J. AMER. SOC. HORT. SCI. 113(2):269–272. 1988.

Endosperm Type, Inbred Background, and Leakage of Seed Electrolytes During Imbibition in Sweet Corn

D.H. Schmidt and W.F. Tracy

Department of Agronomy, University of Wisconsin-Madison, Madison, WI 53706

Additional index words. *Zea mays*, sugary (*su*), dull (*du*), waxy (*wx*), sugary-2 (*su2*), shrunken-2 (*sh2*), seed quality

Abstract. **Endosperm mutants of maize often exhibit poor seed quality, as indicated by poor germination and seedling vigor. The measurement of seed leachate electrolyte conductivity (SLEC) is a rapid method of evaluating seed quality. Generally, high SLEC indicates poor seed quality. Other endosperm types in addition to sugary (*su*) are becoming important in the sweet corn industry. To facilitate the conversion of inbreds to new endosperm types and maintain acceptable levels of seed quality, it would be useful to determine the relationship between endosperm type and SLEC. The objective of this study was to determine the effects of inbred background, endosperm type, and inbred × endosperm interactions on SLEC and to determine the relationship between seed weight and SLEC. Ten seed weight and SLEC of six near-isogenic lines differing for 10 endosperm types were measured. Ten combinations of the following endosperms were used; sugary (*su*), waxy (*wx*), sugary-2 (*su2*), dull (*du*), and shrunken-2 (*sh2*). Significant differences in SLEC were found among endosperm types: *sh2* had the highest SLEC (186.1 $\mathrm{dS\cdot m^{-1}}$) and *Su su2* the lowest (62.9 $\mathrm{dS\cdot m^{-1}}$). Over endosperm types, 10-seed weight and SLEC were negatively correlated ($r = 0.84^{**}$). This negative relationship may be due to damage suffered by the pericarp during the collapse of the endosperm of the lighter endosperm types. Significant differences in SLEC also were found among inbreds. Values ranged from 162.3 $\mathrm{dS\cdot m^{-1}}$ to 55.7 $\mathrm{dS\cdot m^{-1}}$. Among inbreds, SLEC and 10-seed weight was positively correlated ($r = 0.82^{*}$). Endosperm by inbred interactions had significant effects on SLEC. This interaction is of importance to those converting inbreds to different endosperm types and should be considered when choosing seed parents for hybrid production.**

Acceptance of sweet corn (*Zea mays* L.) hybrids having shrunken-2 (*sh2*) endosperm or amylose-extender (*ae*), dull (*du*), waxy (*wx*) endosperm has been limited because of low seed quality as indicated by poor germination and seedling vigor (2, 3, 9). In certain backgrounds, sugary (*su*) endosperm has resulted in reduced germination and shorter seedlings than has starchy (*Su*) endosperm (8). Dull (*du*) endosperm resulted in significantly lower germination and reduced shoot length than waxy (*wx*) endosperm in the sweet corn inbred Ia5125 (9).

In addition to the importance of endosperm type in determining seed characteristics, inbred background strongly affected germination and seedling vigor (9). Further, significant effects on germination and seedling vigor were due to endosperm × inbred interactions (9). Changes in moisture levels and carbohydrate synthesis and accumulation during kernel development of 10 endosperm genotypes in seven near-isogenic sweet corn lines showed significant endosperm × line interaction (11). Pericarp thickness also is affected by endosperm × inbred interactions (13).

Leakage of seed electrolytes during imbibition has been associated with seed quality in several crop species. Increased seed leachate electrolyte conductivity (SLEC) has been associated with decreased seed viability in garden peas (5), soybean (4), and artificially aged barley seed (1). Among 13 sweet corn hybrids with *su* endosperm, field emergence and electrolyte conductivity were negatively correlated ($r = -0.58^{**}$), whereas field emergence and standard laboratory germination tests were not significantly correlated ($r = -10.18$) (16).

Within the limited number of endosperm types examined, endosperm type has an effect on SLEC (12, 15, 16). Among three sweet corn hybrids, each with a different endosperm type, SLEC was greater from seed with endosperm genotypes *sh2* or *ae du wx* ('Florida Staysweet' and 'Pennfresh ADX', respectively) than the *su* hybrid 'Iochief' (15).

Sweet corn eating quality traditionally has been based on the *su* allele. Recently, endosperm types including *sh2, ae du wx*, brittle (*bt*), and others have become important in the sweet corn industry (3). SLEC has been established as a rapid and accurate method of determining seed quality in maize (12, 15, 16). Due to seed quality problems associated with *sh2, ae, du, wx,* and *bt* endosperm types (2, 3, 9), it would be useful for sweet corn breeders and seedsmen to understand the factors that affect SLEC. The objectives of this research were to determine the effects of inbred background, endosperm type, and inbred x endosperm interactions on seed quality in sweet corn as measured by SLEC and average seed weight.

Materials and Methods

Sixty near-isogenic maize lines developed by Soberalske and Andrew (10) were used in this study. Sweet corn inbreds C23, C40, C68, P39M94, Ia453, and Ia5125 a were used as the recurrent parents. Endosperm mutants *du, wx,* sugary-2 (*su2*), and *sh2* and the mutant combination *du wx* were incorporated in these inbreds with the *Su* or *su* allele at the sugary locus. The *sh2* mutant was incorporated with the *Su* allele but not the *su* allele, because the *su sh*2 combination is nearly lethal. The standard sugary (*su*) version of each inbred was included for a total of 10 endosperm genotypes in each of the six backgrounds.

Seeds used were from self-pollinated ears of the near-isogenic lines grown in single-row plots on a Plano silt loam (Typic Argiudolls) at Arlington, Wis. in 1980 and 1985. Selfed ears were harvested ≈45 days after pollination, dried to ≈10% moisture, and stored in a cool temperature/low moisture facility. Seeds were hand-shelled. Each year, seeds from the selfed ears

---

Received for publication 9 Apr. 1987. Contribution from the Dept. of Agronomy, Univ. of Wisconsin Agr. Exp. Sta., Madison. Research supported by the College of Agriculture and Life Sciences, Univ. of Wisconsin, Madison; The Wisconsin Alumni Research Foundation; and the Wisconsin Food Processors Assn. We thank S.H. Duke, Dept. of Agronomy, Univ. of Wisconsin, Madison, for his assistance and advice. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

were bulked within rows. Average seed weight was estimated by making three weight determinations on 10 seeds of each of the 60 genotypes in each year.

SLEC was measured using a modified version of the method developed by Waters and Blanchette (16). Vials containing 10 seeds of a genotype were filled with 50 ml of deionized water. Conductivity readings were taken after exactly 24 hr using a Beckman SD-412I Solubridge conductivity indicator. Four replicates within each year were analyzed. Each replicate consisted of vials of the 60 genotypes and three deionized water controls. Room temperature (25° ± 2°C) was held constant throughout the experiment.

Results were analyzed as a split-split plot in a randomized complete block design with years as main plots, inbreds as subplots, and endosperm types as sub-sub-plots. All effects were considered random. The design was used to account for the physical layout of the experiment in which endosperm types were grouped within inbreds. This grouping was done to focus precision on endosperm effects. The Waller–Duncan mean separation test criterion was used for inbreds and endosperm types. Comparison of all starchy versus sugary endosperms (*Su* or *su*) and comparison between *du, wx, su2,* and *du wx* endosperms were also conducted.

Results and Discussion

Highly Significant effects on SLEC due to inbred and endosperm main effects and endosperm × year, inbred × endosperm, and year × inbred × endosperm interactions were detected (Table 1). Significant effects were found for years. Highly significant endosperm × year, inbred × year, and year × inbred × endosperm interactions and significant year effects may be due to environmental effects on carbohydrates of the different genotypes. Styer and Cantliffe (12) found significant differences for SLEC and percent carbohydrate in *sh2* and *su* kernels grown in two different environments. Significant year effects are often a function of seed aging (1). Although seeds used in the study were processed in the same manner in both 1980 and 1985, it is not possible to determine if the difference in SLEC due to years was due to seed production in different environments or to seed aging. However, if the significant effects of years is due to seed aging, the response to aging varies according to both endosperm and inbred, as indicated by the significant interaction terms. Due to the established relationship between SLEC and seedling vigor, endosperm and inbred effects were expected based on results of previous studies in corn (12, 14–16) and soybean (4). However, we have identified differences in SLEC over an expanded number of endosperm types. Inbred × endosperm interaction effects on SLEC had not been previously identified. Significant inbred × endosperm interactions have been noted for kernel characteristics, such as germination, seed quality, vigor, and carbohydrate synthesis, which are related to SLEC (6, 9, 11). Highly significant inbred × endosperm interactions for SLEC indicate that inbred backgrounds respond differently when converted to new endosperm types, and such interactions may have important effects on seed viability.

Table 1. Mean squares from analysis of variance for seed electrolyte conductivity and 10-seed weight for six inbred lines varying for 10 endosperm genotypes.

	SLEC		Ten-seed wt	
Source	df[z]	MS	df	MS
Year (Y)	1	261.08*	1	0.0007
Error A	6	14.56*	4	0.0062
Inbred (I)	5	1123.49**	5	5.2694**
I × Y	5	25.04**	5	0.0388**
Error B	30	5.14**	20	0.0073
Endosperm (E)	9	606.73**[y]	9	2.6269**[y]
E × Y	9	102.67**	9	0.0440
I × E	45	43.90**	45	0.5192**
Y × I × E	45	20.93**	45	0.0379**
Error C	324	3.12	216	0.0049

[z] df = degrees of freedom.

[y] Satterthwaite approximation used to determine significance.

*, **Significant differences at the 5% and 1% levels, respectively.

Inbred and endosperm main effects and inbred × endosperm, and inbred × year, and year × inbred by endosperm interactions had highly significant effects on 10-seed weight (Table 1). The lack of year effects in this experiment indicated that seed weight was a stable trait over environments. It is obvious that inbreds vary in seed weight and that endosperm type also affects seed weight, as indicated by the descriptors for some endosperm types, e.g. shrunken and collapsed. The observed inbred × endosperm effects on seed size indicated a differential response of inbred backgrounds when converted to different endosperm types.

In comparing the endosperm types, *Su sh2* had the highest SLEC values, which was 189% of the SLEC of *Su du wx*, the next highest endosperm type (Table 2). The high SLEC from *su sh2* is consistant with previous reports (12, 15, 16). The endosperm type that exhibited the lowest SLEC was *Su su2* (62.9 $dS\cdot m^{-1}$). By using the Waller–Duncan mean separation criterion, we were able to separate the 10 endosperm types into four SLEC groups. The groups had no apparent relationship to endosperm type based on either the allele at the *su* locus or the other endosperm mutants. Endosperm type *Su wx* had significantly lower SLEC than did *su wx*, whereas *Su du wx* had significantly higher SLEC than did *su du wx*. Ten-seed weight among endosperms varied from 1.05 g for *Su sh2* to 2.10 g for *Su wx* (Table 2). In all instances except for *su du wx* vs. *Su du wx*, the starchy endosperm version was heavier than the sugary endosperm version. Seven endosperm types had significantly lower kernel weight than *su*.

Inbred backgrounds also had a wide range of SLEC (Table 3). Inbred C40 had the highest SLEC at 162.3 $dS\cdot m^{-1}$, and Ia453 had the lowest at 55.7 $dS\cdot m^{-1}$. The ranking of the inbred lines according to their SLEC averaged over *Su* (excluding *Su sh2*) or *su* endosperms and averaged over *du, su2, wx,* or *du*

Table 2. Endosperm genotype mean separation for seed leachate electrolyte conductivity (SLEC) and 10-seed weight combined over six inbred backgrounds and 2 years.

Endosperm genotype	SLEC ($dS\cdot m^{-1}$)	Weight of 10 seeds (g)
Su sh2	186.1 a[z]	1.05 f
Su du wx	98.4 b	1.52 e
su du	85.1 c	1.53 de
Su du	84.1 c	1.56 d
su su2	84.0 c	1.57 d
su du wx	82.1 c	1.63 c
su wx	78.6 c	1.56 d
Su wx	67.7 d	2.10 a
su	66.5 d	1.64 c
Su su2	62.9 d	1.89 b

[z] Means separated by the Waller–Duncan multiple range test, $P = 5\%$.

Table 3. Mean separation among inbred lines for seed leachate electrolyte conductivity and 10-seed weight in grams averaged over 10 endosperm types and 2 years.

Inbred line	SLEC for endosperm types within inbreds[z] ($dS\cdot m^{-1}$)	Weight of 10 seed (g)
C40	162.3 a[y]	2.15 a
C23	87.4 b	1.47 d
C68	86.1 b	1.54 c
Ia5125a	74.9 c	1.54 c
P39M94	70.9 c	1.28 e
Ia453	55.7 d	1.65 b

[z] Each inbred line contained 10 endosperm types.

[y] Means separated by the Waller–Duncan multiple range test, $P = 5\%$.

wx were the same as the overall rankings, indicating the importance of inbred background in determining SLEC in sweet corn. Rowe and Garwood (9) found germination percentage differed significantly for inbreds, indicating the importance of inbred background on seedling vigor.

SLEC for the average of sugary endosperm, *su du, su su2, su wx,* and *su du wx,* ($82.8\ dS\cdot m^{-1}$) was not significantly different from SLEC averaged over *Su* endosperms, *Su du, Su su2, Su wx,* and *Su du wx,* $78.3\ dS\cdot m^{-1}$). The lack of significant difference for SLEC may be because the recurrent parents were sweet corn inbreds. The sweet corn backgrounds are adapted to the sugary allele and thus *su* may not confer as great a disadvantage with respect to electrolyte leakage, as would be the case in dent backgrounds.

Significant differences in SLEC were found among *du, su2, wx* and *du wx* endosperms. Sugary-2 ($73.5\ dS\cdot m^{-1}$) was significantly different from *du wx* and *du*. Dull endosperm had significantly higher SLEC ($84.6\ dS\cdot m^{-1}$) than *wx* (73.2 18 $dS\cdot m^{-1}$). Within this group, the mutant combination *du wx* had the greatest SLEC ($90.7\ dS\cdot m^{-1}$) and was significantly different from *du* and *wx*. Rowe and Garwood (9) found that, for inbred Ia5125, *du* had a significantly lower germination and shoot length (59.8% and 10.5 cm) than *wx* (88.7% and 13.8 cm). They also reported that for inbred S3-61, *du wx* had significantly lower germination and shoot length than *du* or *wx* (9).

Differences in SLEC among endosperm types were negatively correlated with 10 seed weight ($r = -0.84$**). When endosperm *Su sh2*—which is extreme in both traits—was deleted, a significant negative correlation persisted ($r = -0.72$*). The significant relationship between the characters may be due to two factors related to the physiology of endosperm types. Mature seed of different endosperm types has different proportions of carbohydrates (3). Shrunken-2 is low in starch, whereas *Su wx* is high, especially in the amylopectin starch component. The different proportion of endosperm constituents may result in differences in SLEC as reported here. However, a second factor involved in the SLEC differences may be the disruption of membranes and damage to the pericarp during the collapse of defective kernel types, such as *Su sh2* (12). In addition to lighter weight kernels, kernel collapse results in the separation of the pericarp from the endosperm. Styer and Cantliffe (12) found more airspace between the pericarp and the endosperm in *Su sh2* kernels than in *su* kernels. A separation between the pericarp and endosperm would allow increased mechanical damage to the pericarp. Kernels with damaged pericarps germinate poorly, result in weaker seedlings, and have greater SLEC (7, 12, 15) than those with undamaged pericarp.

Significant differences were found for 10-seed weight among inbreds averaged over endosperms (Table 3). C40 had the heaviest seed (2.15 g), whereas P39M94 had the lightest seed (1.28 g). The 10-seed weight and SLEC traits were significantly correlated ($r = 0.82$*) in the six inbreds. Andrew (2) reported that among inbreds used as seed parents, seed weight was not related to germination rates or seedling vigor, but that within a seed parent, the largest seeds resulted in improved germination and seedling vigor.

Our results indicated that years, inbred backgrounds, and endosperm types affected SLEC. Endosperm types affected kernel characteristics such as pericarp thickness (6, 13), carbohydrate and protein synthesis (3, 10, 11), seed size (2, 14), and kernel phenotypes (3). All of these factors could alter SLEC. Further, highly significant inbred × endosperm interactions indicated some of the difficulties expected when converting an inbred with a particular endosperm to a different endosperm type. Significant year × endosperm and year × inbred interactions may indicate that differential deterioration of the genotypes occurred in storage and might be useful in identifying seed parents resistant to deterioration over time. This factor is an important consideration for the sweet corn industry.

Literature Cited

1. Abdul-Baki, A.A. and J.D. Anderson. 1970. Viability and leaching of sugars from germinating barley. Crop Sci. 10:31–34.
2. Andrew, R.H. 1982. Factors influencing early seedling vigor of shrunken-2 maize. Crop Sci. 22:263–266.
3. Boyer, C.D. and J.C. Shannon. 1983. The use of endosperm genes for sweet corn improvement. Plant Breeding Rev. 1:139–161.
4. Duke, S.H., G. Kakefuda, C.A. Henson, N.L. Loeffler, and N.M. Van Hulle. 1986. Role of the testa epidermis in the leakage of intracellular substances from imbibing soybean seeds and its implications for seedling survival. Physiol. Plant. 68:625–631.
5. Flentje, N.T. and H.K. Saksena. 1964. Pre-emergence rotting of peas in South Australia. Austral. J. Biol. Sci. 17:665–675.
6. Helm, J.L., D.V. Glover, and M.S. Zuber. 1970. Effect of endosperm mutants on pericarp thickness in corn. Crop Sci. 10:105–106.
7. Koehler, B. 1957. Pericarp injuries in seed corn. Ill. Agr. Expt. Sta. Bul. 617.
8. Nass, H.G. and P.L. Crane. 1970. Effect of endosperm mutants on germination and early seedling growth rate in maize (*Zea mays* L.). Crop Sci. 10:139–140.
9. Rowe, D.E. and D.L. Garwood. 1978. Effects of four maize endosperm mutants on kernel vigor. Crop Sci. 18:709–712.
10. Soberalske, R.M. and R.H. Andrew. 1978. Gene effects of kernel moisture and sugars of near-isogenic lines of sweet corn. Crop Sci. 18:743–746.
11. Soberalske, R.M. and R.H. Andrew 1980. Gene effects on water soluble polysaccharides and starch of near-isogenic lines of sweet corn. Crop Sci. 20:201–204.
12. Styer, R.C. and D.J. Cantliffe. 1983. Changes in seed structure and composition during development and their effects on leakage in two endosperm mutants of sweet corn. J. Amer. Soc. Hort. Sci. 108:721–728.
13. Tracy, W.F. and D.H. Schmidt. 1987. The effect of endosperm type on pericarp thickness in near-isogenic lines of sweet corn. Crop Sci. 27:692–694.
14. Wann, E.V. 1980. Seed vigor and respiration of maize kernels with different endosperm genotypes. J. Amer. Soc. Hort. Sci. 105:31–34.

15. Wann, E.V. 1986. Leaching of metabolites during inbibition of sweet corn seed of different endosperm genotypes. Crop Sci. 26:731–733.

16. Waters, L. and B. Blanchette. 1983. Prediction of sweet corn field emergence by conductivity and cold tests. J. Amer. Soc. Hort. Sci. 108:778–781.

J. AMER. SOC. HORT. SCI. 113(2):272–276. 1988.

Comparison of Two Recurrent Selection Procedures For Yield in Two Pickling Cucumber Populations

J. Nienhuis[1] **and R.L. Lower**[2]

Department of Horticulture, University of Wisconsin, Madison, WI 53706

Additional index words. reciprocal full-sib recurrent selection, S_1 line recurrent selection, *Cucumis sativus, Cucumis sativus* var. *hardwickii*, population improvement, fruit number, yield

Abstract. **A "gynoecious synthetic" (GS) population, developed by random mating of 50 adapted *Cucumis sativus* L. cultivars and breeding lines, and a "hardwickii semi-exotic" (HSE) population, developed by open-pollinating an F_2 population derived from a cross between a *Cucumis sativus* var. *hardwickii* (R.) Alef. accession LJ 90430 and a gynoecious inbred line GY 14, were subjected simultaneously to S_1 line (S_1) and reciprocal full-sib (RFS) recurrent selection. S_1 selection resulted in increased fruit number per plant in the GS and HSE populations, and in the GS × HSE population hybrid. In contrast, RFS selection did not result in increased fruit number per plant in the GS and HSE populations or their hybrid. The contrasting responses to S_1 compared to RFS selection suggests that additive gene effects were more important than nonadditive effects in the expression of fruit number per plant. Correlated responses to selection resulted in increased number of days to harvest in the GS population, and in reduced percentages of gynoecious plants and pistillate flowers in the HSE population. No change in fruit firmness, and a reduction in length : diameter ratio of fruit only in the GS × HSE population hybrid developed through S_1 selection, suggests that selection for increased fruit number per plant should not adversely affect these fruit quality characteristics in either the GS or HSE populations.**

The shift to mechanical harvesting of pickling cucumbers has been slow because harvesters often skip small-diameter cucumber fruit. Thus, concurrent with the development of harvesters that harvest small fruit, one objective of our pickling cucumber breeding program is to develop high-yielding cultivars that are adapted to once-over mechanical harvesting.

Yield in pickling cucumbers is best expressed as marketable yield, which is the sum of products of the value by the weight of various grade sizes. However, because of the time and resources required to grade and weigh individual plots, yields of pickling cucumber plots often are evaluated more efficiently as marketable fruit number, a trait highly correlated with marketable yield (19).

Significant additive and dominance variances for yield and yield components in cucumber have been reported in crosses among adapted lines (7, 8). However, Smith et al. (19) reported that narrow-sense heritability for fruit number, in a population derived by random mating of 18 monoecious lines, was low (0.17), suggesting that the additive genetic variance for fruit number in existing breeding populations might need to be increased prior to initiating selection. Smith et al. (19) suggested incorporation of exotic, multiple-fruiting genotypes into the current germplasm pool might be a means of increasing genetic variance for yield.

One source of multiple-fruiting genotypes in cucumbers is *Cucumis sativus* var. *hardwickii* (R.) Alef., a noncultivated, annual, monoecious cucumber (4, 21). Numerous differences in morphology, flowering, and fruit setting characteristics between cucumber cultivars and LJ 90430, (obtained from G.W. Bohn, La Jolla, Calif.), the *C. sativus* var. *hardwickii* accession used in our breeding program, have been described previously (11, 12, 14, 15). Accession LJ 90430 was selected for use in our breeding program because it sets large numbers of seeded fruit per plant (10). Lower et al. (15) investigated the types of gene action involved in the inheritance of yield in populations derived from a cross between LJ90430 and a gynoecious inbred line GY 14. Additive gene effects as well as additive-by-additive epistatic interactions were significant sources of variation among generation means for mature fruit number per plant, which suggests that recurrent selection might be effective in increasing fruit yield within this population (15).

Recurrent selection is a powerful tool for improving population performance (3, 5, 6, 9, 10, 13, 20). S_1 line selection (S_1) is a recurrent selection procedure designed for improvement of populations by selection based on additive genetic variance (10). It has been investigated most extensively in maize and has been found to be superior or equal in effectiveness to half-sib testcross procedures for population improvement (6, 13). In addition, because selfing may expose deleterious recessive genes, S_1 is more effective than half-sib procedures, where recessives may be masked. Reciprocal full-sib (RFS) recurrent selection, a modification of the original reciprocal recurrent selection procedure, is designed to improve both general and specific combining ability simultaneously in two populations (3, 9). The primary practical advantage of RFS over simultaneous S_1 selection in two populations is that only half as many progeny rows need to be evaluated to maintain the same selection intensity and effective population size (10).

Received for publication 27 Jan. 1987 The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

[1] Former Graduate Assistant. Presently: Scientist, N.P.I., University Research Park, Salt Lake City, UT 84108.

[2] Professor.