Revista Brasileira de Milho e Sorgo

Brazilian Journal of Maize and Sorghum

ISSN 1980 - 6477

Journal homepage: www.abms.org.br/site/paginas

GENETIC IMPROVEMENT IN POPCORN

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How to cite

CARANHATO, A. L. H.; TRINDADE, R. W. R.; UHDRE, R. S.; PINTO, R. J. B.; SCAPIM, C. A.; PATERNIANI, M. E. A. G. Z. Genetic improvement in popcorn. **Revista Brasileira de Milho e Sorgo**, v. 21, e1272, 2022.

Abstract – Popcorn consumption in Brazil has grown significantly over the years, and genetic improvement is essential to obtain sustainable gains in multiple traits to supply this increasing demand. Thus, the objective of this review was to contribute information concerning the process of popcorn breeding in tropical regions, germplasm availability, popcorn breeding plans, the main characteristics related to popcorn quality and yield, and advances and perspectives in the process of popcorn improvement. The main focus of breeding programs is to obtain hybrids from inbred lines with high popping expansion (>40 mL g^{-1}) and yield (>4.000 kg ha^{-1}). The genetic improvement performed in Brazil has presented significant advances, mainly due to work developed in public institutions with the development of new hybrids that present more significant popping expansion and yield. However, the number of cultivars is still low, and most of them are controlled by private companies. Therefore, intrapopulation methods are recommended to develop open-pollinated varieties with high popping expansion, and this trait can be used as an early predictor of promising inbred lines to obtain superior hybrids for grain quality. Furthermore, popping expansion can be quickly recovered in backcrosses involving the cross of common maize with an inbred popcorn line.

Keywords: *Zea mays* L. var. everta; Germplasm; Breeding Plans, Popping Expansion; Yield.

MELHORAMENTO GENÉTICO DE MILHO PIPOCA

Resumo - O consumo de milho-pipoca no Brasil tem crescido significativamente ao longo dos anos e para suprir esse aumento de demanda, o melhoramento genético é essencial para a obtenção de ganhos sustentáveis em múltiplas características. Assim, o objetivo desta revisão foi contribuir com informações sobre o processo de melhoramento da pipoca em regiões tropicais, disponibilidade de germoplasma, planos de melhoramento do milho-pipoca, principais características relacionadas à qualidade e produtividade do milho-pipoca e avanços e perspectivas no processo de melhoramento do milho-pipoca. O foco principal dos programas de melhoramento é a obtenção de híbridos de linhagens com alta capacidade de expansão (>40 mL g^{-1}) e produtividade (> 4.000 kg ha^{-1}). O melhoramento genético realizado no Brasil apresentou grandes avanços, principalmente devido aos trabalhos desenvolvidos em instituições públicas com o desenvolvimento de novos híbridos que apresentam maior capacidade de expansão e produtividade. No entanto, o número de cultivares ainda é baixo e a maioria delas é controlado por empresas privadas. Métodos intrapopulacionais são recomendados para o desenvolvimento de variedades de polinização aberta com alta capacidade de expansão e esta característica pode ser usada como um preditor inicial de linhagens promissoras para obtenção de híbridos superiores para qualidade do grão. A capacidade de expansão pode ser facilmente recuperada em retrocruzamentos envolvendo o cruzamento de milho comum com uma linhagem de milho-pipoca.

Palavras-chave: *Zea mays* L. var. everta; Germoplasma; Planos de Melhoramento; Capacidade de Expansão; Rendimento de Grãos.

DOI: https://doi.org/10.18512/rbms2022v21e1272

The main characteristic of popcorn is its grain hardness and small length, which can burst and turn into popcorn after heating (Sawazaki, 1995). This phenomenon occurs because, due to vaporization of moisture and gelatinization of starch grain subjected to temperatures >150ºC. In addition, the expansion of water molecules in the form of steam creates internal pressure in the grain to the point where the pericarp ruptures, exposing the endosperm, thus forming the white and soft mass known as popcorn (Zinsly & Machado, 1987).

The importance of popcorn comes from its profitability in the market, with growing consumption and widespread acceptance of the final product. In addition, its consumption is usually associated with leisure time, such as fairs and movie theaters (Amaral Júnior et al., 2013). In the USA, approximately 15 billion *quarts* (almost 17 billion liters) of popcorn are consumed annually (Matzke, 2021). In 2016, the popcorn market was around $9.06 billion, and it is projected to reach $15 billion by the end of 2023 (Dawande, 2018).

Between 2014 and 2019, an increase of 223% in areas sown with popcorn was observed in Brazil (Kist et al., 2019), which has become the second-largest producer of popcorn in the world, producing approximately 320,000 tons. Approximately 70% of this production is intended for domestic consumption and the remainder for export (Blecher, 2019). However, there is still a vast market for popcorn cultivation in Brazil.

Genotypes with superior characteristics are required to promote the popcorn production chain from both the agronomic and commercial approaches of the final product. All improvement breeding methods applied to standard corn can also be used in popcorn, emphasizing popcorn quality evaluation. According to Sawazaki (1995), knowledge of all the factors that affect popcorn quality and consumer preferences is fundamental for the success of the improvement breeding program.

However, over the years, the supply of seeds of improved cultivars of popcorn in Brazil has not followed the improvement shown by common maize. The Brazilian institutions and universities carrying research focused on popcorn improvement consist of the Agronomic Institute of Campinas (IAC), Embrapa Maize and Sorghum Research Center (Embrapa Milho e Sorgo – Brazilian Agency for Agricultural Research), the State Universities of Maringá (UEM), and Norte Fluminense (UENF), the Agriculture Superior School "Luiz de Queiroz" (ESALQ), and the Federal Universities of Viçosa (UFV) and Lavras (UFLA).

This review aims to contribute to information concerning the process of genetic improvement of popcorn in tropical regions, emphasizing germplasm availability, popcorn breeding programs, main characteristics related to popcorn quality and yield, methodologies for popcorn quality evaluation, and advances and perspectives in the process of popcorn breeding.

1. Germplasm

Some authors agree that the popcorn was one of the first improved races during the maize domestication process (Wellhausen et al., 1951; Contreras et al., 2006) because popcorn presents some characteristics considered as wild, such as smaller grain size, higher prolificacy, thicker pericarp (Ziegler, 2001), and, in some races, narrow grains (Silva et al., 2020).

Since the germplasm choice is crucial in conducting a breeding program, information found in the literature regarding some of the most relevant popcorn germplasm at national and global levels will be presented below.

1.1. South American Races

The term race refers to a group of related individuals with enough characteristics in common to permit their recognition as a group (Anderson & Cutler, 1942).

The center of origin of popcorn is Latin America, where a great diversity of indigenous races exist, but only three races are well documented. The first is the Pororo race from Bolivia (Ramírez et al., 1960), which has white, small, rounded kernel, low to medium height plants, with tillers, and high prolificacy (Vencovsky, 1987). The second is the Pisankalla race, originating in Bolivia, Paraguay, and Argentina, producing white and narrow grains (Ramírez et al., 1960). Finally, the Brachytic Pop Corn race is found in mountainous regions of the Andes and has brachytic plants, oval ears, small and thin grains, generally dark red, with white endosperm, and colorless aleurone (Brieger et al., 1958).

1.2. Indigenous open-pollinated variety (OPV)

Indigenous Composite: Obtained from more than 40 open-pollinated varieties (OPV) of indigenous corn collected in various regions of South America, recombined for more than eight generations, followed by mild selection. As a result, it has substantial genetic variability involving several characteristics and excellent material for popcorn improvement (Zinsly & Machado, 1987).

Guarani: This OPV has significant variability in terms of grain color characteristics. It has medium-height plants with tillers, high prolificacy, and a semi-early production cycle (Sawazaki, 1995). Therefore, the Guarani OPV is critical in providing alleles of interest for improving popcorn, being utilized as a parent in hybrids such as IAC-112.

1.2. Improved OPV

South American Mushroom (SAM): The Instituto Agronômico de Campinas (IAC) developed it in 1941, and its pedigree came from Argentina. After mass selection, it was commercially released in 1947 (Sawazaki, 1995).

Composite CMS-42 and **Composite CMS-43**: They originated from 25 OPV of yellow round grains and 33 white grains, respectively, and were obtained from the germplasm bank of Embrapa. These have resistance to *Exserohilium turcicum* and *Puccinia spp*. with tremendous genetic variability for plant and grain characteristics (Pacheco et al., 1998).

Yellow and White Popcorn: These were obtained from the IGEN-2 composite, with three cycles of stratified mass selection for yield, other agronomic characteristics, and popping expansion (PE). They are early plants with high prolificacy, PE of 26 mL g^{-1}, an average plant height of 1.60 m, an ear height of 0.9 m, and yield equivalent to half that of hybrid IAC HMD 7974 (Zinsly & Machado, 1987).

UFRGS-20 and **UFRGS-18**: Open-pollinated variety obtained from advanced generations of North American hybrids (Sawazaki, 1995).

BRS Angela: Open-pollinated variety originated from six cycles of intrapopulation recurrent selection on the popcorn composite CMS 43. It has a white, rounded kernel and PE of 26 mL g^{-1} (Pacheco et al., 2001).

UNB-2: Obtained from a selection of the "Indigenous Composite" that first originated de population UNB-1, that was crossed with the popcorn population "Americana." The progeny obtained was

DOI: https://doi.org/10.18512/rbms2022v21e1272

crossed again with a popcorn variety named "High-yielding Yellow Popcorn" with yellow kernel and resistance to northern leaf blight (*Exserohilum turcicum*) followed by two cycles of mass selection. Finally, this population was backcrossed three times with the popcorn "Americana" originating the UNB-2 population (Amaral Júnior et al., 2013).

UENF 14: Was developed in five cycles of recurrent selection of the UNB-2U population. The cultivar has a yellow kernel and produces 3.047 kg ha^{-1} and has a PE of 35.69 mL g^{-1}(Amaral Júnior et al., 2013).

1.3. Hybrids from inbred lines

IAC-112: Material with high popping expansion (>40 mL g^{-1}) and good yield (>3.000 kg ha^{-1}), with pearl grain format and yellowish color. Developed by the Agronomic Institute of Campinas (IAC), it is a simple hybrid obtained from crossing Guarani x IAC 64 varieties (Sawazaki, 2001).

IAC-125: A top-cross hybrid, the kernel color, and shape are orange and pearl. It was developed by the Agronomic Institute of Campinas (IAC) with inbreed lines of SAM, IAC 64, and an advanced generation of an American hybrid (Sawazaki, 2001).

Zélia: A three-way cross hybrid adapted to tropical and temperate environments developed by Pioneer. Its kernel color is yellow, has a precocious cycle and good yield potential (>3000 kg ha^{-1}), and high popping expansion (>35 mL g^{-1}) (Scapim et al., 2002).

IAC-268: A three-way hybrid developed by the Agronomic Institute of Campinas (IAC), has a high PE (>45 mL g^{-1}) and yield (>4.500 kg ha^{-1}). It has a light yellow kernel and stands out with high resistance to foliar diseases and *Pratylenchus brachyurus* nematode (Paterniani et al., 2020).

IAC-367: A three-way hybrid developed by the Agronomic Institute of Campinas (IAC), with orange and pearl type kernels, high PE (>45 mL g^{-1}), and yield (>4.500 kg ha^{-1}) (Paterniani et al., 2020).

1.4. Exotic Germplasm

Exotic germplasm for applied breeding programs means all germplasm that is not immediately useful without selection for adaptation for a given area (Hallauer & Miranda-Filho, 1988).

Jap Hulless: It is a variety having good popcorn quality; its plants have short and thick cobs, rows of 30-40 kernels, and long, thin, whitish-colored kernels (Sawazaki, 1995).

South American: Originally from Argentina and introduced in the United States in 1920, the popcorn formed by popping its kernels is mushroom-type and has suitable PE, with good popcorn attractiveness due to its aleurone coloration being mottled golden yellow (Sawazaki, 1995).

Super gold (Sunburst, Yellow Pearl): Developed by the Kansas Experiment Station through mass selection for PE on the Queen Golden variety, it has small, conical spikes, small and glassy grains, with suitable PE (Sawazaki, 1995).

1.5. Current Germplasm

At the National Register of Cultivars (RNC) of the Ministry of Agriculture, Livestock and Food Supply - Brasil (2021), there are 137 registered cultivars (Table 1). However, a few cultivars have been effectively seeded in commercial crops.

Table 1. List of cultivars (hybrids and OPV) and inbred lines registered for popcorn and their respective holding companies in the National Cultivar Register.

Keeper	Record Type		
	Cultivar	**Parental Inbred lines**	**Parental Single Hybrid**
Agristar do Brasil Ltda.	12	-	-
Atlântica Logística e Armazenagem Ltda. ME.	2	-	-
ATS - Agricultura, Tecnologia e Serviços Ltda	1	-	-
Basso Comercio de Sementes, Importação e Exportação Ltda.	-	3	-
Comercial Cianorte Ltda.	6	-	-
Seeds, Seedlings and Matrices Department - DSMM/CATI	2	-	-
Elemar Reinoldo Haas	1	-	-
Felipe Bresolin Ltda.	4	5	-
Feltrin Sementes Ltda	1	-	-
Feltrin Sementes Ltda. Vidasul Sementes Ltda. Agristar do Brasil Ltda. Isla Sementes Ltda.	1	-	-
General Mills Brasil Alimentos Ltda.	9	-	4
Agronomic Institute of Campinas - IAC	7	3	3
Lodéa Consultoria e Comércio De Sementes Ltda. ME.	4	-	-
Marcelo Ananias	1	-	-
Pipolino Indústria Comércio Ltda.	20	-	-
Seedco Do Brasil Agricultura Ltda.	3	-	-
Sementes Boa Esperança Ltda.	4	-	-
SG Nutri - Sementes, Grains and Nutrientes Comércio e Serviços Ltda.	4	-	-
TSV Sementes De Vegetais Ltda.	1	-	-
Universidade Estadual Do Norte Fluminense Darcy Ribeiro - UENF	17	-	-
Yoki Alimentos S/A	19	-	-

Source: Brasil (2021).

Based on Table 1, it is possible to observe the predominance of private companies in the national seed market. Most seeds used by producers are derived from foreign germplasm, mainly from the United States and Argentina (Sawazaki et al., 2000; Miranda et al., 2012). The restricted access to these seeds, coupled with the low availability of popcorn cultivars in the national scenario, result in a narrow genetic base and end up compromising the development of new cultivars in breeding programs (Scapim et al., 2002; Silva et al., 2017; Seledes et al., 2019).

Indigenous maize of landraces can be an essential source of germplasm for developing new cultivars. These materials have high genetic diversity, mainly due to differences in cropping systems and the selection applied to the plants that vary according to the needs at each location (Silva et al., 2017; Seledes et al., 2019).

Costa et al. (2016) proposed that the Far West region of Santa Catarina could be considered a micro center of genetic diversity for popcorn. The region presents an extensive presence of popcorn races considered wild and high local human activity, contributing to the high genetic diversity of popcorn (Ogliari & Alves, 2007; Vogt et al., 2010; Ogliari et al., 2013). Silva et al. (2017) evaluated the PE of 85 open-pollinated varieties local of popcorn from this region and obtained values ranging from 2.5 to 24.7 mL mL^{-1}, demonstrating the high potential of genetic gains with selection in these local varieties for this trait.

According to Lee (1995), *heterotic groups* can be defined as a germplasm collection that, when crossed with germplasm from another group, tends to exhibit higher levels of heterosis than when crossed with members of its group. Santacruz-Varela et al. (2004) evaluated different popcorn populations from the USA and Latin America based on morphological and molecular descriptors and observed the formation of three main groups: Yellow Pearl, Pointed Rice, and North American Early. Blanco et al. (2005) evaluated popcorn germplasm from Iowa State University and defined three heterotic groups: Amber Pearl, South American, and Supergold.

In Brazil, there are several studies of genetic diversity to identify different groups of popcorn for improvement (Dandolini et al., 2008; Trindade et al., 2010; Saavedra et al., 2013; Resh et al., 2015; Silva et al., 2015; Santos et al., 2017).

The PE is one of the most critical traits for popcorn improvement. Thus, in the next section, we will discuss its definition, cause, and the type of inheritance governing this trait.

2. Popping expansion (PE)

PE is the ratio between the volume of popped popcorn and the volume or mass of kernels used for popping. Its units can be expressed as volume/volume (mL mL^{-1}) or volume/grams (mL g^{-1}), according to the units of measurement of popcorn kernel sample (Miranda et al., 2003). Different systems for assessing popcorn expansion should be used in individual and family selections. The hot air popcorn pumper is an efficient system in which 10 g of the kernel can be used to evaluate plants, and up to 90 g of the kernel can be used to evaluate families in the trials. The microwave oven is equivalent to the hot air popcorn pumper. Kraft paper bags can be used in the microwave oven. For plant evaluation, 10 g of a kernel with 140 seconds is recommended. For progenies evaluation, 30 g to 90 g of a kernel with 220 seconds can be used (Matta & Viana, 2001).

According to Green Júnior and Harris Júnior (1960), popcorn cultivars with PE indices < 25 mL

DOI: https://doi.org/10.18512/rbms2022v21e1272

$g^{-1}$are considered poor, good if between 25 and 30 mL $g^{-1,}$ and very good if between 30 and 35 mL g^{-1}. Populations of popcorn with PE indices > 35 mL g^{-1} are considered excellent.

The PE is determined by the resistance of the pericarp, associated with the presence of oil and moisture. When heated to high temperatures (>150ºC), vaporization of moisture and gelatinization of starch present in the grain takes place. Thus, the expansion of water molecules in vapor and oil creates internal pressure within the grain to the point where the pericarp ruptures, exposing the endosperm (Zinsly & Machado, 1987).

The flakes that originated after the popcorn explosion can be classified as the Mushroom or Flake Butterfly type. The first usually presents a regular round format, with yellow coloration, and is commonly sold in the format of popped popcorn. The second presents a less regular format, white or yellow coloring (D'Croz- Mason & Waldren, 1990).

Seed moisture is one of the factors that most influence PE. The moisture associated with maximum PE depends on the cultivars and the method adopted for its determination (Luz et al., 2005). The ideal average moisture of grains for marketing should be around 13.5% to 14%, which provides good PE (Sawazaki et al., 2000).

Concerning the genetic inheritance of PE, there is a predominance of additive variance (Table 2). The selection of superior individuals is a good strategy that can be adopted in a breeding program using simple methods and that the selection gains for the trait will be effective

3. Factors affecting kernel and popcorn quality

The improvement process of popcorn is slower than that of common maize, mainly because of the additional need to work with characteristics related to popcorn quality. Information about the legislation involved in classifying grains and the main characteristics related to popcorn quality are presented below.

3.1. Characteristics related to grain quality

In Brazil, popcorn classification follows Normative Instruction Nº61/2011 (Brasil, 2011) that defines its classification according to quality and identity requirements. The quality requirements for popcorn are defined according to the color of the grains (yellow, white, colored, or mixed) and the maximum tolerance limits and are set out in Table 3.

Straw stalking is highly correlated with the percentage of fungal grain infections. Poorly compacted varieties have a higher percentage of infected ears than those with better compactness. Another factor that favors reductions in the incidence of fungal attacks is stalk development. This factor causes the cob to yield after the ripening period, with its tip facing downwards, preventing water entry (Sawazaki, 1995) and preventing fungus development.

Factors related to harvest, processing, and grain storage influence the popcorn quality. Pacheco et al. (1996) state that mechanical damage in popcorn grains drastically decreases PE. Corrêa et al. (2001) concluded that drying air temperatures > 40°C cause a significant decrease in the PE values.

DOI: https://doi.org/10.18512/rbms2022v21e1272

Table 2. Results of variance component of the PE trait in popcorn.

Predominance of genetic variance	References:
Additive	Lyerly (1942)
Additive	Dofing et al. (1991)
Additive	Pacheco et al. (1998)
Additive	Larish and Brewbaker (1999)
Additive	Pereira and Amaral Júnior (2001)
Additive	Miranda et al. (2001)
Additive	Scapim et al. (2006)
Additive	Arnhold et al. (2009)
Additive	Arnhold et al. (2010)
Additive	Silva et al. (2011)
Non additive	Oliveira et al. (2018)
Non additive	Lima et al. (2019)
Additive	Possatto Júnior et al. (2021)
Additive	Castro et al. (2022)

Table 3. Popcorn Normative Instruction Nº61/2011 (Brasil, 2011) defines its classification according to quality and identity requirements.

Framework	Maximum value expressed as a percentage (%)						Minimum PE value (mL.g^{-1})
	Damaged grains		Broken grains	Foreign Matter and Impurities		Infestation levels of maize weevil	
	Mouldy and Burnt	Total		Dead Insects	Total		
Type 1	0.20	2.00	2.00	0.30	1.00	1.50	30
Type 2	0.40	3.00	2.50	0.30	1.50	2.00	30
Type 3	0.60	4.00	3.00	0.30	2.00	2.50	30
Out of Type	1.00	6.00	4.00	0.30	2.50	3.00	< 30

Source: Brasil (2011).

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3.2. Characteristics related to popcorn quality

Other factors that should be considered during the improvement process of popcorn are those related to its consumption, such as the presence of unpopped kernels, color, texture, and flavor (Leonello et al., 2009; Sawazaki et al., 1984; Sweley et al., 2013).

Pericarp thickness: The pericarp presents a significant association with PE is responsible for maintaining the internal pressure in the kernel that is generated with heating; therefore, its thickness and integrity are responsible for the explosion and size of the popcorn (Zinsly & Machado, 1987; Mohamed et al., 1993; Sawazaki, 2001). Saito et al. (2021) obtained a positive genotypic correlation of 0.81 and a phenotypic correlation of 0.76 (Table 4) between the variables of pericarp thickness and PE. Simultaneously, Sawazaki (1995) states that selection for this trait should increase pericarp thickness but should exhibit good fragmentation after popping.

Grain length and width: Several studies indicate that grain length and width negatively correlate with PE (Lin & Anantheswaran, 1988; Allred-Coyle et al., 2000). In works developed by Lyerly (1942) and Saito et al. (2021) (Table 4), the genotypic correlations obtained were -0.50 and -0.62 for grain width and -0.60 and -0.78 for grain length, respectively. Thus, the selection of grains with less length and width is indicated to obtain genotypes with more outstanding PE.

Embryo: The embryo does not contribute directly to the PE increase of popcorn, but the smaller the embryo size, the greater the percentage of endosperm present in the kernel. According to Sawazaki (1995), breeding programs seek to develop plants that have reduced embryo size.

Endosperm: Popcorn mainly comprises vitreous endosperm (Allred-Coyle et al., 2000; Shimoni et al., 2002; Sweley et al., 2013). A study by Pordesimo et al. (1991) indicated that the higher the ratio of vitreous endosperm to farinaceous endosperm, the higher the PE.

4. Plant characteristics correlated with yield

In a breeding program, the indirect Selection of more productive plants by correlated responses in other less complex characters can allow more remarkable progress and efficiency in the selection process (Rios et al., 2012). Furthermore, the study of simple correlation, whether genotypic, phenotypic, or environmental, allows quantitative estimates of the influence of one character on another and identifies whether this influence is positive or negative, thus facilitating the selection of combined characters (Daros et al., 2004; Rangel et al., 2011).

Many simple correlation studies in popcorn have already indicated the tendency of PE to present negative genotypic correlation with yield and other traits, hindering the simultaneous improvement of attributes of interest (Zinsly & Machado, 1987; Coimbra et al., 2001; Vendruscolo et al., 2001; Daros et al., 2004). However, in path analysis studies, Rangel et al. (2011) verified the possibility of finding a positive correlated response between PE and yield if plants with smaller grain sizes (width and length) are selected from within the most productive populations.

Estimates of the simple phenotypic (r_F), genotypic (r_G), and environmental (r_A) correlation coefficients between PE and agronomic characters were obtained by Saito et al. (2021), Cabral et al. (2016), and Rangel et al. (2011), and are presented in Table 4.

Through path analysis, Saito et al. (2021)

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Table 4. Estimates of simple phenotypic (r_F), genotypic (r_G), and environmental (r_A) correlation coefficients between PE and agronomic characters were found by Saito et al. (2021) (1), Cabral et al. (2016) (2), and Rangel et al. (2011) (3).

	r_F			r_G			r_A		
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
AltE	-0.37	-0.26	-	-0.38	-0.34	-	-0.13	-0.38	-
Starch	-0.06	-	-	-0.08	-	-	0.13	-	-
CompGr	-0.75	-0.57	-	-0.78	-0.63	-	-0.09	-0.72	-
Difus	0.53	-	-	0.54	-	-	0.07	-	-
EspGr	0.04	0.26	-	0.05	0.31	-	-0.04	0.37	-
EspPer	0.76	-	-	0.81	-	-	-0.05	-	-
WidthGr	-0.60	-0.51	-	-0.62	-0.59	-	-0.08	-0.76	-
M100	-0.57	-0.53	-0.12	-0.59	-0.58	-0.22	-0.23	-0.64	0.08
Nesp	-0.04	-	0.07	-0.05	-	0.08	0.08	-	0.07
Nfil	-0.13	-	-	-0.14	-	-	-0.04	-	-
Oil	-0.27	-	-	-0.30	-	-	-0.01	-	-
Prol	-	0.06	-	-	0.08	-	-	0.03	-
Prot	0.44	-	-	0.45	-	-	0.08	-	-
Yield	-0.50	-0.05	-0.12	-0.54	-0.10	-0.07	0.20	-0.06	0.14

AltE = Height of ear insertion; Starch = Percentage of total starch of the grain; CompGr = Length of the grain; Diffus = Thermal diffusivity of the pericarp; Espr = Thickness of the pericarp; LargGr = Width of the grain; M100 = Mass of 100 grains; Nesp = Number of ears per plot; Nfil = Number of rows of grains in the ear; Oil = Total oil content of the grain; Prol = Prolificity; Prot = Protein content; Yield = yield

concluded that pericarp thickness has a direct effect on PE and that the thermal diffusivity of the pericarp has an indirect effect on pericarp thickness, on PE. The authors also performed a study of canonical correlations to identify better the associations that allow for an increase in the PE of popcorn and found the canonical pair significant and high (r = 0.9541). This result verified that PE was directly proportional to pericarp thickness and thermal diffusivity but inversely proportional to grain length and yield, indicating that increased PE is associated with greater pericarp thickness and thermal diffusivity, shorter grain length, and lower yield.

5. Intrapopulation improvement in popcorn populations

In this topic, the main improvement methods applied to popcorn and some of its particularities will be presented.

5.1. Mass Selection

It is recommended that mass selection be carried out in two stages. The first represents a less intense selection for agronomic characters of interest, and the second constitutes a more rigorous selection for PE (Zinsly & Machado, 1987; Sawazaki, 1995). According to Sawazaki (1995), the success of this method depends on existing genotypic correlations involving the selected traits in the first phase and the PE.

5.2. Selection among and within half-sib families

The most widely used intrapopulation improvement method in popcorn in Brazil is selection among and within half-sib families (Paterniani, 1967). Pacheco et al. (1998), considering the second cycle of Selection among and within CMS-42 and CMS-43 populations, obtained selection gain expectations between 16.8% for PE and 3.06% in yield in CMS-42, and 19.12% and 3.15% in CMS-43. Researchers performed selection among families of the population DFT1- Ribeirão, and a predicted gain of 9.58% in PE was estimated, where selection was performed based on independent levels of elimination (Coimbra et al., 2002). Matta and Viana (2003) observed an improvement in quality, but not in production levels, when performing selection among and within families of the Beija-Flor open-pollinated variety.

Selection indices were applied to data sets of 169 half-sib families of the popcorn composites UEM-Co1 and UEM-Co2 in four cycles of recurrent selection. Genetic gains for popping expansion and grain yield were estimated based on selection indices and truncation selection (Vieira et al., 2017).

There are several papers showing the effects of recurrent selection on yield and popping expansion of populations themselves (Sawazaki, 1996; Daros et al., 2004; Santos et al., 2008; Vilela et al., 2008; Rangel et al., 2011; Ribeiro et al., 2012; Freitas et al., 2014).

6. Hybrids from inbred lines

One of the objectives of breeding programs involving popcorn, in the long-term, is to obtain hybrids from inbred lines, thus enabling the exploitation of hybrid vigor. Howeveer, the method generally used in obtaining homozygous inbred lines is artificial self-mating, generating depression by inbreeding depression (Lima et al., 1984; Simon et al., 2004; Scapim et al., 2006). Thus, the value of a population as a source of inbred lines is dependent on the inbreeding depression when compared to the various characteristics, especially yield, limiting the generation of superior inbred line for the subsequent establishment of vigorous hybrids (Lima et al., 1984; Arnhold et al., 2007).

For PE, the loss by inbreeding is lower than that of yield due to the lower genetic complexity of the characters and the predominance of additive effects resulting in a more outstanding contribution of loci being in homozygosity than loci in heterozygosity for this trait (Dofing et al., 1991; Pacheco et al., 1998; Larish & Brewbaker, 1999; Miranda et al., 2008; Arnhold et al., 2010). For example, Simon et al. (2004) obtained inbreeding depression values of 27% for PE and 68% for yield.

In classics works carried out with popcorn, it was found that selection based on PE should be practiced during the phase of obtaining inbred lines (Vilarinho et al., 2002, 2003; Santos et al., 2004; Arnhold et al., 2007, 2009, 2010; Viana, 2009). The selection based in PE is feasible because crossings between high PE inbred lines tend to produce hybrids with high PE, while those between high and low PE inbred lines tend to produce hybrids with intermediate values (Lyerly, 1942; Pereira & Amaral Júnior, 2001; Simon et al., 2004; Scapim et al., 2006). Therefore, there should also be the selection of productive inbred lines decreasing the seed cost. However, simultaneous improvements to PE and yield characteristics are difficult due to the negative genotypic correlation (Bombonato et al., 2020). This obstacle can be circumvented by using selection indices (Coimbra et al., 2002; Granate et al., 2002). The use of top crosses hybrids in popcorn has been a good option for the breeders (Sawazaki et al., 2003; Pinto et al., 2004; Viana et al., 2007; Scapim et al., 2008; Barreto et al., 2012; Rodovalho et al., 2012; Lima et al., 2016; Miotto et al., 2016; Pena et al., 2016).

Another option for obtaining inbred lines is the use of haploid-inducing inbred lines. This technique obtains haploid individuals and subsequent genome duplication (Prigge & Melchinger, 2011).

7. Backcrossing

Backcrossing is a very efficient method for transferring characters of simple inheritance aiming to correct defects in an inbred line with desirable agronomic characteristics, and used as a recurrent parent (Miranda Filho & Viegas 1987).

It is common to introduce dent corn germplasm to increase several agronomic characteristics in popcorn. However, crossings between high and low PE plants tend to produce offspring with intermediate PE characteristics. The PE can be recovered by backcrossing with parents with high PE. Studies show that PE is recovered with few backcrossings due to its mode of inheritance.

8. Marker-assisted selection

The recurrent selection method has been used in breeding programs for many decades (Hallauer et al., 2010; Ribeiro et al., 2016). With improvements to techniques and the acquisition of new molecular markers, it became possible to improve this breeding technique further. The availability of genetic data for each generation in the selection process and its rapid development cycle make recurrent selection assisted by markers an excellent tool to identify the maximum possible genetic variation in most regions of the genome (Pereira et al., 2006; Berilli et al., 2011; Guimarães et al., 2018).

Coan et al. (2018) sought to identify genomic regions and possible candidate genes associated with resistance to ear rot caused by *Fusarium* spp. in 183 tropical and popcorn maize inbred lines, and a set of 267.525 SNP-type markers were obtained using genotyping by sequencing (GBS). In this work, fourteen significant SNPs associated with the disease explained 15% to 25% of the phenotypic variation observed.

9. Quantitative characteristics loci (QTLS) and popping expansion

Mapping QTLs can be a valuable tool to reduce the disadvantages of phenotype-based PE determination tests. In addition, the discovery of different QTLs for PE in different germplasm sources offers ample room for efficient approaches to the use of gene pyramiding and the employment of marker-assisted selection (Lu et al., 2003; Li et al., 2007b; Senhorinho et al., 2019).

To be considered good candidates for marker-assisted Selection, obtaining QTLs with good stability between populations and environments is desirable. However, it is possible to observe that some QTL, even if related to the same trait, present considerable inconsistency in different research settings. Therefore, some studies have tried to demonstrate which factors may affect the results of QTL mapping, for example, density and type of marker, population structure (Stuber et al., 1992), generation (Austin & Lee, 1996; Li et al., 2009), and environment (Li et al., 2003).

Table 5 presents several studies that sought to determine QTLs related to PE.

Additive variance seems essential in the expression of PE, being influenced by a small number of genes (Dofing et al., 1991; Larish & Brewbaker, 1999; Lima et al., 2019). In addition, QTLs related to high PE are located on different chromosomes (Amaral Júnior et al., 2016), and several studies indicate the presence of at least one QTL related to PE located on chromosome 1 (Lu et al., 2003; Babu et al., 2006; Li et al., 2007b). Once these molecular markers are validated, they will be helpful in marker-assisted selection and better understanding of popping expansion.

10. The use of new statistical techniques in popcorn improvement

Since 2000, researchers have been using more refined statistical techniques to genetically improve popcorn. These include the use of multivariate analysis AMMI (Miranda et al., 2003; Gonçalves et al., 2014), the use of BLUP (Viana et al., 2011, 2014; Freitas et al., 2013; Vittorazzi et al., 2017), the use of Bayesian statistics for analysis of genetic parameters of PE and yield in popcorn (Rodovalho et al., 2014; Schwantes et al., 2019), Bayesian clustering via Markov chains aiming at genetic diversity studies to identify different groups of popcorn for improvement (Saavedra et al., 2013; Silva et al., 2015), and Bayesian analysis of genetic parameters for quantitative traits in families of full-sib families of popcorn (Amaral Júnior et al., 2016).

Conclusions

When analyzing the current situation regarding popcorn cultivation in Brazil, it can be seen that the focus of breeding programs is to obtain hybrids from inbred lines with high PE and yield.

The consumption of popcorn by the Brazilian population is growing exponentially. The genetic improvement performed in Brazil has presented significant advances over the years, mainly due to work developed in public institutions with new hybrids that present more outstanding PE and yield. However, the number of cultivars is still low, and most of them are controlled by private companies.

Intrapopulation methods are recommended to

Table 5. QTL mapping studies for the trait PE in popcorn.

Reference	Number of QTL's	Phenotypic variation explained (%)
Lu et al. (2003)	4	45
Babu et al. (2006)	4	62
Li et al. (2007b)	6	54
Li et al. (2009)	4	-
Senhorinho et al. (2019)	4	-
Thakur et al. (2021)	3	78

develop open-pollinated varieties with high popping expansion.

Popping expansion can be an early predictor of promising inbred lines to obtain superior hybrids for popping expansion.

Popping expansion is quickly recovered in backcrosses involving the cross of common maize with an inbred popcorn line.

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