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SEED VIGOR, AGING, AND OSMOPRIMING AFFECT ANION AND SUGAR LEAKAGE DURING IMBIBITION OF MAIZE (*ZEA MAYS* L.) CARYOPSES

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Conductivity was significantly increased by aging and decreased by osmopriming of maize (*Zea mays* L.) caryopses. Chloride, phosphate, and sulfate were the main anions that leaked out of maize seeds; their leakage was closely related to conductivity, increased by aging, and decreased by osmopriming. The anion leakage of isolated embryos correlated closely to seed vigor and was more sensitive to aging and priming than that of the whole seed. Anion leakage may be a more sensitive measure for seed vigor than bulk conductivity readings. Aging did not increase the sugar leakage of whole seeds but significantly increased the sugar leakage of isolated embryos. Sugar leakage was not closely related to total soluble sugar content of seeds. While priming decreased seed conductivity, the decreased anion and sugar leakage of the primed seeds was mainly caused by the washing effect during priming. The total anions or sugars left in the polyethylene glycol (PEG) solution after priming and in the conductivity solution of the primed seeds was almost the same as in the conductivity solution of the unprimed seeds alone.

Keywords: anion leakage, sugar leakage, *Zea mays* L., maize, aging.

Introduction

As seeds take up water during imbibition, there is rapid leakage into the surrounding medium of solutes such as sugars, organic acids, ions, amino acids, and proteins. The rate of this leakage can be used to express the degree of cell membrane damage and repair in response to aging (Simon 1974; Pearce and Samad 1980). Electrical conductivity measurements of seed leachates are routinely used to determine seed vigor in a number of species (Pandey 1992; Hampton and TeKrony 1995).

Ion leakage (e.g., K^+, Mg^{2+}, Cl^-, Ca^{2+}, and Mn^{2+}) has been shown to relate to seed viability and vigor (Lott et al. 1991; Dias et al. 1996; Rehman et al. 1999). However, there are few data on the detailed composition of seed electrolyte leakage, especially that of anions. There are also few experiments in which leakage from embryos and endosperm has been studied separately (Simon 1974). Larson (1968) reported that isolated embryos of pea (*Pisum sativum* L.) leaked more rapidly than intact seeds, but it is not clear whether the electrolyte leakage of endosperm and the embryo are equally important to seed vigor. Leakage of sugars is considered a less reliable index of membrane integrity than the leakage of electrolytes (Simon 1974). Abdul-Baki and Anderson (1970) concluded that sugar measurement was not a reliable index for barley (*Hordeum vulgare* L.) seed viability. However, there are few experiments where sugar composition has been analyzed in detail, so it is still not clear whether all the sugars or only some special sugars correlate to seed vigor. It is also not clear if sugar leakage from the embryo and endosperm are equally important for seed vigor.

Osmotic priming is widely used to improve seed quality. Priming decreases solute leakage during seed imbibition (Chojnowski et al. 1997). The composition and quantity of membrane phospholipids may also change during priming (Basra et al. 1988). However, it is uncertain whether the reduction in electrolyte leakage is caused by changes in membrane structure or simply by washing electrolytes from seeds during priming (Welbaum et al. 1998).

More than 10 anions and 10 soluble sugars of whole maize grains and isolated embryos were measured separately in this study. The objectives were: (1) to understand better the effects of seed vigor, aging, and osmopriming on anion and sugar leakage during imbibition; (2) to see if leakage of whole seeds and embryos was equally important for seed vigor; (3) to determine the relationship between the leakage of anions, sugars, and conductivity; and (4) to test the hypothesis that the decreased leakage of primed seeds was mainly caused by washing effects.

Material and Methods

Seed Lots

Five untreated dent maize seed lots (3697-25, 3697-2, 296, 188, and 3697-61) were kindly provided by the Dutch seed company Advanta. They were renamed in order of increasing seed vigor as A (low), B, C, D, and E (high), according to the results of cold germination test at 10°C (table 1). The seed vigor of seed lot A was significantly lower than that of the others, but the other seed lots were not significantly different. Standard germination tests were applied to all seed lots according to the International Seed Testing Association (1996).

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Table 1

Germination Percentage and Seedling Length of Five Maize Seed Lots (A–E) Germinated at 10°C for 11 d

	A	B	C	D	E
Germination (%)	86.2 ± 3.4	88.7 ± 3.2	90.9 ± 2.3	94.1 ± 2.6	97.5 ± 1.0
Seedling length (mm)[a]	26.4 ± 4.6	32.9 ± 4.2	33.2 ± 5.4	35.2 ± 5.8	37.7 ± 3.5

[a] From root tip to shoot crown.

Artificial Aging

Artificial aging was applied to all seed lots. Seeds (500) were put on plastic plates (20 × 12 cm^2) and incubated at 40° ± 1°C in a saturated atmosphere (100% RH) for 4 d. These aged seeds were named by adding "-4" after their original name (e.g., E-4). Some seeds of seed lots C and D were artificially aged at 40° ± 1°C and 100% RH for 12 d. They were named C-12 and D-12. After aging, the seeds were dried at 20°C in moving air for 2 d. Seed moisture content was determined before and after artificial aging plus drying (International Seed Testing Association 1996) and was about 10% on a dry-weight basis for all the seed lots.

Seed Osmopriming

Seeds were primed by immersing in −1.5 MPa PEG 6000 solution (Michel 1983) and incubating at 20°C for 24 h, then rinsed with distilled water and redried at 25°C in moving air for 2 d. The final moisture contents were equilibrated to about 10% dry weight. These seeds were named by adding "p" after the original name (E-4p).

Conductivity Test

Three replicates of 50 preweighed seeds of each seed lot were soaked in 250 mL of deionized water in plastic cups covered with caps to prevent evaporation loss and entry of foreign matter. A cup of deionized water without seeds was prepared as the control. All the cups were incubated at 20°C for 24 h. Conductivity was measured with an electrical conductivity meter (model-P310, Bentley, United Kingdom). The results were expressed on a seed or embryo dry-weight basis (μS/cm/g).

Anion and Sugar Analysis

The anion and sugar contents were determined for the imbibition solutions after the conductivity test of whole seeds, the PEG solutions used to prime the seeds, and the imbibition solutions of isolated embryos. For the latter, four replicates of 10 preweighed embryos were surgically isolated from dry seeds without damage, and their surfaces were cleaned with tissue paper. These four were next submerged in 10 mL deionized water in covered plastic tubes at 20°C for 24 h.

All the solutions were centrifuged at 14,000 *g* for 10 min, and 200 μL of the supernatant was transferred to small tubes. Thirteen anions (chloride, phosphate, citric, succinic/malic, sulfate, oxaloacetic, nitrate, isocitric, glutamic, α-ketoglutaric, oxalic, fumaric, and cis-aconitic anions) and 10 soluble sugars (glucose, fructose, sucrose, raffinose, arabinose, melezitose, trehalose, stachyose, rhamnose, and L-serine) were determined at 18° ~ 20°C using a Dionex DX500 chromatography system with PeakNet computer software (Dionex, PeakNet version 3.0, Sunnydale, Calif.). Anion and sugar contents were determined according to the known standards and expressed on seed or embryo dry-weight basis.

For the determination of total soluble sugars, whole seeds and isolated embryos were ground in liquid nitrogen. The ground tissue (50 mg) was suspended in 50 mL of 95% (v/v) alcohol and incubated in a water bath at 80°C for 1 h, then centrifuged at 14,000 *g* for 10 min, and the sugars were determined by the method above.

Statistical Analysis

The statistical significance of the differences between seed lots and treatments was determined using SPSS (SPSS). Germination data were arcsine transformed before analysis.

Results

Conductivity and Germination

There were significant differences in both conductivity and germination percentage among the seed lots (table 2). The conductivity of low-vigor seed lot A was significantly higher than

Table 2

Conductivity and Germination Percentage of Maize Seeds Tested at 20°C

Seed lot	Conductivity (μS/cm/g)	Germination (% ± SD)
A	20.70^{**}	93.2 ± 3.6
B	15.32	94.5 ± 2.6
C	15.05	94.0 ± 3.5
D	16.24	96.0 ± 1.6
E	16.72	98.7 ± 1.4
A-4	21.29^{**}	90.5 ± 5.8
B-4	18.08^{*}	90.0 ± 3.7
C-12	19.64^{**}	89.0 ± 4.1
D-12	20.77^{**}	88.0 ± 2.3
E-4	17.73^{*}	92.0 ± 2.6
A-p	11.22^{*}	92.0 ± 2.9
B-p	9.98	93.0 ± 2.2
C-p	13.20^{**}	89.0 ± 3.4
D-p	9.05	96.0 ± 1.8
E-p	7.99	96.0 ± 1.6
B-4p	10.58^{*}	88.0 ± 4.2
C-12p	14.51^{**}	85.0 ± 5.3
D-12p	9.84	91.0 ± 3.2

Note. Tukey *b*-test after ANOVA. Multiple comparisons were made among the primed and unprimed seeds separately. A–E are original seed lots; A-4 through D-12 are aged seeds; and A-p through D-12p are primed seeds.

* $P < 0.05$.

** $P < 0.01$.

that of the other seed lots ($P < 0.01$). Artificial aging increased the conductivity and decreased the germination percentage of all the seed lots. Compared with the unaged seeds, the mean conductivity of the aged seed lots increased 16.04% (significant at $P < 0.01$), and the germination percentage decreased 5.98%. Higher-vigor seed lots were more sensitive to aging; after aging, the conductivity of higher-vigor seed lot (B-4 and E-4) was increased more. Their germination percentage was decreased more than that of lower-vigor seed lot (A-4), but the conductivity of A-4 was still significantly higher than that of B-4 and E-4. The negative correlation between conductivity and germination percentages of the unprimed seeds was significant ($r = -0.671$; $P < 0.05$).

The conductivity of the primed seeds was significantly lower than that of the unprimed seeds ($P < 0.01$). For the primed seeds, the conductivity of higher-vigor seed lot E-p is still significantly less than that of lower-vigor seed lot A-p. The conductivity of the aged seeds B-4p is also higher than that of unaged seeds B-p. Priming decreased the conductivity of the aged seeds more significantly than that of the unaged seeds (table 2). There was no clear difference between the germination percentages of primed seeds and unprimed seeds of the same seed lot.

Anion Leakage of Whole Seeds

Chloride, phosphate, and succinic/malic anions were the main anions that leaked out of maize seeds during imbibition and that showed significant differences between seed lot A and E (table 3). For seed lots A and E, the total anion leakage of their aged seeds was significantly higher than that of the unaged seeds and that of the primed seeds was significantly lower than that of the unprimed seeds ($P < 0.01$). The leakage of chloride and phosphate anions showed the same situation for the aged and primed seeds and that of seed lot A was significantly higher than that of seed lot E. Succinic and malic acid were different; their leakage of seed lot E was more than that of seed lot A. Oxalic/acetic anion was not found in the imbibition solution of seed lot E. The correlation between the conductivity and the total anion leakage of whole maize seeds was significant ($r = 0.907$; $P < 0.01$). The correlation coefficients of the conductivity and the anions of chloride, phosphate, and isocitric acid were highly significant ($P < 0.01$), but the correlation of conductivity and the other anions were not significant.

Anion Leakage of Isolated Embryos

The correlation coefficients of the conductivity of whole seeds and the leakages of phosphate, chloride, and sulfate anions and the total anions of the isolated embryos were significant ($P < 0.05$). All the anion leakages were significantly increased by aging and decreased by priming (table 4). The anion leakage of the isolated embryos of C-12 and D-12 was significantly more than that of C and D. For the anion leakage of the isolated embryos, the primed seeds C-12p and D-12p were less than half of the unprimed seeds C-12 and D-12 (significant at $P < 0.01$). The isolated embryos leaked more anions than the whole seeds. The phosphate anion consisted of 60%–70% of the total anion leakage of the isolated embryos and was about 50 times more than that of whole seeds. Sulfate anion leakage of the isolated embryos was about 40 times more than that of whole seeds, increased by aging and decreased by priming.

Sugar Leakage of Whole Seeds

The total sugar leakage of lower-vigor seed lot A was about 14% higher than that of seed lot E (significant at $P < 0.05$) for unaged and aged seeds (table 5). This difference was mainly caused by glucose and sucrose. But for the other sugars, including fructose, there were no clear differences between the two seed lots, even for their aged or primed seeds. The correlation of conductivity and sugar leakage of whole maize seeds was not significant ($r = 0.404$). The sugar leakage of maize seeds was significantly decreased either by aging or priming ($P < 0.01$). The sugar leakage of the aged seed lot A-4 and E-4 was significantly lower than their unaged seed lot A and E. The total sugar contents in the leachate of the primed seeds were less than half of the unprimed seeds. Trehalose and melezitose were not found in the leachate of primed seeds.

Table 3

Anion Leakage (μg/g DW) of Whole Maize Seeds

Seed lot	Chloride	Phosphate	Sulfate	Succinic/malic	Isocitric acid	Oxalic/acetic	Total anions ± SD[a]
A	111.6^{b*}	121.0^{**}	8.2	11.3	26.3	5.3	284.2^{*} ± 23.0
A-4	148.5^{**}	152.1^{**}	5.6	6.9	39.7^{*}	6.6	386.8^{**} ± 52.0
A-p	48.3	37.6	5.5	12.6	0.0	4.8	108.8 ± 32.0
E	67.6	75.1	11.0	74.1^{**}	27.2	0.0	255.0^{*} ± 17.0
E-4	93.8^{*}	116.1^{**}	8.8	105.0^{**}	41.0^{*}	0.0	354.8^{**} ± 58.0
E-p	33.3	57.8	5.1	19.3	0.0	0.0	115.5 ± 22.0
$r^{\clubsuit}$	0.929^{**}	0.884^{**}	0.429	0.113	0.887^{**}	0.460	0.907^{**}

Note. A and E are original seed lots; A-4 and E-4 are aged seeds; and A-p and E-p are primed seeds. $r^{\clubsuit}$ is the correlation coefficient of anion and conductivity with significance at $P < 0.01$.

[a] Includes fumaric, cis-aconitic, nitrate, glutamic, citri, and α-ketoglutaric.

[b] Tukey *b*-test after ANOVA.

* $P < 0.05$.

** $P < 0.01$.

Table 4

Anion Leakage (μg/g DW) of Isolated Embryos

Seed lot	Phosphate	Chloride	Sulfate	Succinic/malic	Oxalic/acetic	Isocitric acid	Total anions ± SD[a]
C	6466	860	376	780	380	230	9392 ± 1290
C-P	5170	570	284	850	410	230	7513 ± 230
C-12	6727	970	803	1030	760	320	10,637 ± 1460
C-12p	2883	320	179	430	280	70	4168 ± 180
D	5449	620	62	730	460	240	7619 ± 550
D-p	3038	540	50	840	630	360	5467 ± 260
D-12	6666	1180	84	1370	970	610	10,878 ± 470
D-12p	2752	330	50	460	450	170	4206 ± 340
r^{*}	0.824**	0.804**	0.466	0.669*	0.553	0.497	0.790**

Note. C and D are original seed lots; C-12 and D-12 are aged seeds; and C-p, C-12p, D-p, and D-12p are primed seeds. For the total anion, phosphate, chloride, and sulfate anion pairing comparison shows that their seed lot C leakage was significantly higher than seed lot D ($P < 0.05$); aged seeds C-12 and D-12 leaked more anions than their unaged seeds C and D ($P < 0.05$); and the primed seeds C-p, D-p, C-12p, and D-12p significantly leaked more anions than their unprimed seeds C, D, C-12, and D-12. r^{*} is the correlation coefficient of anion leakage and conductivity.

[a] Includes fumaric, cis-aconitic, nitrate, glutamic, citri, and α-ketoglutaric.

* $P < 0.05$.

** $P < 0.01$.

Sugar Leakage of Isolated Embryos

The effect of aging on the sugar leakage of isolated embryos was different from that of the whole seeds. The leakage of the total soluble sugars and all their components of the isolated embryos was consistently increased by aging (table 6). The sugar leakage of isolated embryos of seed lot C-12 and D-12 was 46.4% and 42.3% more than those of the unaged seed lots C and D, respectively (significant at $P < 0.01$). The total sugar leakage of the isolated embryos was about five to six times more than that of the whole seeds. The leakage of sucrose and raffinose of the isolated embryos was about 40 and 300 times more than those of the whole seeds, respectively.

Priming reduced the sugar leakage of the aged embryos significantly. The sugar leakage of the isolated embryos of C-12p and D-12p was significantly lower than that of C-12 and D-12, respectively (significant at $P < 0.01$), but priming did not reduce, or reduced very little, the sugar leakage of unaged embryos.

Table 5

Sugar Leakage (mg/g DW) of Maize Seeds

Seed lot	Glucose	Fructose	Sucrose	Total sugar ± SD[a]
A	1.12**	1.01**	0.22**	2.38** ± 0.27
A-4	0.74	0.61	0.15	1.53 ± 0.03
A-p	0.41	0.40	0.06	0.88 ± 0.01
E	0.98**	0.95**	0.08**	2.08** ± 0.40
E-4	0.63	0.61	0.05	1.33 ± 0.02
E-p	0.44	0.40	0.04	0.90 ± 0.08

Note. A and E are original seed lots; A-4 and E-4 are aged seeds; and A-p and E-p are primed seeds. Compared with the untreated seeds, both aging and priming decreased the sugar leakage significantly.

[a] Includes raffinose, trehalose, arabinose, melezitose, stachyose, rhamnose, and L-serine.

** $P < 0.01$.

Washing Effect of Osmopriming

Osmopriming decreased anion leakage of maize seeds, and these decreased anions could be found in the PEG solutions that primed the seeds. Phosphate, chloride, succinic/malic, and isocitric were the main anions found in the PEG solutions (fig. 1*a*). Some anions (e.g., citric anion) were not found in the conductivity solutions but were found in the PEG solutions.

The total anions in the PEG solution and conductivity solution of the same seed sample was a little more than, or did not differ from, that in the conductivity solution of the unprimed seeds alone (fig. 1*a*). Pairing comparison shows that there were no statistical significant differences between the sugar leakage in the conductivity solution of the unprimed seeds and the total sugars in the PEG solution and in the conductivity solution of the primed seeds. The total anions in the PEG solution and conductivity solution of the primed seed lot C-p was $0.362 + 0.197 = 0.559$ mg/g DW, which is more than the anions in the conductivity solution of the unprimed seed lot C (0.527 mg/g DW). All the main anions (phosphate, chloride, succinic/malic, and isocitric, etc.) showed the same results.

The washing effect of osmopriming on sugar was more significant than on anions. The sugars found in the PEG solutions were significantly more than those in the conductivity solutions for the primed seeds (figure 1*b*). The total sugars in the PEG solution and in the conductivity solution of the primed seeds was a little less than the sugars in the conductivity solution of the unprimed seeds alone, but the differences were not statistically significant.

Discussion

The results presented confirm that the conductivity test can be used to detect differences in maize seed vigor and demonstrated that anion leakage was significantly increased by aging and decreased by osmopriming. Anion leakage was a more sensitive measure than bulk conductivity readings.

Table 6

Sugar Leakage (mg/g DW) of Isolated Embryos

Seed lot	Glucose	Fructose	Sucrose	Raffinose	Total sugar ± SD[a]
C	9.19	10.21**	8.48	3.86	32.12 ± 0.57
C-p	7.57	8.00	8.88	5.77	30.62 ± 4.61
C-12	10.88**	11.95**	16.31**	7.27**	47.03** ± 4.43
C-12p	8.62	7.59	10.30	4.46	31.82 ± 0.90
D	7.96	8.65	11.54	4.70	33.14 ± 3.29
D-p	8.38	8.53	15.11	4.08	36.36 ± 3.86
D-12	11.13**	11.29**	17.69**	6.41**	47.16** ± 1.18
D-12p	8.39	7.66	15.19	5.15	36.75 ± 0.87

Note. C and D are original seed lots; C-12 and D-12 are aged seeds; and C-p, C-12p, D-p, and D-12p are primed seeds. Pairing comparison shows that all the sugar leakage of the aged seeds C-12 and D-12 was significantly more than the unaged seeds C and D ($P < 0.01$); priming reduced the sugar leakage of the aged embryos ($P < 0.01$) but not the unaged embryos.

[a] Includes trehalose, arabinose, melezitose, L-serine, etc.

** $P < 0.01$.

Many authors have demonstrated that the total seed lipid and phospholipid contents consistently decline with seed aging and that this leads to an increase in membrane permeability (Koostra and Harrington 1969; Powell and Matthews 1981; Petruzzelli and Taranto 1984; Wilson and McDonald 1986; Senaratna et al. 1988; Kalpana and Rao 1996). In this study, the increased leakage of phosphate anion of low-vigor and aged seeds may provide further evidence of phospholipid degradation and membrane damage. Most of the chlorine in seeds is in the chloride ion, and the increased leakage of this anion from aged and low-vigor seeds indirectly confirmed that membrane permeability was increased. Most sulfate in plants is formed in proteins (specifically in the amino acids cysteine and methionine) and in the vitamin thiamin, biotin, and coenzyme A (Epstein 1972). Sulfate anion leakage of isolated embryos was increased by aging and was well related to conductivity that indicated that some amino acids and vitamins in embryos are degraded during seed aging.

Aging decreased the sugar leakage of whole seeds, but sugar leakage of whole seeds was not related to conductivity or anion leakage. This further confirmed the conclusion that sugar leakage is a less reliable index of membrane integrity and not clearly related to the loss of seed viability (Abdul-Baki and Anderson 1970; Simon 1974; Horbowicz 1997). Abdul-Baki and Anderson (1970) explained that sugar leakage appears to be regulated primarily by the rate of utilization of such sugars during germination rather than by changes in membrane permeability of dry seed. Horbowicz (1997) reported that the levels of sucrose, raffinose, stachyose, and myoinositol did not change during aging.

This study provided new evidence that sugar leakage of isolated embryos was significantly increased by aging and correlated to anion leakage. Raffinose became one of the main sugars detected, and its leakage significantly increased by aging. This result is consistent with the conclusion of Bernal-Lugo and Leopold (1992, 1995), who demonstrated that the decline of maize seed vigor is associated with a marked decline in monosaccharides and in raffinose. Agrawal (1977) reported that leaching of sugars relates to the total soluble sugars present in seeds, but our results showed there was no close relationship. The total soluble sugars of the aged seeds were about 10% higher than the unaged seeds, but the sugar leakage of the aged seeds was about 15%–30% less than that of the unaged seeds.

It is generally agreed that the increased leakage of deteriorated seeds can be attributed to membrane damage. Membrane damage is a continuous process during seed deterioration and can be divided into several stages. During the first stage, phospholipid degradation begins, a large part of the membrane structure becomes loose, and membrane permeability increases, but its integrity is not lost. At this stage, small molecular materials, like ions, can pass through the membrane, but larger molecular materials, like sugars, cannot pass through, and the seed has not lost viability. Conductivity is the reflection of ion leakage and can measure the change at this early stage, so it is very sensitive. During the second stage, a large part of the membrane loses its integrity, small molecular organic materials can pass through, and the conductivity and the leakage of most soluble materials are increased. Seed viability and germinability are decreased. At the last stage, the membrane structure disintegrates with the loss of its function. The seed has lost its viability and cannot germinate. Because

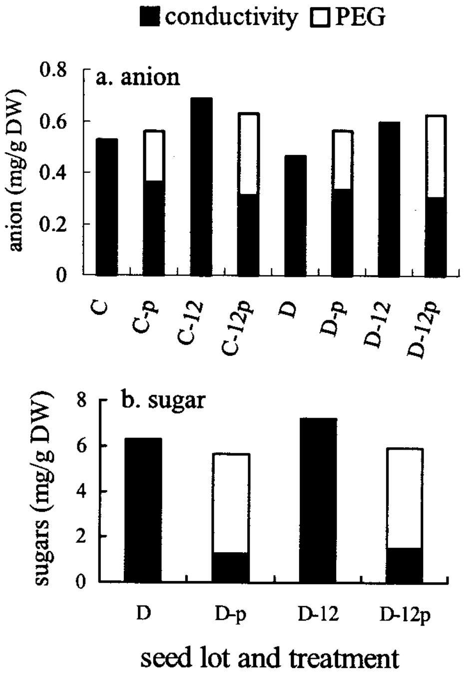

Fig. 1 Total anion and sugar leakage of maize seeds in the conductivity solutions and PEG solutions that primed seeds. C and D are original seed lots; C-12 and D-12 are aged seeds; and C-p, C-12p, D-p, and D-12p are primed seeds. Pairing comparison shows that there were no significant statistical differences between the anions in the conductivity solution of the unprimed seeds and the total anions in the conductivity solution of the primed seeds plus that in the PEG solution that primed the seeds (*a*). Pairing comparison also shows that there were no significant statistical differences between the sugars in the conductivity solution of the unprimed seeds and the total sugars in the conductivity solution of the primed seeds plus that in the PEG solution that primed the seeds (*b*).

sugars are larger molecules than ions, sugar leakage occurs after ions during seed deterioration, and the leaked sugars may be reabsorbed by seeds during imbibition. This may explain why sugar leakage is not closely related to anion leakage and conductivity.

Embryos usually comprise about 11%–12% of maize seed dry weight, but the sugar and anion leakage of embryo per unit dry weight was about 30 and 50 times more than the whole seeds, respectively. This implies that embryos play an important role in the leakage conductivity. The embryo is very different chemically being composed primarily of proteins, while the endosperm is almost all starch. It is not surprising that embryos leak more ions than endosperm, but the aged embryo also leaked more sugars than the endosperm. Though excision may damage the embryos, the difference between the leakage of aged and unaged embryos was more significant than that of whole seeds, which may mean that the embryo was more sensitive to aging than the endosperm.

Seed priming decreased electrolyte leakage, but it was mainly caused by the washing effect during priming. A quantity of anions and sugars were washed out of seeds and could be found in the used PEG solutions. The total anions left in the PEG solutions and in the conductivity solutions of the primed seeds was a little more than that in the conductivity solutions of the unprimed seeds alone. The total sugars in the two solutions of the primed seeds was a little less than that in the conductivity solutions of the unprimed seeds. Therefore, the decreased leakage cannot be used as evidence of the recovery of damaged membranes and so improved vigor following seed priming.

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