Seed Vigor and Respiration of Maize Kernels with Different Endosperm Genotypes

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Abstract. Seed vigor in sweet corn (Zea mays L.) was compared among cultivars with the triple recessive endosperm mutant gene combination amylose-extender (ae), dull (du) and waxy (wx), the shrunken-2 (sh2) gene, their sugary (su) counterparts and an open-pollinated cultivar of normal genotype. Dry weight was significantly lower for F1 kernels of the high-sugar genotypes ae du wx and sh2 than for their su counterparts or the normal cultivar. The endosperm:embryo dry weight ratio was also low in the high-sugar lines due primarily to their small endosperm. Seedling dry weight at 10 days was correlated with endosperm:embryo ratio. Comparisons were made among the cultivars for shoot, radicle, and seminal lateral root growth from intact seeds and from excised embryos on nutrient agar. The normal genotype showed superior seed vigor when evaluated by seedling growth from intact kernels, but not when embryos were grown on agar, suggesting that vigor in normal was due to large endosperms. Respiration rate (µl O2 uptake/kernel-hr) of the germinating seeds did not account for growth differences among the genotypes. Respiration at 24 hr after imbibition was negatively correlated with seedling dry weight at 10 days. Respiration at 48 and 72 hr showed no significant correlations with growth rates. Low seed vigor in high-sugar genotypes apparently was related to their small endosperms. The genotype of the embryo also was important in seedling vigor, but low vigor in high-sugar cultivars could not be attributed wholly to genetic inferiority of the embryo.

The quality of sweet corn has been enhanced in recent years by the introduction of one or more mutant genes affecting carbohydrate metabolism in the endosperm in place of the standard sugary (su) gene (5, 7, 9, 12, 13, 14). Certain combinations of the endosperm mutants produce a 1-to-3 fold increase in total sugars over the standard su genotype with a concomitant decrease in the WSP (water-soluble polysaccharides) and starch fractions in the kernels at edible maturity (5, 6, 9, 13, 14). They also have the effect of prolonging high quality in fresh market sweet corn for several days after harvest (13, 14). The high-sugar types have been accepted mostly for home-garden and fresh market use.

The shrunken-2 (sh2) gene has been used to produce several sweet corn hybrids with the high-sugar characteristic (9, 14). A high-sugar sweet corn hybrid was recently introduced by The Pennsylvania Agricultural Experiment Station that possessed the triple recessive combination of the amylose-extender (ae), dull (du) and waxy (wx) genes. Like the sh2 hybrids, it contained about twice the amount of sugar as standard su hybrids (7).

A major limiting factor to the acceptance and success of the high-sugar types by the sweet corn industry has been low seed vigor. Woodstock (15) defined seed vigor as "that condition of active good health and natural robustness in seeds which, upon planting, permits germination to proceed rapidly and to completion under a wide range of environmental conditions." Germination and robustness are generally lower in high-sugar than in standard sweet (su) types, and seedling vigor is lower during early stages of growth (4, 11, 13, 14).

The cause of low seed vigor in the high-sugar genotypes is not fully understood. Recent research has shown, however, that selection among lines containing the high-sugar genotypes is effective for improving the seed quality (4, 11). Crane (4) reported that the ae gene had a slight disadvantage in seedling emergence and in early seedling growth. He also reported that sizable differences among ae pedigrees in seedling emergence in cold muck soil indicated that the characteristic could be improved by selection. Rowe and Garwood (11) studied the effect of endosperm mutant genes ae, du, su and wx individually and in all combinations on seed vigor in an isogenic series from three sweet corn inbreds. They found large differences among the sweet corn inbreds in their ability to impart good seed vigor to the mutant genotypes. Their work suggested that the problem of slow seed vigor in the ae du wx genotype might be alleviated by using recurrent parents in the breeding process that are capable of enhancing seed vigor and by selecting vigorous inbreds for seed parents in the production of hybrid seed.

Woodstock and Feeley (16) found that rate of seedling growth during the first 3-4 days of germination was significantly correlated with growth rates 4-6 days after planting and that seedling growth during the first week of germination was correlated with growth between 2 and 3 weeks after planting. They also found that respiration determinations during the first stages of germination could be used to predict subsequent shoot growth. Abdul-Baki and Anderson (2) determined that respiration (O2 uptake and CO2 production), uptake of glucose or leucine, synthesis of carbohydrates and proteins, and leaching of metabolites all correlated with seed vigor in excised embryonic axes of soybean.

Usually, low seed vigor in crop plants is attributed to aging of the seed, or to some physical injury that impairs the ability of the seed to germinate. In the high-sugar genotypes in sweet corn, however, it is not known whether the low seed vigor is due to a small reserve of nutritive materials in the endosperm or whether the embryo itself is genetically inferior and incapable of exhibiting strong vigor. Identifying the nature of this low seed vigor should help breeders establish selection criteria to improve seed quality within the high-sugar genotypes.

This paper reports the results of tests to determine whether low seed vigor in high-sugar genotypes was due to a limited carbohydrate reserve in the endosperm, or whether the embryos carrying the mutant alleles were genetically inferior to the normal or their su counterparts.
Materials and Methods

Seed samples from self-pollinated F1 ears of 'Golden Cross Bantam', 'Iochief', 'Florida Sweet', 'Pennfresh ADX' and experimental hybrid M6464 were selected for uniform size and weight. All tests were conducted with F2 kernels that had been produced under identical conditions in order to circumvent variations that might have resulted from differences in age, production or handling of the commercial F1 hybrid seeds. ‘Florida Sweet’ is the sh2 counterpart of ‘Iochief’ (14), ‘Pennfresh ADX’ is the ae du wx counterpart of ‘Iochief’ and M6464 is also an ae du wx hybrid similar in plant, ear and kernel type to ‘Golden Cross Bantam’. ‘Truckers Favorite’, an open pollinated starchy corn, was included as a normal check cultivar. The F1 hybrid, M6464, was produced at this Laboratory from 2 experimental breeding lines that had been selected for several generations for improved germination and seedling vigor. All F1 ears (50 of ‘Truckers Favorite’) were harvested at 40-45 days after pollination and stored without further drying in open trays in a seed storage room at 20°C and 45% RH. The tests were made 3-4 months later when moisture content of the seeds had equilibrated at 10-11%.

Measurement were made of kernel dry weight, seedling growth, endosperm and embryo dry weight, root and shoot elongation from intact seeds and from excised embryos grown on a nutrient agar medium, and seed respiration during first 72 hr of germination. Seedling dry weights were determined in a greenhouse from seeds planted at a uniform depth in builders sand in Speedving trays with 2.5 x 2.5 x 7.5 cm cells. A single kernel was planted in each cell with 20 kernels/line and 4 replications. At 10 days the seedlings were removed from the trays, counted, washed, and dried to a constant weight in an oven at 90°C.

For determination of the ratio of endosperm to embryo dry weight, 50 uniform kernels selected from each cultivar were soaked for 20-24 hr in tap water. Next, the embryo axis was removed from the remainder of the seed, and both fractions were dried to a constant weight in an oven at 90°C and weighed.

Samples of 4 kernels/cultivar replicated 5 times were used for this determination. Kernel dry weight was reported as the sum of the embryo and endosperm weights.

The lengths of shoots, radicles, and seminal lateral roots were measured at 120 hr after imbibition from intact seeds germinated in rolls of non-toxic germination paper at 25°C, and from excised embryos grown under identical conditions except that they were grown on Murashige and Skoog agar medium, and seed respiration during first 72 hr of germination. Seedling dry weights were determined in a greenhouse from seeds planted at a uniform depth in builders sand in Speedving trays with 2.5 x 2.5 x 7.5 cm cells. A single kernel was planted in each cell with 20 kernels/line and 4 replications. At 10 days the seedlings were removed from the trays, counted, washed, and dried to a constant weight in an oven at 90°C.

Results and Discussion

Kernel dry weight differed significantly for each endosperm genotype represented, except that ‘Golden Cross Bantam’ had significantly lighter kernels than other su hybrids, ‘Iochief’ and ‘Florida Sweet’ (Table 1). ‘Truckers Favorite’ had significantly heavier kernels than the other cultivars. Kernel dry weights of the 2 ae du wx hybrids, M6464 and ‘Pennfresh ADX’, were similar, and significantly heavier than the weight of ‘Florida Sweet’, the lightest of the group. In general, the high-sugar genotypes, ae du wx and sh2, had lighter kernels than their su counterparts. The differences in dry weight of endosperm followed closely those of the whole kernels with significant differences between all cultivars, except ‘Iochief’ and ‘Iochief’ (Table 1).

Embryo dry weight also differed significantly among the cultivars. Although ‘Truckers Favorite’ had the heaviest kernels and endosperms, its embryos were significantly lighter than those of su or ae du wx genotypes. Only ‘Florida Sweet’ had lighter embryos than ‘Truckers Favorite’.

The endosperm:embryo weight ratio reflects the relative amounts of nutrient reserve available to the embryo during germination (Table 1). ‘Truckers Favorite’ had large endosperms and relatively small embryos giving it a significantly higher endosperm:embryo ratio than the other cultivars. ‘Florida Sweet’ and, to a lesser extent, ‘Pennfresh ADX’ and M6464 had shrunk kernels with small endosperms in relation to embryos, so that seedling dry weight at 10 days (Table 1) also showed significant differences among cultivars and was correlated with the endosperm:embryo ratio (r = 0.904**). In these tests, seedling dry weight at 10 days probably most accurately reflected the actual seed vigor of the cultivars represented.

The data in Table 1 suggest that differences in vigor might be closely related to weight of endosperm. To test this hypothesis, I measured seedling growth from intact seeds on germination paper and also from excised embryos on a nutrient medium (Table 2). At 120 hr after imbibition there were significant differences among cultivars for shoot length from the intact kernels, but none for shoots from embryos on the nutrient medium. ‘Truckers Favorite’ showed a distinct superiority over the other cultivars for shoot growth from intact seeds, but that superiority was not evident from the excised embryos. Significant differences for radicle length also were found among cultivars, and again the superiority of the normal genotype from intact seeds was not evident from the excised embryos (Table 2). There also were significant differences among cultivars for seminal lateral root lengths, but these differences were similar from intact seeds and embryos.

Early seedling growth of the su cultivars was generally greater than that from their respective ae du wx or sh2 counterparts but the differences were not statistically significant, except that seedling dry weight at 10 days (Table 1) and seminal lateral root growth in ‘Iochief’ and ‘Iochief’ was significantly greater than that from ‘Pennfresh ADX’ and ‘Florida Sweet’, respectively (Table 2). ‘Truckers Favorite’ was clearly superior to the sweet lines for seed vigor but that superiority was not evident when its excised embryos were grown on agar. This suggests that the high seed vigor in ‘Truckers Favorite’ was due to its large endosperm. Elongation of seminal lateral roots was greatest for ‘Truckers Favorite’ and ‘Iochief’ and generally much less for the high-sugar genotypes. ‘Golden Cross Bantam’...
also had slow lateral root development, yet its seedlings were among the most vigorous, according to seedling dry weight (Table 1). The importance of seminal lateral roots for seedling establishment needs further investigation.

The respiration rate of kernels during the first 72 hr of germination (Table 3) could not be easily reconciled with seedling growth (Tables 1 and 2). Respiration rate at 24 hr was negatively correlated with seedling dry wt at 10 days ($r = -0.797^*$) but not at subsequent times. There were some significant differences among the 7 cultivars tested, but no clear-cut differences were attributable to genotype. 'Truckers Favorite', the normal genotype and most vigorous for seedling growth, had the lowest respiration rate at 1 and 24 hr after imbibition. 'Florida Sweet', one of the least vigorous lines, showed a high respiration rate throughout 72 hr. A possible explanation for this seemingly inconsistent reaction may be that kernels of the high-sugar genotypes (sh2 and ae du wx) released more soluble sugars upon hydration than normal thereby providing a quick energy source for respiration. 'Truckers Favorite', on the other hand, has low sugar in its endosperm (unpublished data) and depended upon enzymatic action to degrade the starch granules and release soluble sugar for respiration.

Ingle et al. (8) reported that during germination progressive hydration and associated change of insoluble to soluble constituents occurred. They found that soluble carbohydrates constituted the major portion (50-75%) of the total soluble fraction of the seed during the 5-day germination period. Creech and McArdle (6) reported that mature kernels of the genotype ae du wx contained, on a dry weight basis, 7.13% total sugars, sh2 contained 5.90% and su, 6.33%, compared to 1.40% in normal (starchy) kernels of 'Truckers Favorite' might explain why its respiration rate was relatively low early in germination but increased to rank among the highest at 72 hr. On a limited
number of kernels, we followed the respiration rate to 96 and 120 hr (unpublished data). During that period respiration rate increased more rapidly in 'Truckers Favorite' and the su cultivars than in either of the high-sugar cultivars.

The data on respiration appear to contrast with those of Woodstock and Feeley (16) and Woodstock and Grabe (17). They found that respiration rate during the first hours of germination was positively correlated with subsequent seedling growth. They, however, imposed seed aging treatments and compared seed respiration and seedling growth rates within cultivars, and their tests were not intended for comparisons between genotypes. Results reported here are somewhat analogous to those of Cohn and Obendorf (3). They were unable to correlate slightly elevated respiration rates in corn kernels treated as high-moisture controls with any subsequent growth differential. They suggested that elevated respiration rates might have been associated with hydration level of the kernels.

Respiration rates varied greatly within seed samples having low germination percentages. Data reported here, however, were taken only from kernels that germinated readily, with non-germinating seeds being eliminated from the test. The normal genetic variation in the F2 kernels was not considered important during germination.

I conclude from these studies that the deleterious effect of the high-sugar genotypes on seed vigor was associated with small endosperms that did not sustain vigorous seedling growth. The data indicated also that the genotype of the embryo was important in seed vigor, but low vigor in the high-sugar genotypes could not be attributed wholly to genetic inferiority in the embryo. Nutrient reserves and their availability to the embryo probably are the major factors in seed vigor and might also affect embryo development and maturation of the seed. Selection to increase seed weight and the endosperm:embryo weight ratio should improve seed vigor in the high-sugar genotypes for sweet corn.

Literature Cited


Effect of Calcium in offsetting Defoliation Induced by Ethephon in Pecan1

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Abstract. A greenhouse screening system was developed with 'Curtis' seedlings of 'Curtis' pecan (Carya illinoensis (Wang) K. Koch) to test the effect of Ca in reducing defoliation caused by foliar applications of (2-chloroethyl)-phosphonic acid (ethephon). Ethephon alone at 2000 ppm induced 100% abscission, but the effect could be offset by applications of Ca from several sources. The added Ca increased the freely available Ca in treated leaves. As pH of the solutions containing ethephon alone increased from 2.0 to 8.0, less defoliation occurred.

Practical uses for ethephon in plant science are many and varied (9), and in most cases, deleterious side effects from ethephon treatment are inconsequential. However, excessive
defoliation induced by ethephon has precluded its commercial use as a harvest fruit loosener for pecan and olive (4, 8).

Poovaiah and Leopold (7) showed that Ca reduced the abscission-inducing effects of ethylene. Their report led us to test the influence of Ca on pecan leaf abscission induced by ethephon.

Our purposes were 2-fold: a) to develop a greenhouse screening system with pecan seedlings, and b) to test sources and rates of Ca to offset-ethephon-induced abscission.

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