Genetic Analysis of Pericarp Thickness in Progenies of Eight Corn Hybrids

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Abstract. Pericarp thickness in maize (*Zea mays* L.) was analyzed by generation mean analysis for backcross and F₂ populations from eight hybrids, derived from two thin-pericarped sweet corn inbreds—AA8 and 677a (55 and 51 μ m)—crossed with four field corn inbreds—B37, B68, H55, and Hi26 (range 82–132 μ m). Average heterosis was –12.5% and segregating progeny distributions were skewed toward those of thin-pericarped parents. Narrow-sense heritability was high, averaging 55.2%, and the number of effective factors was low, ranging from 1.4 to 5.9 and averaging 3.3. Epistatic effects were as large as additive or dominance effects in many crosses, urging caution in applying models that exclude gene interactions to determine variance components and heritabilities. The mode of action in reducing pericarp thickness appeared to differ among the two thin parents, with AA8 affecting the differential thickening of germinal vs. abgerminal walls, and 677a reducing the number of pericarp cell layers. All genetic parameters suggested that genetic progress in backcross conversions to thin pericarp in sweet corn breeding would be rapid irrespective of the pericarp thickness of exotic parents.

Temperate corn hybrids are based on a relatively small fraction of the available germplasm of *Zea mays*. American sweet and supersweet corns have a particularly narrow gene base. They trace back primarily to two sugary (gene *su*) cultivars of the northeastern United States, Papoon and Black Sweet (Galinat, 1971). This narrow base is especially apparent when American sweet corns are brought to the tropics, where their poor vigor and lack of disease and insect resistance make them ineffective for commercial production (Kim and Brewbaker, 1988).

Attempts to broaden the gene base for sweet corn improvement necessarily involve wild-type or "field" corns that lack endosperm mutants such as *sugary* that reduce starchiness (although a few such mutants are known among the primitive tropical races of maize). Crosses to field corns are generally avoided in sweet corn improvement due to concern about the introduction of genes for thick pericarp, which is the major component of perceived tenderness in vegetable corns (Ito and Brewbaker, 1981). This concern results in part from the fact that most temperate field corns have very thick pericarps (Helm and Zuber, 1972; Ito, 1981). Tropical sweet corns have been produced with acceptable pericarp thickness from conversions of tropical field corns to sweet genes, however (Brewbaker, 1977). Many tropical races were used as "green" or "elote" corns and have relatively thin pericarps (Brewbaker, 1982; Ito and Brewbaker, 1981).

Pericarp thickness is implicated in several important roles relating to kernal quality, including tenderness of food corns (Bailey and Bailey, 1938; Ito and Brewbaker, 1981), quality of popcorn (Richardson, 1960), drying due to water movement from the kernel (Purdy and Crane, 1967), and resistance to pathogens (Wolf et al., 1952).

Genetic studies of pericarp thickness were first conducted by Richardson (1960) in popcorn. The F₁ hybrids from a five-entry diallel showed partial dominance of the thin pericarp. F₂ plants

from a single cross (60 vs. 91 μ m) provided evidence of a single dominant gene for thinness, with modifying genes of relatively minor importance. Helm and Zuber (1972) perfected pericarp measurement techniques and analyzed two sets of diallel hybrids based on Southern Corn Belt dent inbreds. They interpreted thickness to be quantitatively inherited, with thin pericarp partially dominant in one set of crosses but not in a second. Broad-sense heritability exceeded 80%, and epistatic effects (additive $\times$ additive) were significant. Ho et al. (1975) provided support for the dominant-thinness theory. Average thickness of F₁, F₂, and BC₁ progenies of their Canadian field corn inbreds was not significantly different from that of the thin parent (61 μ m) in a cross with a thick-pericarped inbred (106 μ m). Mean heterosis was estimated from a five-entry diallel to be 8.3%, ratios of general to specific combining ability were high (9:1), and narrow-sense heritability was high (72%).

Previous studies have used only field corn genotypes. The present study involved both sweet and field corn inbreds, with the general concept of converting field corns to sweetness. The objective of this study was to determine the genetic control of pericarp thickness in field corn $\times$ sweet corn progeny.

Materials and Methods

Parents included two sweet corn inbreds with relatively thin pericarps and four field corn inbreds with thick pericarps (Table 1). All inbreds were derived from Hawaiian conversions for virus resistance (Brewbaker et al., 1989). The Hawaiian BC₅ conversions of these inbreds had somewhat thinner pericarps (Table 1) than the originals. Helm and Zuber (1972), for example, found the pericarp thickness of H55, Hi26, and B37 to be 123, 99, and 160 μ m, respectively. Tracy et al. (1978) re-

Table 1. Pedigrees of parental inbreds.

Inbred	Pericarp thickness (μ m)	Institution	Pedigree
677a (Hi)	50.5	Univ. of Illinois	442a BC
AA8	54.6	Univ. of Hawaii	Hawaiian Sugar
H55 (Hi)	82.0	Purdue	(Mo21A $\times$ Hy)Hy
Hi26	98.5	U.S. Dept. Agr.	(K577C $\times$ Hy)Hy BC2
B37 (Hi)	107.7	Iowa State Univ.	BSSS
B68 (Hi)	132.3	Iowa State Univ.	(Arg.Flt. $\times$ B14)B14BC3

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ported that sweet corn inbred 677a had a pericarp 57 μm thick (abgerminal surface), distinguished by fewer cell layers (four to six vs. six to 13 for most sweet corns). Values in the table are the averages of germinal and abgerminal surfaces.

All experiments in the present study were planted in 1979 at the Waimanalo Research Station of the Univ. of Hawaii, located at 21 N latitude on the island of Oahu. Management practices followed those of Univ. of Hawaii year-round breeding nurseries (Ito and Brewbaker, 1981). A randomized complete block design was planted with a total of three 20-hill rows for each of the P_1 , P_2 , and F_1 . Four rows were planted of each backcross and seven of each F_2 . Ten mature ears were sampled per row ≈ 6 weeks after pollination, providing 30 ears of P_1 , P_2 , and F_1 progenies, 40 ears of each backcross (labeled B_1 and B_2 to the two parents P_1 and P_2 , respectively), and 70 ears each of the F_2 progenies.

Pericarp thickness was measured from germinal and abgerminal sides at a medial position on five kernels per ear, generally following methods of Helm and Zuber (1972) as modified by Ito and Brewbaker (1981). Ears were air-dried to 15% moisture and sampled uniformly by the removal of contiguous kernels on two neighboring rows from the center of the ear. The kernels were soaked in tap water for 20 h at room temperature. The crown and tip caps of five kernels per ear were removed with a razor blade, and the pericarp slit along the edge of the kernel and peeled off with tweezers. The resulting rectangular strips were placed overnight in a solution of 2 water : 1 glycerin (v/v) in an evacuated chamber. They were then blotted dry between hand towels, rolled with a bottle, and equilibrated at room humidity (60%) overnight before measurement with an Ames no. 56212 micrometer (Ames, Inc., Waltham, Mass.). Remaining aleurone tissue, if present, was removed by scraping.

Generation mean analysis was conducted under the conventional assumptions of no epistasis or linkage. Additive and dominance (nonadditive) genetic variances (σ_A^2 and σ_D^2) and narrow-sense heritability (h^2) were estimated following the method of Warner (1952), in which $\sigma_A^2 = 2\sigma_{F_2}^2 - (\sigma_{B_1}^2 + \sigma_{B_2}^2)$, $\sigma_D^2 = \sigma_{F_2}^2 - (\sigma_A^2 + \sigma_E^2)$ and $h^2 = \sigma_A^2/\sigma_{F_2}^2$. Environmental variance was calculated by $\sigma_E^2 = (\sigma_{P_1}^2 + \sigma_{P_2}^2 + 2\sigma_{F_1}^2)/4$ and broad-sense heritability (b^2) was calculated by $(\sigma_{F_2}^2 - \sigma_E^2)/\sigma_{F_2}^2$ (Mather and Jinks, 1971).

Gene effects were based on a six-parameter model (Hayman, 1958, 1960). Estimates of gene effects (m = mean, a = additive, d = dominance or nonadditive, others = epistatic) were presented using the notation of Gamble (1962) and derived as follows:

$$\begin{aligned} m &= F_2 \\ a &= B_1 - B_2 \\ d &= -(P_1)/2 - (P_2)/2 + F_1 - 4F_2 + 2B_1 + 2B_2 \\ aa &= -4F_2 + 2B_1 + 2B_2 \\ ad &= -(P_1)/2 + (P_2)/2 + B_1 - B_2 \\ dd &= P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2 \end{aligned}$$

Significance of the estimates was tested by the standard error was of each of the six parameters.

Results

Effect of endosperm genotype and location of measurement. Pericarp thicknesses were compared between sweet corn (*su*)

and normal kernels from the same open-pollinated F_1 ears (Table 2). The two endosperm genotypes proved identical, indicating that pericarp thickness is not influenced by the starch composition of the endosperm. These data were taken as the basis for pooling data from the two endosperm genotypes in the generation mean analyses.

Pericarps from seven of the eight crosses were studied to assess the effects of the position of measurement on the kernel and of endosperm genotype. Values for the abgerminal surface of the kernel averaged 71.7 μm , while those for the germinal surface averaged 62.7 (Table 3). However, highly significant differences occurred among the hybrids in this comparison. The 677a hybrids consistently showed thicker abgerminal surfaces, while two of the three AA8 hybrids showed no difference between the two surfaces. This differential effect on the germinal and abgerminal surfaces from different crosses could have contributed to discrepancies to be reported in the quantitative genetic analyses.

Population means. Means and their SE for parental, F_1 , F_2 , and backcross generations were derived from two readings each on 9600 pericarps from progenies generated by the eight crosses (Table 4). Means of the F_1 s were consistently closer to the mean of the thin pericarp parent, with an average heterosis of -12.5%.

Frequency distributions. Frequency distributions of the six generations for each of the eight crosses are graphed in 10- μm intervals in Fig. 1. Parental distributions normalized and were nonoverlapping in most cases. The F_1 distributions normalized, but those of F_2 were generally shifted heavily toward the thinner parent (more noticeably in 677a crosses). Backcross distributions overlapped and were also shifted toward thinner parents, but were distinctive for almost every cross. The F_2 means were less than those of F_1 s in all eight comparisons, and significantly less in four cases. The failure of the F_2 means to shift back toward the midparent seemed to implicate gene interaction or epistatic effects (Fig. 1, Table 4). The backcross means generally reverted toward means of the recurrent parent. A major exception was provided by backcrosses of H55, which were

Table 2. Pericarp thickness for sweet and field corn kernels.

Position	Endosperm type	Pericarp thickness		No.
		Mean $\pm$ SD (μm)	CV (%)	
Germinal	<i>su</i>	63.0 $\pm$ 11.91	18.9	984
	+	62.3 $\pm$ 11.31	18.2	971
Abgerminal	<i>su</i>	71.8 $\pm$ 19.29	28.9	984
	+	71.5 $\pm$ 17.20	24.1	971
Mean	<i>su</i>	67.4 $\pm$ 16.52	24.7	1968
	+	66.9 $\pm$ 15.27	22.8	1942

Table 3. Pericarp thicknesses of germinal and abgerminal positions in seven F_1 hybrids.

Hybrid	Germinal (Mean $\pm$ SD)	Abgerminal (Mean $\pm$ SD)	Difference (%)
		μm	
AA8 $\times$ Hi26	62.7 $\pm$ 8.7	76.9 $\pm$ 16.8	22.6
AA8 $\times$ B68	68.0 $\pm$ 8.5	68.7 $\pm$ 9.1	1.0
AA8 $\times$ H55	54.8 $\pm$ 6.9	48.7 $\pm$ 19.3	-12.5
677a $\times$ Hi26	56.4 $\pm$ 10.2	64.5 $\pm$ 13.2	14.4
677a $\times$ B68	72.2 $\pm$ 8.5	91.7 $\pm$ 10.2	27.0
677a $\times$ H55	56.6 $\pm$ 9.2	65.3 $\pm$ 11.4	15.4
677a $\times$ B37	67.9 $\pm$ 12.7	85.9 $\pm$ 13.1	26.5
Mean	62.7 $\pm$ 5.3	71.7 $\pm$ 8.6	14.4

Table 4. Pericarp thickness for parents (P₁, P₂), F₁, F₂, and backcross (B₁, B₂) generations.^a

Thin parent (P ₁)	Generation	Pericarp thickness (μm)			
		Thick parent (P ₂)			
		Hi26	B68	B37	H55
AA8	P ₁	54.6 ± 1.1	54.6 ± 1.1	54.6 ± 1.1	54.6 ± 1.1
	P ₂	98.5 ± 2.3	132.3 ± 2.3	107.7 ± 2.2	82.0 ± 1.4
	F ₁	68.9 ± 1.8	68.6 ± 1.1	74.3 ± 1.6	51.3 ± 1.3
	F ₂	58.9 ± 1.7	74.7 ± 1.6	71.6 ± 1.7	59.9 ± 1.5
	B ₁	51.2 ± 1.6	63.5 ± 1.9	64.7 ± 1.7	57.5 ± 2.0
	B ₂	73.3 ± 1.5	78.8 ± 2.0	67.6 ± 1.7	54.2 ± 1.3
677a	P ₁	50.5 ± 1.2	50.5 ± 1.2	50.5 ± 1.2	50.5 ± 1.2
	P ₂	98.5 ± 2.4	132.3 ± 2.3	107.7 ± 2.2	82.0 ± 1.4
	F ₁	59.9 ± 1.8	81.1 ± 1.4	77.1 ± 1.9	61.4 ± 1.2
	F ₂	57.3 ± 1.5	61.3 ± 1.7	62.1 ± 2.2	52.1 ± 1.3
	B ₁	54.0 ± 2.0	52.2 ± 2.1	63.5 ± 1.7	49.6 ± 1.5
	B ₂	69.8 ± 2.4	103.2 ± 3.0	102.6 ± 2.4	61.1 ± 1.5

^aData are means of 30 (P₁, P₂, F₁), 40 (B₁, B₂), or 70 (F₂) ears with SE of the means.

exceptionally thin for both progenies, confirming the observation of Helm and Zuber (1972) that H55 has "negative line heterosis," or potency for thin pericarp.

Crosses involving the tropical thin-pericarped AA8 were generally marked by similar F₁ and F₂ distributions—intermediate to parents yet skewed toward thinness—and by backcross distributions that were both skewed toward thinness (Fig. 1). The F₁ and F₂ distribution of crosses involving Illinois inbred 677a were also skewed to thinness, but backcrosses were less strongly skewed. The B₂ backcrosses (to thick-pericarp parent inbreds labelled P₂) were of particular interest, as they represent the traditional approach in conversion of a thick-pericarped inbred to thinness. Segregations of B₂ crosses differed greatly from cross to cross, however, allowing no generalized predictions. The factorial combination of parents normally permits conclusions about general combining ability patterns common to all crosses involving a given parent, but such patterns were few and were marred by inconsistencies.

Gene effects. Generation mean analysis provided estimates of six parameters (gene effects) for each of the eight crosses (Table 5). Mean effects (m) were calculated simply as the mean of the pertinent F₂ progeny. Additive (a) effects, derived by comparing B₁ and B₂ progenies (Gamble, 1962), were commonly significant and toward the thin parent. All 677a crosses showed significant additive effects, but two of the four AA8 crosses were not significant. The relative magnitudes of additive effects were generally larger in 677a crosses than in AA8 crosses.

Dominance or nonadditive gene effects were significant in three of the AA8 and two of the 677a crosses (Table 5). The significant dominance gene effects for AA8 crosses were negative, i.e., toward the parent with thinner pericarp. In contrast, those of 677a crosses were all positive, suggesting that 677a contains genes for thick pericarp that were expressed particularly in the B37 and B68 crosses. Dominance effects were significant for all B37 and B68 crosses, but were not significant in the CI21E crosses. The relative magnitudes and significance of additive and dominance effects depended on the cross involved, allowing few generalizations.

Epistasis effects (parameters aa, ad, dd) were commonly significant, suggesting a major influence of gene interactions (Table 5). Additive × additive (aa) effects, based on the comparison of F₂ and backcross means, were commonly large, positive (toward thick parent), and statistically significant for 677A crosses. The aa effects for AA8 crosses were smaller and variable in

sign. Additive × dominance (ad) and dominance × dominance (dd) effects were commonly large, positive, and significant for AA8 crosses, but variable, often negative, and less commonly significant for 677a crosses. The signs of these estimates for AA8 crosses with B37 and B68 were consistently opposite those of the 677a crosses, as noted for the dominance (d) effects. These differences correlate with the unique B₂ distributions of AA8 crosses (Fig. 1), that showed little or no shift toward the thicker parent.

Variance components and heritability estimates. The additive genetic variances (σ_A^2) were generally much larger than dominance variance (σ_D^2), but differed greatly from cross to cross (Table 6). Large variations were observed for both components, with σ_A^2 ranging from -47.6 to 263.6 and σ_D^2 from -85.0 to 134.6. Negative variances were common (five of 16 estimates) and were interpreted as zero (Robinson et al., 1955), and environmental variances were relatively large. The phenotypic variance, averaged over all crosses, contained 48.7% additive genetic variance, 3.0% dominance variance, and 48.3% environmental variance. Mean heritability estimates of nH = 41.8% and bH = 59.5% were derived by equating negative variance values to zero (Table 6). Genetic gain values (Gs) for 5% selection ranged up to 32 μm per generation. Values are provided in Table 6 for log conversions of pericarp data (lnGs). Estimates of genetic gain were large only for those crosses involving large differences between parental values.

The minimum number of effective factors was estimated by both the Wright and Castle-Wright formulas (Table 7), and averaged 3.3 effective factors over all crosses. Values were similar for the two methods, and suggest a major genetic difference (five factors) only in the case of inbred B68, which at 132 μm had the thickest pericarp in the study.

Discussion

Our results confirm that pericarp thickness is controlled by oligogenes (Helm and Zuber, 1972; Ho et al., 1975), but argue against generalizations, since segregations are very different from parents of similar pericarp thickness. Gene number estimates averaged 3.3 and ranged from 1.4 to 5.9 for the eight crosses. No single genes of major effect were observed, as also concluded by Richardson (1960).

All hybrids showed partial dominance for thin pericarp, and high additive variances were observed that should permit rapid

Fig. 1. Frequency distributions of pericarp thickness in corn ears derived from eight crosses (P_1 and P_2 = parents; B_1 and B_2 = backcrosses to these parents; F_1 and F_2 = hybrids and advanced generation from these hybrids).

genetic gains toward thinness. F_2 and backcross distributions were often shifted toward those of the thin-pericarped parent, as noted also by Ho et al. (1975). We conclude that direct

backcrossing and selection likely will satisfactorily reduce pericarp thickness but will be more effective if supplemented by interspersed F_2 populations.

Table 5. Estimates (μm) of the six gene effects for pericarp thickness from eight crosses.

Parameter	Gene effects for progenies							
	AA8	AA8	AA8	AA8	677a	677a	677a	677a
	x Hi26	x B68	x B37	x H55	x Hi26	x B68	x B37	x H55
m	58.9	74.7	71.6	59.9	57.3	61.3	62.1	52.1
a	-22.1**	-15.3**	-2.9	3.4	-15.7**	-50.9**	-39.1**	-11.5**
d	6.0	-38.9**	-28.9**	-33.0**	3.6	55.4**	81.9**	8.2
aa	13.7	-14.0	-22.0**	16.0*	18.2*	65.7**	83.9**	13.0*
ad	-0.2	23.5**	23.7**	17.0**	8.2**	-10.0**	-10.5**	4.3*
dd	28.1**	53.6**	68.5**	31.9**	3.1	-31.4*	-103.7**	20.9*

*,**Significant at $P = 0.05$ and 0.01 , respectively.

Table 6. Estimates of additive (σ_A^2), dominance (σ_D^2), and environmental (σ_E^2) variances, broad (bH)- and narrow (nH)-sense heritabilities, and genetic advance through selection (Gs) for pericarp thickness.

Cross	Variance components			Heritabilities		Selection gains	
	σ_A^2	σ_D^2	σ_E^2	bH	nH	Gs	lnGs
AA8 x Hi26	219.5	-85.1	69.2	76.0	76.0	31.7	26.8
AA8 x B68	66.4	31.0	75.7	56.3	38.3	10.4	10.4
AA8 x B37	193.4	-81.1	93.7	67.4	67.4	27.8	26.1
AA8 x H55	69.1	16.1	57.2	59.9	48.6	11.9	7.3
677a x Hi26	-47.6	106.5	112.1	48.7	0.0	0.0	4.6
677a x B68	-24.8	134.2	94.8	58.6	0.0	0.0	13.3
677a x B37	263.4	-79.7	111.1	70.4	70.4	13.2	45.9
677a x H55	33.3	5.1	60.6	38.7	33.7	6.9	6.0
Mean	96.6	5.9	95.7	59.5	41.8	12.7	17.5

Table 7. Minimum number of genes controlling pericarp thickness.

Cross	Effective factors ^a (no.)		
	CW	W	Mean
AA8 x Hi26	2.2	2.3	2.3
AA8 x B68	5.3	6.4	5.9
AA8 x B37	2.7	2.8	2.8
AA8 x H55	1.0	1.8	1.4
677a x Hi26	3.8	4.4	4.1
677a x B68	5.6	5.8	5.7
677a x B37	2.1	2.1	2.1
677a x H55	2.3	2.4	2.3

^aCW = Castle-Wright formula; W = Sewall-Wright formula.

We conclude that at least three different morphological changes were involved in pericarp thickness polymorphism: 1) the number of pericarp cell layers, which can range from two to 20, lower values being found only in teosintes (Tracy et al., 1978), 2) differential thickening of cells on germinal and abgerminal surfaces, and 3) the thickening of individual pericarp cell walls.

The two sources of thin pericarp used in this study, AA8 and 677a, were high combiners for thin pericarp (Brewbaker, 1968) but appear to differ in at least two important ways. The 677a inbred had distinctly fewer cell layers in the pericarp, about half that of most sweet corns (Tracy et al. 1978). The AA8 inbred is shown here (Table 3) to confer on its hybrids a particularly thin pericarp on the abgerminal sides of kernels, as contrasted with 677a and most other corns. In a survey of 85 races of maize, most showed thicker abgerminal pericarp, 42 of them significantly so (J.L.B., unpublished).

All types of digenic epistasis were shown by generation mean analysis to be important in affecting inheritance of pericarp

thickness. Generalizations could not be made, however, since the type of gene effects depended on the cross involved. Additive $\times$ additive epistasis was significant in Helm and Zuber's study (1972), while the dominance $\times$ dominance interaction predominated in the cross studied by Ho et al. (1975). It is clear, therefore, that genetic models that assume no epistasis do not accurately describe the quantitative genetics of pericarp thickness. A reasonable model for epistasis is that of interaction of genes governing the three morphological changes associated with pericarp thickness described above.

Narrow-sense heritability estimates averaged 41.8% for our data and 58.6% for the log-transformed data (Ito, 1981). These values were lower than the 72% of Ho et al. (1975) and 80% of Helm and Zuber (1972), that were based on regression of offspring on midparent values. When our values were used to calculate offspring-parent regressions, a higher narrow-sense heritability estimate (72%) was also obtained.

A narrow-sense heritability estimate can also be made from our previous tenderness selection study (Ito and Brewbaker, 1981), using the formula for calculating gain from selection: $G_s = k nH \sigma_p^2$, where k is the selection intensity in SD, nH is narrow-sense heritability, and σ_p^2 is the phenotypic variance. Average genetic gains and SD were 8.3 and 15.2 μm , respectively. A selection intensity of 10% was applied, leading to a k value of 1.76 and $nH = 8.3 \mu\text{m}/(1.76)(15.2 \mu\text{m}) = 0.32$. The realized heritability was lower than the narrow-sense heritability estimated in our current study. We attribute this to epistasis, which normally is assumed to be zero in producing estimates of heritability (Comstock, 1955).

Genetic gains with the selection index of 5% are calculated to be 11.5 and 17.5 μm per generation, using nH estimates from the original and the log-transformed data in the present study, respectively. These values can be compared with the average gain of 8.3 μm for cycles 2 and 3 of our selection experiment (Ito and Brewbaker, 1981). Pericarp data for 85 races of maize ranged from 36 to 124 μm , vs. 35 to 55 μm for superior sweet corns (J.L.B., unpublished). These values suggest that pericarp thicknesses of many exotic lines may be reduced to those of average sweet corns with little difficulty, an inference borne out by our ease in breeding tropical supersweets (*bt* gene) based on direct conversion of tropical flints (Brewbaker, 1982). This result does not imply that continued reduction in thickness can be made, because it may lead to problems with osmotic burst and pathogen invasion.

Conclusions from quantitative genetic studies are naturally reinforced by use of multiple locations or seasons, labor permitting. In our extensive experience breeding thin-pericarped corns in Hawaii, however, kernels from lines that mature under diverse conditions differ negligibly in pericarp thickness (Ito,

1981). This is evidenced also in the present study by the identity of pericarp thickness values on seeds of different endosperm genotypes (Table 2).

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