsmond *et al.*, 2011).

Comparison of means from locations

Table 10. Comparison of the means of the pollen grain morphology of different maize (*Zea mays* L.) genotypes.

Location	DPG (μm)	DP (μm)	EXT (μm)
Atenco	92.81 a	5.74 a	1.09 a
Montecillo	87.70 b	5.85 a	0.97 b
HSD (0.05)	1.97	0.23	0.59

Means with the same letter are statistically equal (Tukey; $p \leq 0.05$); HSD: honest significant difference. DPG: pollen grain diameter; DP: pore diameter; EXT: exine thickness.

CONCLUSIONS

Deacclimatization in the highlands of central Mexico reduces the agronomic yield of the North American Yellow Pearl Popcorn race in traits such as earliness, tassel, and ear morphology. However, these changes do not limit the ability of the pollen produced, since its viability and morphology have no effect on its role as a male parent, allowing for the production of ears with the same characteristics as when pollen from native varieties is used. Therefore, the North American Yellow Pearl Popcorn race is an alternative that can be used in breeding for local popcorn varieties.

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