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The effect of genotype x pollination mode interaction on kernel modification in quality protein maize (QPM) genotypes

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Abstract

Kernel vitreousness or texture is one of the most important prerequisites for successful adoption of the Quality Protein Maize (QPM) genotypes by the farmers. The present study was carried out to analyze in detail the effects of pollination mode (controlled- versus open-pollination) on different kernel attributes (endosperm modification, crown modification and ear appearance) in a set of QPM inbred lines and their experimental crosses. QPM genotypes were found to differ significantly with respect to kernel modification, indicating genetic heterogeneity for endosperm modifier genes. Analysis of ears obtained from different pollination modes indicated significant interaction of the genotypes with the pollination mode, suggesting the importance of the source of pollen and its genetic constitution in conferring the kernel texture. The study also demonstrates that the data derived using controlled-pollination could be more reliable than those using the open-pollination mode for analyzing the effects of complementation of endosperm modifier genes in QPM cross combinations. Ascertaining the kernel modification potential of the QPM genotypes would aid in proper selection of genotypes during QPM breeding.

Key words: Endosperm modification, QPM, maize, pollination mode, interaction effects

Introduction

The average protein content in the maize kernel is about 9-10%, which is intermediate between rice and wheat [1]. The endosperm constitutes bulk of the grain, thereby contributing as much as 80% of the total kernel protein. However, the endosperm proteins are particularly deficient in two essential amino acids, lysine and tryptophan [2]. Therefore, healthy diets for monogastric animals, including humans, must include alternate source of these amino acids [3].

The *opaque2,* a recessive mutant, alters the amino acid composition of the endosperm protein, resulting in enhanced concentration of lysine and tryptophan [4]. In India, three *opaque2* composites, namely Shakti, Rattan and Protina were released under the All-India Coordinated Research Project (Maize) during 1970s. However, negative pleiotropic effects of this mutation, namely soft endosperm, low yield and increased susceptibility to insect-pests and pathogen, coupled with mechanical damage due to soft and chalky kernel texture, led to the non-preference of these cultivars by the farming community [5]. Later, breeders at CIMMYT (International Wheat and Maize Improvement Center), Mexico, successfully combined the high-lysine potential of *opaque2* with the genetic endosperm modifiers, releasing new maize genotypes, which are collectively referred to as “Quality Protein Maize” (QPM) [1, 5].

Kernel modification in QPM genotypes is quantitatively inherited and was found to be dosage-dependent [1] with significant genotype x environment interaction [6]. Endosperm hardness and the degree of kernel vitreousness were correlated with increased synthesis of gamma-zein [7] in the endosperm. Several reports [6, 8-10] indicated preponderance of additive gene action for kernel modification. Due to the complex genetic control of kernel modification and lack of reliable molecular markers linked to endosperm modifier genes, the only effective approach at present is to physically screen the kernels using a ‘light box’ for identification of promising QPM genotypes with desirable kernel modification attributes. Information regarding the kernel modification is essential for breeders to utilize the QPM germplasm effectively in the breeding programmes.

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The objectives of the present study were (i) to analyze the variability of kernel modification in a selected set of elite QPM lines (developed in India and at CIMMYT, Mexico) and their hybrid combinations, and (ii) to explore the possible effects of the pollination mode (controlled- versus open-pollination) on the kernel modification in the QPM genotypes.

Materials and methods

Genetic materials

The genotypes selected for the study comprised (i) a set of 14 QPM inbred lines, of which 13 were developed from high-lysine *opaque2* composites, such as Shakti-1, developed by Directorate of Maize Research (DMR), New Delhi, under the All-India Coordinated Research Project (Maize); these lines were designated as 'DMRQPM' lines, and (ii) three elite QPM inbred lines developed at CIMMYT, Mexico [designated as 'CML' (CIMMYT Maize Line)]. Details about the pedigree and source(s) of these inbred lines are provided in Table 1.

To analyze the complementation effects of kernel modifier genes from different parents, experimental crosses were derived using Line x Tester (L x T) mating design [11]. A L x T (14 x 3) set, comprising a selected set of CMLs as testers and a set of DMRQPM inbreds as lines, was analyzed for various kernel modification attributes.

Field evaluation

The QPM crosses, along with the parents, were evaluated in a trial at the IARI Experimental Farm, New Delhi, during *kharif* (monsoon season) 2003, in a randomized complete block design with three replications per entry. Plots were 5-m rows, spaced 75 cm apart. 'Shakti-1' was used as a QPM check. The same set of experimental material was maintained in two trials: one in open-pollination mode and another through controlled-pollination (bulk-sibbing). The trial was isolated from the normal-endosperm maize by time of planting and by QPM border rows. Standard agronomic practices were followed, and the material was hand-harvested.

Analysis of kernel modification

Kernel modification of the QPM genotypes including the hybrids and their parental lines (involved in the L x T set) were rated, using a procedure suggested by Bjarnason and Vasal [1]. Three attributes of kernel modification, namely (a) endosperm modification (extent of opaqueness in the entire endosperm), (b) crown opaqueness (presence of opaqueness only on the crown region of the kernel), and (c) ear appearance (in terms of opaqueness/vitreousness) were evaluated in each genotype. For analysis of endosperm modification, the backlit kernels were rated on a scale of 1-5, with 1 indicating 100% normal (vitreous), 2 indicating 25% opaque, 3 indicating 50% opaque, 4 indicating 75% opaque, and 5 indicating 100% opaque (Fig. 1A). Endosperm modification scores were derived based on analysis of 100 randomly chosen kernels from the ears of QPM genotypes. The number of kernels rated in a specific each class was multiplied by its corresponding rank (1, 2, ...5), and the values so obtained were summed up to derive a cumulative score. Crown opaqueness was evaluated in terms of percent kernels showing crown opaqueness when screened using the back-lit procedure. The ears were also rated on a scale of 1-5, with 1 indicating 0% opaque kernels in an ear, 2 indicating 25% opaque kernels, 3 indicating 50% opaque kernels, 4 indicating 75% opaque kernels and 5 indicating 100% opaque kernels.

Statistical analysis

The data were analyzed for ANOVA, and LSD (Least Significant Difference) was determined to rank the genotypes based on the kernel modification, using SAS Version 6.12. Cumulative index of kernel modification, using the scores for the three different kernel modification attributes, for each genotype was computed, following the procedure suggested by Arunachalam and Bandopadhyay [12].

Results and discussion

ANOVA revealed significant differences among the QPM genotypes for the three kernel modification attributes namely endosperm modification, crown modification and ear appearance (Table 2), indicating genetic heterogeneity with respect to endosperm modifier genes in the QPM genotypes under study. The study also showed that the effects of 'lines', 'testers' as well as 'line x tester' were significant for all the three kernel modification attributes, indicating considerable variability among the lines as well as testers for kernel texture. Significant 'line x tester' interaction reveals that the different lines and testers have contributed complementary endosperm modifiers. An analysis of contributions of 'lines', 'testers' and 'line x testers' to the overall variation indicated that for all the three traits (considering both open- and controlled-pollinations), the 'line x tester' contribution was the highest (around 50%), suggesting the importance of genetic complementation of kernel modifier genes in the QPM cross combinations.

Table 1. Pedigree and source of the QPM inbred lines used in the present study

S. No.	Genotypes	Pedigree	Source of seed material	Grain type
1.	DMRQPM-17-1	28 full sib families (MS) 6 HECC Bulk-1	DMR, New Delhi	YF
2.	DMRQPM-17-4	28 full sib families (MS) 6 HECC Bulk-4	-do-	YF
3.	DMRQPM-28-3	Shakti (SO) HE 25 # CC Bulk 50 % f-#-⊗-1-3-4 ⊗ BB-3	-do-	YF
4.	DMRQPM-28-5	Shakti (SO) HE 25 # CC Bulk 50 % f-#-⊗-1-3-4 ⊗ BB-5	-do-	YF
5.	DMRQPM-45	Rattan SOHS 47 # SO # SN CC 25%-f-###	-do-	YF
6.	DMRQPM-56	SN Comp. Bulk SN5 CC Bulk ⊗-12-1-BB	-do-	YF
7.	DMRQPM-58	SN Comp. Bulk 2 Bulk SN5 CC Bulk ⊗-16-4-BB	-do-	YF
8.	DMRQPM-60	28 full sib families (MS) 6 HECC Bulk ⊗-15-1-BB	-do-	YF
9.	DMRQPM-65	SO/SN Comp. Category 'O' ⊗-1-1-B-B	-do-	YF
10.	DMRQPM-401	28 full sib families (MS) 6 HECC Bulk ⊗-1-4-BBBB	-do-	YF
11.	DMRQPM-402	28 full sib families (MS) 6 HECC Bulk 2 ⊗-16-4-BBBB	-do-	YF
12.	DMRQPM-403	Shakti SO/SN HE 25 CC Bulk 50 % f-#- #-10-3-B-1-B	-do-	YF
13.	DMRQPM-404	SO/SN Comp Bulk 2 Bulk SN5 CC Bulk 2 ⊗-16-4-BBBB	-do-	YF
14.	Tuxpeno Carrib.	Tuxpeno Carrib. HE/o2 -f-#- #-⊗-4-⊗	-do-	WF
15.	CML166	Pob66c1HC215-4-1-2-B-B-2-B-B-B	CIMMYT, Mexico	YF
16.	CML167	G25QSINT-37-3-2-2-B-B	-do-	YF
17.	CML189	G34QMH17-2-1-1-B	-do-	YF
18.	Shakti-1	Selection from Shakti composite	DMR, New Delhi	YF

YF: Yellow flint; WF: White flint

Table 2. ANOVA of kernel modification attributes of the QPM genotypes

Sources of variation	d.f.	Mean sum of squares		
		EM	CM	EA
Pollination mode	1	0.2735	0.0007	1.0197*
Replication	2	0.1352	0.0020	0.5536
Genotypes	58	2.8029**	0.0441**	1.2262**
Pollination mode x genotype	58	0.5792**	0.0328**	0.6059**
Error	234	17.5999	0.0040	0.2317

d.f.: degrees of freedom; EM: endosperm modification; CM: crown modification; EA: ear appearance; *Significant at P = 0.05; ** Significant at P = 0.01

A comparison of the mean values for various attributes revealed better kernel texture for majority of the QPM inbred lines and their experimental crosses over the QPM 'check' Shakti-1 (Table 3). Since most of the DMRQPM lines were isolated from Shakti-1, the results suggest that selection procedures led to accumulation of favourable combinations of endosperm modifier genes in the DMRQPM lines. However, none of the QPM lines exhibited complete kernel vitreousness, indicating significant scope for further accumulation of favourable endosperm modifiers in the QPM inbred lines, as was also reported by Kassahun and Prasanna [13].

An important objective of the present study, which was hitherto not explored in previous experiments on QPM, was to ascertain the effects of pollination mode on various kernel modification attributes. The analysis clearly revealed that pollination mode (open vs. controlled) alone had no significant effects on endosperm modification and crown opaqueness, except on ear appearance (Table 2). However, there was a significant interaction of the pollination mode with the genotypes in influencing kernel modification attributes. For instance, among the inbred lines, CML189 (1.08), DMRQPM-403 (1.38) (Fig. 1B & C), DMRQPM-65 (1.38) (Figs. 1B & C) and DMRQPM-56 (1.45) showed excellent endosperm modification under controlled-pollination, as compared to the open-pollination mode (Table 3). Similar pattern was observed for the crosses, DMRQPM-403 x CML166, DMRQPM-28-5 x CML167, DMRQPM-403 x CML189, and DMRQPM-45 x CML189.

In contrast, DMRQPM-404 x CML167 (2.63), DMRQPM-17-1 x CML167 (1.63) and DMRQPM-58 x CML189 (2.05) exhibited more vitreousness in the endosperm under open-pollination than under controlled-pollination. However, the rest of the genotypes showed comparable endosperm modification under both the pollination modes.

Among the kernel modification attributes, the ear appearance and crown modification have direct and visible effect, thereby impacting consumer acceptance of the genotype. Therefore, proper selection of genotypes not only for endosperm modification but also for crown modification and ear appearance assumes importance. In the present study, DMRQPM-403 (0.03) and CML166 (0.03) showed better crown modification, followed by DMRQPM-56, DMRQPM-404, DMRQPM-402, DMRQPM-58, CML167 and Tuxpeno Carrib., under controlled-pollination. The crown modification scores of some genotypes, such as DMRQPM-56 (0.04), DMRQPM-60 (0.09), DMRQPM-402 (0.04) and Tuxpeno Carrib. (0.04), were relatively better under controlled-pollination than under open-pollination (Table 3). Similar trend was also observed in case of QPM crosses like DMRQPM-401 x CML166, DMRQPM-401 x CML189, DMRQPM-404 x CML189, DMRQPM-65 x CML189, and DMRQPM-17-1 x CML189. However, a reverse pattern was observed in case of DMRQPM-28-5, DMRQPM-401 x CML167, DMRQPM-404 x CML167 and DMRQPM-28-5 x CML189 wherein ears from open-pollination revealed better crown modification than those from the controlled-pollination.

In case of ear appearance, the interaction between genotypes and the pollination modes was again clearly apparent. For instance, DMRQPM-60, DMRQPM-401, DMRQPM-402, and DMRQPM-17-1 exhibited better ear modification under controlled-pollination than under open-pollination. Conversely, ears from open-pollination revealed better modification in case of DMRQPM-404 x CML167, DMRQPM-401 x CML167, and Tuxpeno Carrib. x CML189 than under controlled-pollination.

Cumulative indices for kernel modification computed for the genotypes, based on LSD ranks for the individual attributes, indicated CML166 (2.71) and CML167 (2.81) as the best inbreds among the CIMMYT inbred lines. Several DMRQPM lines displayed high kernel opaqueness (Table 3). DMRQPM-403 was found to be highly promising for kernel texture. The effects of specific testers (CML166, CML167 and CML189) on kernel modification attributes on the common set of 14 DMRQPM genotypes (lines) were also analyzed. The mean CI values for CML166-based, CML167-based and CML189-based QPM crosses under controlled- and open-pollination modes were 2.09 and 2.27, 1.43 and 1.59, and 1.71 and 1.65, respectively. Thus, the analysis revealed that in crosses with DMRQPM, better complementary combination of endosperm modifiers could be derived using CML166, as compared to CML167 and CML189.

Among the QPM hybrids, DMRQPM-45 x CML166 showed the highest cumulative index (Table 3) both under controlled-pollination (2.86) as well as open-pollination (3.00), indicating that the genotype has an excellent combination of endosperm modifier genes, and under open-pollinated conditions, the foreign pollen had little effect. The influence of pollination mode x genotype interaction could be particularly discerned in the QPM crosses (Table 3). For example, DMRQPM-404 x CML167 exhibited a high cumulative index (CI) of 2.27 under open-pollination, but the same performed poorly (CI = 0.56) under controlled-pollination. Similar trend was also observed in case of DMRQPM-17-1 x CML167, and Tuxpeno Carrib. x CML189. In contrast, DMRQPM-403 x CML189 showed high cumulative index (2.36) under controlled-pollination, while the kernel modification was relatively lower (CI = 1.99) under open-pollination (Table 3).

High kernel modification or vitreousness in the QPM kernels derived through controlled-pollination could be attributed to the accumulation and complementation of favourable endosperm modifiers (particularly in case of QPM crosses). In cases where the CI for kernel modification was significantly reduced in a QPM genotype under open-pollination as compared to controlled-pollination, there could have been dilution of the effects of favourable endosperm modifier genes, since kernel modification is polygenic and dosage-dependent. In contrast, in those cases where the QPM genotypes exhibited better kernel vitreousness under open-pollination than under controlled-pollination, the plausible explanation could be that these genotypes derived favourable endosperm modifiers from other QPM genotypes in the vicinity. Studies undertaken so far to understand kernel modification in QPM genotypes were primarily based on open-pollinated QPM trials that were spatially/temporally isolated from the normal (non-QPM) maize [6, 10, 14]. Pixley and Bjarnason [15] reported no significant xenia effect, while Wessel-Beaver and Lambert [8] indicated the presence of xenia effect in an experiment involving S2 lines derived from a modified-*o2* synthetic.

Table 3. Mean values for kernel modification attributes of selected QPM genotypes

S. No.	Genotypes	EM		CM		EA		CI	
		C	O	C	O	C	O	C	O
1	DMRQPM-56	1.45	2.63	0.046^{II}	0.223	2.00^{III}	2.00	2.19	1.37
2	DMRQPM-60	2.95	3.09	0.096	0.553	2.00^{III}	4.00	1.61	0.18
3	DMRQPM-401	3.12	3.13	0.326	0.373	2.00^{III}	3.33	0.94	0.46
4	DMRQPM-28-3	1.63	2.22	0.076	0.190	2.00	2.66	1.88	1.34
5	DMRQPM-403	1.38	2.67	0.033^{I}	0.010^{I}	1.33^{I}	1.33^{II}	2.66	2.04
6	DMRQPM-404	3.25	2.41	0.076^{III}	0.013^{II}	1.66	1.33^{II}	1.71	2.18
7	DMRQPM-402	3.27	3.09	0.043^{II}	0.166	2.00^{III}	3.00	1.66	0.92
8	DMRQPM-58	2.63	2.77	0.040^{II}	0.053	1.33^{I}	1.66^{III}	2.17	1.77
9	DMRQPM-65	1.38	2.95	0.086	0.093	2.00^{III}	2.33	2.16	1.41
10	DMRQPM-17-4	3.22	2.69	0.120	0.036^{III}	2.00^{III}	1.66^{III}	1.41	1.86
11	DMRQPM-17-1	3.16	3.09	0.203	0.446	2.33	3.66	0.99	0.32
12	DMRQPM-28-5	3.61	2.54	0.180	0.033^{III}	2.00^{III}	1.66^{III}	1.11	1.99
13	DMRQPM-45	3.04	2.68	0.123	0.123	2.66	2.00	1.13	1.52
14	Tuxpeno Caribb	1.45	1.89^{III}	0.040	0.226	1.33^{I}	2.00	2.53	1.59
15	CML166	1.34^{III}	1.71^{II}	0.033^{I}	0.030^{III}	1.33^{I}	1.66^{III}	2.71	2.45
16	CML167	1.20^{II}	1.49^{I}	0.046^{II}	0.066	1.33^{I}	1.33^{I}	2.81	2.51
17	CML189	1.08^{I}	2.13	0.096	0.030^{III}	2.00^{II}	2.00	2.33	2.03
18	DMRQPM-56 x CML166	1.36	1.59	0.023^{2}	0.053	1.66^{2}	1.66^{3}	2.58	2.45
19	DMRQPM-401 x CML166	1.26^{3}	1.35^{3}	0.066	0.240	2.00^{3}	2.66	1.92	1.68
20	DMRQPM-28-3 x CML166	1.36	1.25^{2}	0.046	0.000^{1}	1.33^{1}	1.00^{1}	2.64	2.95
21	DMRQPM-403 x CML166	1.00^{1}	1.59	0.030^{3}	0.010^{2}	2.00^{3}	1.33^{2}	2.57	2.67
22	DMRQPM-58 x CML166	1.32	1.54	0.013^{1}	0.060	2.00^{3}	2.33	2.49	2.25
23	DMRQPM-65 x CML166	1.50	2.15	0.040	0.076	1.66^{2}	2.00	2.31	1.95
24	DMRQPM-17-4 x CML166	1.27	1.43	0.023^{2}	0.036	2.00^{3}	1.66^{3}	2.47	2.51
25	DMRQPM-45 x CML166	1.23^{2}	1.00^{1}	0.020^{2}	0.000^{1}	1.33^{1}	1.00^{1}	2.86	3.00
26	DMRQPM-401 x CML167	1.60	1.77	0.380	0.090	2.00^{3}	1.66^{3}	1.26	2.28
27	DMRQPM-404 x CML167	4.13	2.63	0.496	0.000^{1}	2.33	1.00^{1}	0.56	2.27
28	DMRQPM-17-1 x CML167	2.32	1.63	0.290	0.110	2.33	2.00	0.99	2.15
29	DMRQPM-28-5 x CML167	1.45	2.07	0.110	0.160	2.00^{3}	2.66	1.95	1.52
30	DMRQPM-45 x CML167	1.44	1.90	0.050	0.053	1.66^{2}	2.00	2.39	2.13
31	DMRQPM-56 x CML189	1.63	1.80	0.150	0.043	2.33	1.33^{2}	1.47	2.46
32	DMRQPM-60 x CML189	1.56	1.94	0.136	0.016^{3}	2.00^{3}	1.33^{2}	1.75	2.36
33	DMRQPM-401 x CML189	2.90	2.77	0.056	0.276	3.00	2.33	1.30	0.93
34	DMRQPM-403 x CML189	1.00^{1}	2.15	0.096	0.053	2.00^{3}	2.00	2.36	1.99
35	DMRQPM-404 x CML189	3.22	2.95	0.043	0.250	2.00^{3}	2.66	1.66	0.83
36	DMRQPM-402 x CML189	3.16	3.09	0.030^{3}	0.023	1.33^{1}	1.33^{2}	2.07	1.82
37	DMRQPM-58 x CML189	3.35	2.05	0.056	0.140	2.00^{3}	2.66	1.64	1.60
38	DMRQPM-65 x CML189	3.00	2.43	0.063	0.193	1.66^{2}	2.00	1.88	1.50
39	DMRQPM-17-4 x CML189	3.11	2.78	0.026^{3}	0.223	2.00^{3}	3.00	1.76	0.89
40	DMRQPM-17-1 x CML189	3.24	2.65	0.026^{3}	0.056	2.33	2.33	1.54	1.66
41	DMRQPM-28-5 x CML189	3.62	3.06	0.470	0.070	1.66^{2}	2.00	0.95	1.54
42	DMRQPM-45 x CML189	1.39	2.63	0.040	0.053	2.33	2.00	2.09	1.81
43	Tuxpeno Carrib. x CML189	3.38	2.77	0.213	0.013^{3}	3.00	1.33^{2}	0.56	1.95
44	Shakti-1 (QPM check)	3.39	3.54	0.362	0.423	2.66	3.00	-	-

EM: Endosperm modification; CM: Crown modification; EA: Ear appearance; CI: Cumulative Index; O: Open-pollination; C: Controlled-pollination; I, II, III: LSD ranking among inbred lines; 1, 2, 3: LSD ranking among experimental crosses

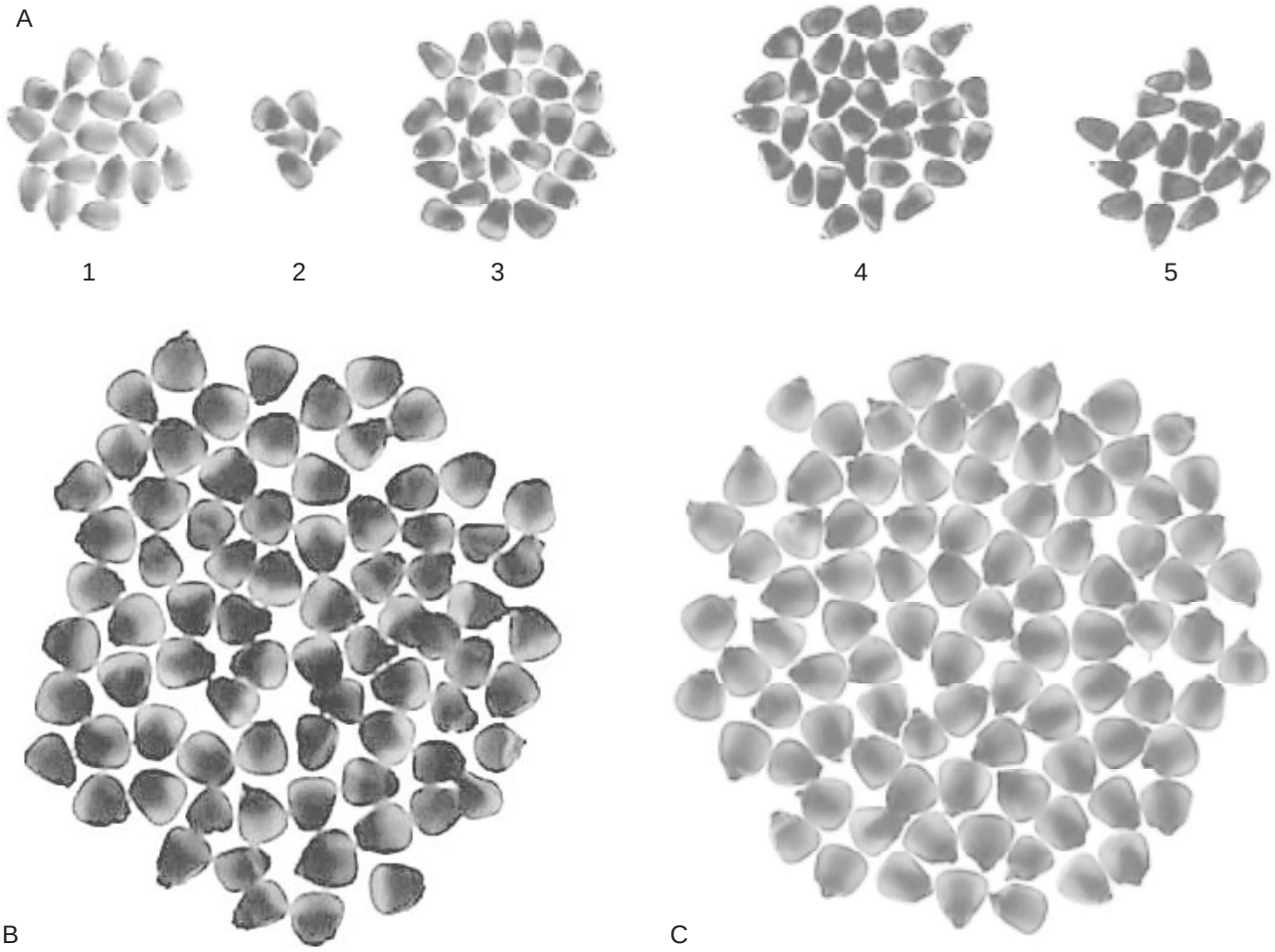

Fig. 1. (A) Kernels from DMRQPM-65 x CML189 (derived from controlled-pollination) displaying all possible range of endosperm modification (1: 100% modified; 2: 25% opaque; 3: 50% opaque; 4: 75% opaque and 5: 100% opaque); (B) DMRQPM-403 kernels from open-pollination exhibiting approximately 50% endosperm modification, while (C) kernels of the same genotype from controlled-pollination showing almost complete modification.

The interaction of genotypes with the pollination mode on the expression of kernel modification in QPM genotypes has two major implications. Firstly, once the breeder identifies a promising QPM cross combination, the entry is further tested for yield, agronomic performance and quality traits, besides kernel texture. For yield, agronomic performance and kernel texture, the data is presently based on an open-pollinated trial, while for quality traits, ears derived from controlled-pollination are tested. The same practice is also being followed for multi-location testing of QPM hybrid entries under the All-India Coordinated Trials. The present study clearly indicates that the practice of using open-pollinated ears for analysis of kernel texture could lead to misleading conclusions about the genotypic potential. Secondly, due to the size scale as well as genetic uniformity, the open-pollination of a maize genotype in a farmer's field is akin to the controlled-pollination of a genotype in the breeder's plot. In such conditions, if a specific QPM hybrid has better potential for kernel modification under open-pollination than under controlled-pollination, and if such a hybrid is released for commercial cultivation, there would be a problem with respect to kernel texture due to the reason mentioned above. However, if a QPM hybrid has better potential for kernel modification under controlled-pollination than under open-pollination, release of such a hybrid for commercial cultivation would not have an

adverse impact since most of the ears will show good modification, except those harvested from the border rows where the chances of foreign pollen contamination is higher.

Therefore, to ascertain the proper potential for kernel modification in the QPM genotypes, particularly cross combinations, it is important that the breeder first compare the data from controlled-pollination *vis-a-vis* the data from an open-pollinated trial, before the entry is tested in multiple locations. The same set of ears (derived by controlled-pollination) under Coordinated Trials at different locations for testing of kernel quality of QPM genotypes can also be effectively utilized for ascertaining the potential for kernel texture. In conclusion, the present study led to (i) analysis of the genetic variability in the QPM lines (DMRQPM and CIMMYT QPM) with regard to kernel modification attributes; and (ii) identification of promising QPM hybrids, such as the DMRQPM-45 x CML166 with excellent potential for kernel modification. Also, the study highlighted the distinct effect of interaction between genotype and pollination mode on the kernel modification attributes in QPM genotypes, and the need for proper analysis of kernel modification potential of QPM hybrids before their release for commercial cultivation.

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