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QTL Influencing Kernel Chemical Composition and Seedling Stand Establishment in Sweet Corn with the *shrunken2* and *sugary enhancer1* Endosperm Mutations

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Abstract. **This study was conducted to identify the chromosomal location and magnitude of effect of quantitative trait loci (QTL) controlling sweet corn (*Zea mays* L.) stand establishment and investigate the impact of dry kernel characteristics on seedling emergence under field conditions. Genetic and chemical analysis was performed on two $F_{2:3}$ populations (one homozygous for *su1* and segregating for *se1*, the other homozygous for *sh2* endosperm carbohydrate mutations) derived from crosses between parental inbreds that differed in field emergence and kernel chemical composition. A series of restriction fragment-length polymorphism (RFLP) and phenotypic markers distributed throughout the sweet corn genome were used to construct a genetic linkage map for each population. $F_{2:3}$ families from the two populations were evaluated for seedling emergence and growth rate at four locations. Mature dry kernels of each family were assayed for kernel chemical and physiological parameters. Composite interval analysis revealed significant QTL associations with emergence and kernel chemical and physiological variables. Improved emergence was positively correlated with lower seed leachate conductivity, greater embryo dry weight, and higher kernel starch content. QTL affecting both field emergence and kernel characteristics were detected in both populations. In the *su1 se1* population genomic regions significantly influencing emergence across all four environments were found associated with the *se1* gene on chromosome 2 and the RFLP loci php200020 on chromosome 7 and umc160 on chromosome 8. In the *sh2* population the RFLP loci umc131 on chromosome 2 and bnl9.08 on chromosome 8 were linked to QTL significantly affecting emergence. Since seedling emergence and kernel sugar content have been shown to be negatively correlated, undesirable effects on sweet corn eating quality associated with each emergence QTL is discussed. Segregating QTL linked to RFLP loci in these populations that exert significant effects on the studied traits are candidates for molecular marker-assisted selection to improve sweet corn seed quality.**

Traditional *sugary1* (*su1*) sweet corn hybrids are characterized by a rapid loss of quality after harvest due to the conversion of sugars to starch and moisture loss. This problem has restricted the location of *sugary1* sweet corn production to areas adjacent to major urban markets due to the loss of quality during extended trans-shipment. Endosperm mutations other than *su1,* which produce qualitative and quantitative differences in kernel carbohydrate metabolism (Azanza et al., 1996a), have been used to develop new commercial sweet corn hybrids. Of importance to the sweet corn industry are the mutants *sugary enhancer1* (*se1*), in combination with *su1*, and *shrunken2* (*sh2*). Hybrids with these endosperm mutations contain 1.5 to 3.0 times more sugar at typical fresh harvest (18 to 22 d after pollination, DAP) (Carey et al., 1984; Douglass et al., 1993) compared to *su1* sweet corn. These hybrids retain higher sugar and kernel moisture content for longer post-harvest periods (Carey et al., 1982; Garwood et al., 1976).

In sweet corn ears at typical fresh harvest, the *se1* allele when homozygous increases total sugar in *su1se1* kernels to levels comparable to those in *sh2* kernels without a reduction in phytoglycogen content (Gonzales et al., 1974; 1976), a water soluble starch that provides a tender and creamy texture. Carbohydrate analysis of genotypes from the three endosperm groups at the mature-dry stage revealed that *se1* kernels were compatible to *su1* in total starch content and to *sh2* in sugar concentration (Douglass et al., 1993). The *sh2* gene results in greatly reduced levels of adenosine 5'-diphosphate glucose pyrophosphorylase (ADGP) (Dickinson et al., 1983). The deficiency of this enzyme leads to the accumulation of sucrose in kernels at the expense of water-soluble polysaccharides and starch, producing a very sweet taste (Boyer and Shannon, 1983). Mature-dry *sh2* seeds contain

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about twice the total sugar content, one-third to one half the starch level, and only trace levels of phytoglycogen in comparison to *su1* seeds (Douglass et al., 1993).

In concert with the desirable attributes of the *sh2* and *se1* mutations on sweet corn eating quality, there is an associated reduction in seedling emergence and growth rate (stand establishment), which have adversely affected their commercial use, particularly at soil temperatures below 15 °C (Andrew, 1982; Douglass et al., 1993; Juvik et al., 1993). Several theories have been proposed to explain the physiological basis of poor seedling emergence associated with these mutations, particularly *sh2* (Young et al., 1997). In *sh2* genotypes the reduced quantity of endosperm and starch results in the formation of air spaces between the endosperm, aleurone, and pericarp tissues during kernel dry-down and gives the seed a collapsed appearance (Styer and Cantliffe, 1983). Douglass et al. (1993) proposed that poor seedling emergence was due to the reduced starch concentration in dry kernels, which results in reduction in the energy reserves required for emergence. Reduced kernel starch content also results in greater cracking of kernel pericarp during *sh2* seed maturation, which is then responsible for more solute leakage during germination (Juvik et al., 1993). Waters and Blanchette (1983) found a significant correlation between kernel water soluble leachate conductivity and field emergence of 13 *su1* sweet corn cultivars although standard laboratory germination tests and field emergence were not significantly correlated. Cell membrane damage associated with high osmotic potential generated by elevated *sh2* kernel sugar concentration and the resulting rapid influx of water during imbibition (Simon, 1978) are also implicated as mechanisms reducing seedling survival. Harris and DeMason (1989) found an association between poor emergence and the lowered activities and amounts of the starch hydrolytic enzyme, α-amylase, in *sh2* compared to *su1* sweet corn. Finally, Headrick et al. (1990) reported that susceptibility of kernels during maturation to infection by fungal pathogens such as *Fusarium moniliforme* was associated with reduced seedling emergence.

The preceding review suggests that seedling emergence and stand establishment are controlled by many genetic factors and environmental conditions. Previous studies with maize have suggested that stand establishment is under polygenic control with relatively low heritability (McConnell and Garner, 1979; Yousef and Juvik, 2001). Improving quantitative traits using a conventional breeding program can be difficult and time consuming. The last two decades have seen a dramatic increase in the use of DNA marker technology as a tool in crop improvement programs. The application of molecular marker technology to quantitative genetics and plant breeding has facilitated the study of complex, quantitatively inherited traits, and made it possible to differentiate the genes controlling these traits into individual Mendelian factors.

Many studies have been conducted to map quantitative trait loci (QTL) of important traits in maize (see Bernardo, 1999). Using saturated linkage maps constructed from DNA markers, it is now possible to estimate the location and magnitude of effect of the loci influencing the expression of quantitative traits (Breto et al., 1994; Tanksley et al., 1996; Xiao et al., 1996). Restriction fragment-length polymorphism (RFLP) loci linked to genes influencing emergence and stand establishment in sweet corn could be used for indirect selection for these traits (Tadmor et al., 1995).

In this current study, two segregating $F_{2:3}$ populations derived from crosses between the sweet corn inbreds IL451b *sh2* x Ia453 *sh2* and between W6786 *su1Se1* x IL731a *su1se1* were evaluated for stand establishment and mature-dry kernel chemical and physiological characteristics. Previous publications have described the linkage map of the W6786 *su1Se1* x IL731a *su1se1* $F_{2:3}$ population and mapped the location of the *se1 gene* (Tadmor et al., 1995) and mapped QTL influencing fresh sweet corn (20 d after pollination) kernel chemical and sensory quality in this same population (Azanza et al., 1996b). In addition, three of the RFLP loci associated with improved emergence in the *sh2* population and described below have been used in an experiment to compare the efficiency of phenotypic versus marker assisted selection (Yousef and Juvik, 2001) and to evaluate effect of the beneficial alleles at these loci on emergence when backcrossed into commercial sweet corn backgrounds (Yousef and Juvik, 2002). The unique objectives of this investigation were to 1) investigate the physiological and genetic relationship between mature-dry kernel chemical composition and field seedling emergence; 2) identify QTL influencing field emergence and dry kernel characteristics in sweet corn with the *se1* and *sh2* endosperm carbohydrate mutations across four environments; and 3) determine which loci associated with emergence can enhance stand establishment with minimal negative effect on sweet corn eating quality.

Material and methods

Plant material. Originally, 65 sweet corn inbreds were evaluated for several characteristics associated with field emergence in field plots at the University of Illinois at Urbana-Champaign in 1989. These inbreds, homozygous for either *sh2*, *se1*, *su1*, or *Su1* endosperm, differed in percent field seedling emergence and growth rates (data not shown). The inbreds with poor seedling emergence but carrying desirable kernel eating quality characteristics were crossed in all possible combinations with inbreds with the best field performance.

Two inbreds with excellent eating quality at fresh harvest (IL731a *su1se1* and IL451b *sh2*) were crossed with two inbreds showing superior emergence and stand establishment (W6786 *su1*, Ia453 *sh2*) (Azanza et al., 1996a). W6786 and Ia453 have relatively low mature-dry kernel sucrose (41 and 52 $mg \cdot g^{-1}$) and high starch (418 and 265 mg/g), but display greater field emergence (62% and 30%) compared to IL731a *su1se1* and IL451b *sh2* in spring plantings. In contrast, IL731a and IL451b displayed high kernel sucrose (140 and 105 $mg \cdot g^{-1}$) and low starch (156 and 215 mg/g), with poor field emergence (30% and 10%), respectively. F_1 plants of these crosses were grown, self-pollinated, and F_2 populations generated. Individual F_2 plants were selfed to create F_3 seeds. The ears were harvested at ≈40 DAP, dried, shelled and the seed was stored at 4°C.

One hundred kernels of each of the $F_{2:3}$ families and the parents in the two populations were sown in flats containing a 1:1:1:2 soil mixture of soil : peat : perlite : vermiculite. Seedlings were hardened off and transplanted into field plots on the University of Illinois' South Farm. At anthesis, 30 to 40 plants in each family were sib-pollinated to provide adequate seed amounts of each $F_{2:3}$ family. Mature-dry seeds were harvested at ≈40 DAP, dried, and bulked. The resulting sib-pollinated $F_{2:3}$ seed was used in the studies described below to provide replicated data for an averaged estimate of individual F_2 plant phenotypic performance. Seed from a total of 214 families was developed for the W6786 *su1Se1* x IL731a *su1se1* population and 117 families from IL451b *sh2* x Ia453 *sh2* population. Hereafter, these two $F_{2:3}$ populations will be referred to as the *sugary enhancer1* (*se1*) and *shrunken2* (*sh2*) populations, respectively.

Evaluation of field seedling emergence. Field evaluations were conducted to determine seedling emergence and growth rate of the $F_{2:3}$ families in four environments (two in Urbana-Champaign, Ill., in 1993 and 1994 (year-1 and year-2); one in Newe Ya'ar, Israel in 1993; and one in Madison, Wisconsin in 1993). Planting dates in Illinois were 7 May 1993 and 16 May 1994 for both *se1* and *sh2* populations. Planting dates in Israel and Wisconsin were 29 Mar. and 18 May 1993 with both populations, respectively. The experimental design was a randomized complete block design (RCBD) with three replications and one hundred kernels per plot. Four weeks after planting at each location, data were collected for seedling emergence and plant height. Percentage emergence was determined by direct count of emerged seedlings of each family in each of the three replications. Heights of 10 plants per plot were recorded and remeasured 2 weeks later. Height of plant was measured from soil level to base of top leaf. Seedling growth rate ($mm \cdot d^{-1}$) was determined by dividing the increase in mean plant height by number of days between the two measurements.

Kernel chemical analyses—carbohydrates. Kernel chemical and physiological analyses were performed using three replicates of one hundred kernel subsamples from 30 to 35 sib-pollinated plants that were bulked within each family in the *sh2* and *se1* populations. The carbohydrate contents including sugars, phytoglycogen, and starch of mature-dry kernels were measured in $mg \cdot g^{-1}$ dry weight and mg/kernel in each $F_{2:3}$ family. Hereafter, the term content will refer to chemical amounts on a mg/kernel basis, while kernel concentration will be presented as mg/g dry weight. Sugars were extracted in 80% ethanol (Juvik and La Bonte, 1988). The fructose, glucose, sucrose, and maltose in dry kernels were assayed by High Performance Liquid Chromatography (HPLC) (Azanza et al., 1996a). Following sugar extraction, pellet samples were used for extraction of phytoglycogen using the phenol sulfuric colorimetric method (Headrick et al., 1990). After the phytoglycogen extraction, pellets were used to quantify kernel water-insoluble starch concentrations. The starch was hydrolyzed with amylase and amyloglucosidase and analyzed by the phenol sulfuric colorimetric method (Headrick et al., 1990).

Kernel chemical analyses—protein and lipids. Protein and lipid concentrations in the mature-dry kernels were measured using a Dickey-John GAC III near-infrared analyzer (Hymowitz et al., 1974). This machine was previously calibrated using freeze-dried kernel powder obtained from mature sweet corn samples. After preliminary quantification of the protein and lipid levels in all the $F_{2:3}$ families, a set of 10 samples covering the range of variation in protein and lipid concentrations were determined by Kjeldahl analysis using the procedure described by Singletary and Below (1990). Quantitative lipid analysis on the same samples was conducted at the Peoria USDA Northern Regional Research Center. The machine, a near infra-red analyzer, was then recalibrated using data from these samples with known concentration and the $F_{2:3}$ samples quantified for protein and lipid concentrations.

Kernel physiological analyses. Kernel dry weight (mg/kernel) was calculated based on the average of 100 randomly selected kernels from each $F_{2:3}$ family. Kernel leachate conductivity measurements were made following procedures outlined by Waters and Blanchette (1983). Three replicates of 40 seeds of each $F_{2:3}$ family were counted, weighed, and submerged in 100 mL of deionized distilled water. After 24 h of soaking, the conductivity of the water from each jar was estimated by measuring the electrical stream passing through the solution in μS units, using a HI 8733 conductivity meter (Hanna Instruments, Singapore). The data were than converted to $\mu S \cdot g^{-1}$ of seed weight. The same seeds used for the kernel leachate conductivity measurements were then soaked for an additional 24 h, after which embryos from ten kernels of each sample were separated from the pericarp and endosperm, weighed, freeze-dried and re-weighed to estimate embryo and endosperm dry weight.

RFLP analyses and genetic mapping. Equal volume amounts of leaf tissue from 25 to 30 $F_{2:3}$ greenhouse grown seedlings of each family were collected, bulked, freeze dried, and stored at –80 °C. Total DNA was isolated from finely ground tissue using the CTAB procedures described by Saghai-Maroof et al. (1984) and Hoisington (1991). Ten micrograms of DNA were digested with 30 units of *Eco*RI, loaded into 0.8% agarose, and subjected to Southern analysis as described by Hoisington (1991).

RFLP probes, maintained as genomic clones, were used in this study. These clones originated from collections of mapped maize clones developed and provided by the University of Missouri-Columbia (umc), Brookhaven National Laboratory (bnl), and Pioneer Hi-Bred International (php). Clones obtained from Pioneer Hi-Bred International also included a set of genomic clones originally from Native Plants, Inc. (npi). Over 200 maize genomic probes were tested for detection of RFLP variants between the parents of the two populations. Of these markers, 62% (125) were found polymorphic. In total, 115 genomic clones (55 unique to the *se1* population, 27 unique to the *sh2* population, and 33 shared) and 3 cDNA clones from known structural genes *SH1* (Sheldon et al., 1983) and *SH2* (Bhave et al., 1990) and *DHN1* (Close et al., 1989) were used for hybridization to DNA from the $F_{2:3}$ families. Genomic and cDNA clones were oligolabeled and hybridized to membranes according to Hoisington (1991).

Two morphological markers (*se1* gene and *a2*) were scored in the *se1* population. The *se1* gene was scored based on kernel color and pericarp texture of mature-dry kernels in the F_3 generation of the cross between IL731a *su1se1* x W6786 *su1* (La Bonte and Juvik, 1990; 1991). The *a2* locus was scored for each family by the recording of red pigmentation in the epicotyl region of seedlings. A total of 93 and 61 marker loci were scored for each of the families in the *se1* (88 RFLP, 3 cDNA, and 2 morphological) and *sh2* (60 RFLP and 1 cDNA) $F_{2:3}$ populations, respectively and subjected to the software program MAPMAKER (Lincoln et al., 1990a; 1990b). Multipoint maximum likelihood linkage analysis was performed (minimum LOD score of 3.0 with a recombination fraction of 4.0). Markers used to construct the genetic map fit the expected segregation ratio for co-dominance or complete dominance at each single locus.

Statistical analyses and quantitative trait loci (QTL) detection. For each of the variables, mean, standard deviation, and range in the segregating $F_{2:3}$ populations and correlation among traits were calculated (SAS, 1991). Phenotypic correlation coefficients (Pearson's correlation) were calculated using $F_{2:3}$ family means of Illinois (year-1) location to study the relationship among different kernel characteristics and field seedling emergence. The putative locations of the QTL were determined by composite interval mapping analysis (CIM) using the PLABQTL software (Utz and Melchinger, 1995), which uses multiple regression of phenotypic on marker genotypic data as proposed by Haley and Knott (1992). The LOD score of >3.0 was chosen for all traits except with seedling emergence (LOD > 2.5) to reduce Type I error and the detection of false-positive QTL. The LOD >2.5 was used for seedling emergence QTL so as to avoid type II error in this targeted trait. Three of the detected QTL at >2.5 were used in a marker-assisted selection program and showed real association

with seedling emergence (Yousef and Juvik, 2002). Using a set of markers as cofactors, CIM increases the power of QTL detection and reduces the bias in the estimated position and effects of QTL (Utz and Melchinger, 1995). The output of the program includes putative QTL location, position of flanking markers, support interval (SI), LOD score, R^2, and the additive and dominance effects for detected QTL. The estimates of QTL location are obtained using the LOD score with support intervals that represent a 1.0 LOD drop off on either side of this position.

Results and discussion

Sweet corn genetic map. The two sweet corn maps for the *se1* and *sh2* populations are presented in Figs. 1 and 2, respectively. Although sweet and dent corn have somewhat distinct origins (Kaukis and Davis, 1986), no significant chromosomal rearrangements were observed between these two sweet corn maps and the field corn map developed at the University of Missouri-Columbia (UMC) (Gardiner et al., 1993). This is expected since crosses between sweet and field corn show full fertility. The estimated total length of the *se1* population gene map was 1779.1 *cM* with an average distance between markers of 18.9 *cM*. Adding conservative linkage distances to the terminal regions of each linkage group in the *se1* population provides for a saturated map that should detect all measurable QTL for the various traits segregating in this population. The *sh2* population with fewer markers had an estimated length of 1032.3 *cM* with an average marker linkage distance of 16.9 cM. Assuming the terminal markers on each chromosome will uncover linkage of at least 30 map units to distally located QTL, total genome coverage is expected to be 1545 *cM*.

Variability in $F_{2:3}$ families for field performance and kernel characteristics. Large differences within the two populations were found for most of the field parameters and kernel characteristics (Table 1). The large range and substantial variability among the families for most of these traits and the lack of any obvious qualitative variation suggest that these traits were influenced by the segregation of several to many gene loci. For example in the *se1* population, seedling emergence in Illinois ranged from 22% to 78%, in Israel from 4% to 82%, and in

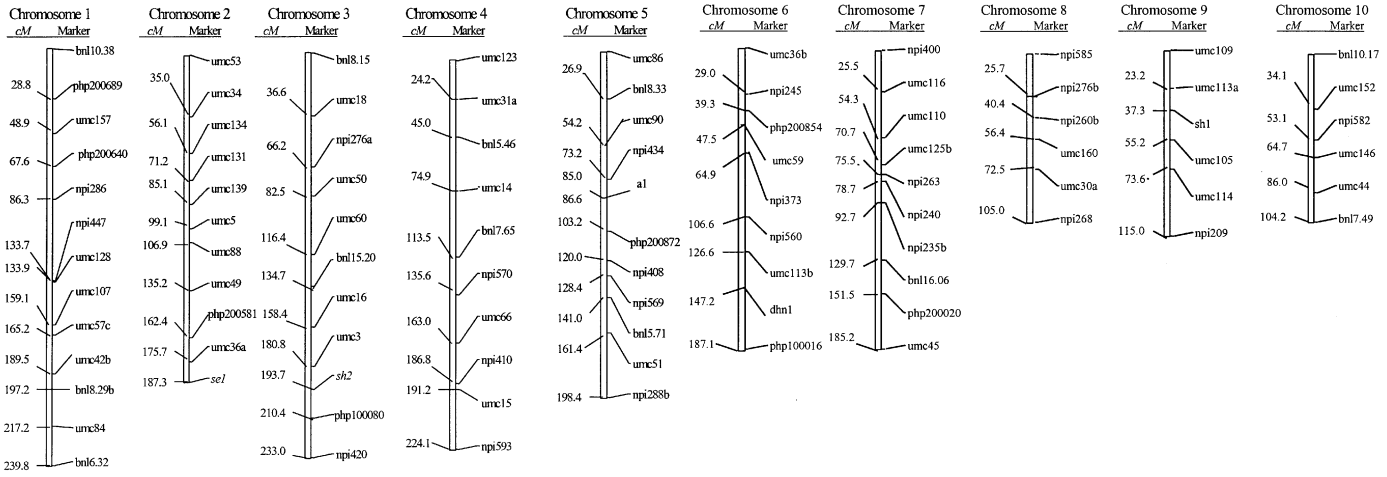

Fig. 1. Genetic linkage map of the *se1* $F_{2:3}$ sweet corn population (W6786 x IL731a).

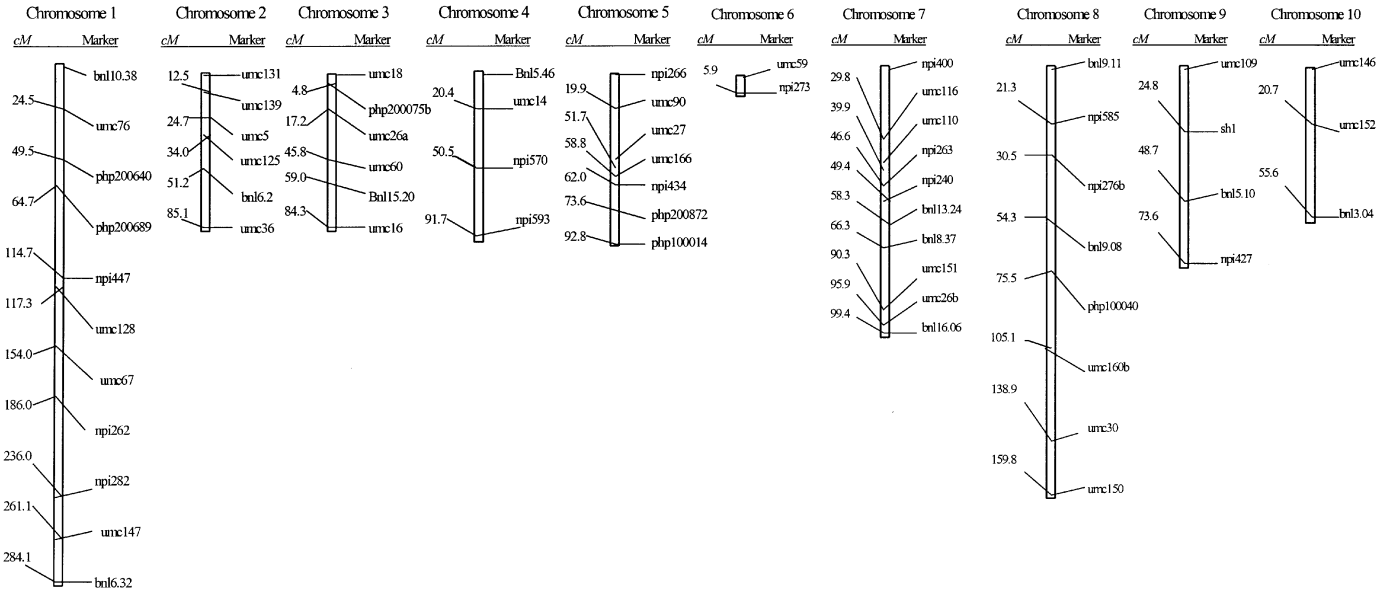

Fig. 2. Genetic linkage map of the *sh2* $F_{2:3}$ sweet corn population (IL451b x Ia453).

Wisconsin from 5% to 76% with plotted means for the families displaying a bell-shaped distribution. In the *sh2* population, seedling emergence measured in Illinois ranged from 2% to 61%, in Israel from 0.3% to 49%, and in Wisconsin from 0% to 55%. Some kernel characteristics (sugars, phytoglycogen and starch) showed transgressive segregation in both populations. A wide range of variability in all of the chemical and physiological kernel variables was also observed in both populations. This suggests that favorable alleles at loci influencing these characteristics are present in both parental inbreds.

Relationship between field emergence and kernel chemical and physiological characteristics. Phenotypic correlation between seedling emergence and kernel chemical and physiological variables in both populations are presented in Tables 2 and 3. The single variable most closely associated with seedling emergence in both populations at all four locations was the conductivity of mature-dry kernel leachate. Negative correlations were observed between conductivity and seedling emergence in both populations and were highly significant (*se1*: $r = -0.50$ to -0.62, $P < 0.001$, *sh2*: $r = -0.49$ to -0.63, $P < 0.001$) at all locations. These results are in agreement with other studies that suggest kernel leachate conductivity is tightly associated with sweet corn seedling emergence (Juvik et al., 1993). The rate of diffusion of water-soluble compounds from mature-dry kernels during imbibition is closely associated with the ability of the seedlings to germinate and emerge from the soil. Leaching of water-soluble components from germinating seed represents a metabolic loss to developing seedling and substrate for invading pathogens.

Another factor associated with emergence and somewhat distinct from conductivity is embryo dry weight. The positive correlation between these two variables in both populations and over environments (*se1*: $r = 0.24$ to 0.29, $P < 0.001$, *sh2*: $r = 0.39$ to 0.43, $P < 0.001$) suggests the larger the embryo size the greater the likelihood of seedling soil emergence, particularly in the *sh2* population. The embryo and scutellum contain a major portion of the seed protein and lipid fractions and therefore these variables were also observed to be positively associated with seedling emergence (protein, for *se1*: $r = 0.18$ to 0.25, $P < 0.001$; for *sh2*: $r = 0.24$ to 0.40, $P < 0.001$ and lipids for *se1*: $r = 0.27$ to 0.36, $P < 0.001$; for *sh2*: $r = 0.24$ to 0.51, $P < 0.001$). Except for kernel sugars, correlations were higher in all carbohydrates, protein, and lipid fractions when calculated on the basis of mg/kernel. Since lipids serve as an energy source for embryo germination and seedling growth, high correlation between these variables

Table 1. Mean, standard deviation, and range for the various traits in the $F_{2:3}$ *se1* and *sh2* sweet corn populations.

		se1 population			*sh2* population		
Trait[z]	Unit	Mean	SD[y]	Range	Mean	SD	Range
Field performance variables							
Seedling emergence							
Illinois (year 1)	%	57.0	11.3	22–78	29.0	13.0	2.3–61
Illinois (year 2)	%	42.0	11.2	15–72	17.0	7.9	2.3–43
Israel	%	49.0	15.1	4–82	13.0	10.4	0.3–49
Wisconsin	%	47.0	15.2	5–76	15.0	9.8	0.0–55
Seedling growth rate							
Illinois (year 1)	$mm \cdot d^{-1}$	6.3	1.1	3.7–9.4	5.3	7.9	3.0-8.6
Israel	$mm \cdot d^{-1}$	5.6	1.5	2.1–10.0	3.3	10.4	0.8–7.0
Wisconsin	$mm \cdot d^{-1}$	7.7	1.4	2.9–12.0	6.2	9.8	1.0–12
Kernel chemical variables (Illinois, year 1)							
Fructose	$mg \cdot g^{-1}$	0.8	1.1	0.0–4.4	1.6	1.9	0.0–11
	mg/kernel	0.1	0.1	0.0–0.6	0.1	0.2	0.0–1.0
Glucose	$mg \cdot g^{-1}$	5.0	3.4	0.0–15	2.1	2.1	0.0–9.6
	mg/kernel	0.6	0.4	0.0–2.1	0.2	0.2	0.0–0.9
Sucrose	$mg \cdot g^{-1}$	42.0	13.5	12–97	38.0	10.9	24–89
	mg/kernel	5.5	1.8	1.4–13	3.5	1.0	2.0–7.7
Maltose	$mg \cdot g^{-1}$	2.8	5.0	0.0–29	1.2	1.4	0.0–9.3
	mg/kernel	0.3	0.6	0.0–4.0	0.1	0.1	0.0–0.9
Total sugars	$mg \cdot g^{-1}$	50.0	17.5	5.0–119	43.0	14.5	25–109
	mg/kernel	5.9	2.3	0.4–16	3.9	1.3	2.1–9.6
Phytoglycogen	$mg \cdot g^{-1}$	391.0	73.1	191–597	14.0	5.8	7.7–41
	mg/kernel	45.0	10.2	23–78	1.3	0.5	0.6–2.9
Starch	$mg \cdot g^{-1}$	201.0	49.5	103–351	310.0	58.7	113–430
	mg/kernel	24.0	8.5	8.8–52	28.0	6.6	9.0–45
Protein	$mg \cdot g^{-1}$	182.0	24.4	118–243	298.0	21.0	255–347
	mg/kernel	22.0	4.9	11–37	28.0	3.9	20–37
Lipids	$mg \cdot g^{-1}$	93.0	4.6	77–107	106.0	5.4	93–119
	mg/kernel	11.0	1.9	6.9–16	10.0	1.2	6.9–13
Kernel physiological variables (Illinois, year 1)							
Kernel dry weight	mg/kernel	117.0	20.3	68–178	91.0	11.2	67–114
Conductivity	$\mu S \cdot g^{-1}$	27.0	9.3	11–74	59.0	20.7	24–133
Endosperm dry weight	mg/kernel	96.0	18.6	53–144	68.0	8.7	38–89
Embryo dry weight	mg/kernel	24.0	4.9	3.7–37	19.0	3.5	10–26

[z]Traits were evaluated in three replications in each environment.
[y]Standard deviations in the population for each trait.

Table 2. Pearson's correlation between field and kernel variables calculated using trait phenotypic values of families in the *se1* population.

Trait	Unit	Seedling emergence (Illinois, year 1)	Seedling emergence (Illinois, year 2)	Seedling emergence (Israel)	Seedling emergence (Wisconsin)	Growth rate (Illinois, year 1)	Growth rate (Israel)	Growth rate (Wisconsin)
Field performance variables								
Seedling emergence								
Illinois, year 1	%	---	0.61**	0.56**	0.69**	0.30**	0.30**	NS
Illinois, year 2	%	0.61**	---	0.47**	0.60**	0.21**	0.23**	NS
Israel	%	0.56**	0.47**	---	0.65**	0.23**	0.58**	NS
Wisconsin	%	0.69**	0.60**	0.65**	---	0.19*	0.40**	0.31**
Seedling growth rate								
Illinois, year 1	mm·d^{-1}	0.30**	0.20*	0.23**	0.19**	---	0.35**	0.18*
Israel	mm·d^{-1}	0.30**	0.23**	0.58**	0.40**	0.35**	---	0.31**
Wisconsin	mm·d^{-1}	NS	NS	NS	0.31**	0.18*	0.31**	---
Kernel chemical variables (Illinois, year 1)								
Fructose	mg·g^{-1}	–0.26**	–0.23**	–0.21*	–0.28**	NS	–0.24**	NS
	mg/kernel	NS	NS	NS	–0.23**	NS	–0.19*	NS
Glucose	mg·g^{-1}	NS	NS	NS	NS	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	0.21*	NS
Sucrose	mg·g^{-1}	–0.21**	–0.27**	NS	–0.23**	NS	NS	NS
	mg/kernel	ns	NS	NS	NS	NS	0.23**	NS
Maltose	mg·g^{-1}	–0.29**	–0.25**	–0.21*	–0.33**	NS	NS	NS
	mg/kernel	–0.23**	–0.21*	–0.18*	–0.29**	NS	NS	NS
Total sugars	mg/g	–0.28**	–0.32**	NS	–0.32**	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	NS	NS
Phytoglycogen	mg·g^{-1}	NS	NS	NS	NS	NS	–0.23**	–0.19*
	mg/kernel	NS	NS	NS	0.27**	NS	NS	NS
Starch	mg·g^{-1}	0.35**	0.27**	0.24**	0.37**	0.25**	0.18*	0.21*
	mg/kernel	0.39**	0.32**	0.34**	0.45**	0.28**	0.31**	0.25**
Protein	mg·g^{-1}	NS	NS	NS	NS	0.25**	ns	NS
	mg/kernel	NS	NS	0.19*	0.25**	0.31**	0.31**	0.19*
Lipids	mg·g^{-1}	NS	NS	NS	NS	NS	NS	NS
	mg/kernel	0.30**	0.28**	0.27**	0.36**	NS	0.32**	NS
Kernel physiological variables (Illinois, year 1)								
Kernel dry weight	mg/kernel	0.31**	0.28**	0.35**	0.40**	0.22*	0.37**	0.20*
Conductivity	μS·g^{-1}	–0.57**	–0.50**	–0.54**	–0.62**	NS	–0.30**	NS
Endosperm dry weight	mg/kernel	0.31**	0.29**	0.33**	0.36**	NS	0.33**	NS
Embryo dry weight	mg/kernel	0.29**	0.26**	0.24**	0.28**	NS	0.34**	NS

NS,*,**Nonsignificant or significant at $P < 0.01$ or 0.001, respectively.

is understandable, particularly in the *sh2* population where the reduced starch content and rates of starch hydrolysis limit energy and carbon translocation from the endosperm to embryo (Young et al., 1997). Other kernel variables were also significantly associated with seedling emergence across populations and locations including kernel dry weight and endosperm dry weight.

Among all variables, endosperm dry weight displayed the second highest correlation with seedling emergence over both populations (*se1*: $r = 0.29$ to 0.36, $P < 0.001$, *sh2*: $r = 0.41$ to 0.50, $P < 0.001$). Endosperm dry weight was highly correlated with kernel starch content (*se1*: $r = 0.75$, $P < 0.001$, *sh2*: $r = 0.59$, $P < 0.001$). Kernel starch content (mg/kernel) appears to represent another factor associated with seedling emergence with a significant positive correlation over all environments in both populations (*se1*: $r = 0.32$ to 0.45, $P < 0.001$; *sh2*: $r = 0.25$ to 0.33, $P < 0.001$). This association is independent of conductivity and embryo dry weight since starch is insoluble in water and is found almost exclusively in the endosperm. Kernel starch is negatively correlated with protein and lipid concentrations suggesting that the particular biochemical pathways leading to the synthesis of the major kernel chemical fractions (starch, protein, and lipids) compete for available photosynthate and other kernel nutrients (Dudley and Lambert, 1992; Singletary and Below, 1990). Endosperm starch and its degradation by α-amylase during germination and early seedling growth is an important source of carbon and energy to the young seedlings. The highly significant positive association of kernel weight with seedling emergence reflects the positive correlation between starch, lipids and protein amount (mg/kernel) with this variable. Seedling growth rates were consistently positively correlated with kernel starch and protein contents on a mg/kernel basis in the *se1* population. No consistent associations between seedling growth rate and other variables were observed in the *sh2* population.

QTL ASSOCIATED WITH FIELD PARAMETERS. Putative QTL affecting measured traits in both *se1* and *sh2* populations are presented in Tables 4 and 5, respectively. Figures 1 and 2 display the map locations of RFLP markers linked to these QTL for the *se1* and the *sh2* populations respectively. For seedling emergence three regions were found to carry significant QTL in the *se1* population in all locations (Table 4). The *se1* gene locus on chromosome 2, php200020 on chromosome 7, and umc160 on chromosome 8 were associated with seedling emergence across all of the environments. Segregation at these three loci across 4 environments accounted for 29.8% of the total variation (adjusted R^2) in seedling emer-

Table 3. Pearson's correlation between field and kernel variables calculated using trait phenotypic values of families in the *sh2* population.

Trait	Unit	Seedling emergence (Illinois, year 1)	Seedling emergence (Illinois, year 2)	Seedling emergence (Israel)	Seedling emergence (Wisconsin)	Growth rate (Illinois, year 1)	Growth rate (Israel)	Growth rate (Wisconsin)
Field performance variables								
Seedling emergence								
Illinois, year 1	%	---	0.56**	0.76**	0.79**	0.47**	NS	0.38**
Illinois, year 2	%	0.56**	---	0.56**	0.54**	ns	NS	0.27*
Israel	%	0.76**	0.56**	---	0.80**	0.48**	0.26*	0.38**
Wisconsin	%	0.79**	0.54**	0.80**	---	0.50**	NS	0.38**
Growth rate								
Illinois, year 1	mm·d^{-1}	0.47**	NS	0.48**	0.50**	---	NS	NS
Israel	mm·d^{-1}	ns	NS	0.26*	NS	NS	---	0.23*
Wisconsin	mm·d^{-1}	0.38**	0.27*	0.38**	0.38**	NS	0.23*	---
Kernel chemical variables (Illinois, year 1)								
Fructose	mg·g^{-1}	–0.24*	NS	NS	–0.25	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	NS	NS
Glucose	mg·g^{-1}	–0.29**	NS	NS	–0.29**	NS	NS	NS
	mg/kernel	–0.24*	NS	NS	–0.25	NS	NS	NS
Sucrose	mg·g^{-1}	–0.24*	NS	NS	–0.24	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	NS	NS
Maltose	mg·g^{-1}	NS	NS	NS	NS	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	NS	NS
Total sugars	mg·g^{-1}	–0.26*	NS	NS	–0.27	NS	NS	NS
	mg/kernel	NS	NS	NS	NS	NS	NS	NS
Phytoglycogen	mg·g^{-1}	–0.40**	–0.29**	–0.43**	–0.29**	–0.26*	–0.32**	NS
	mg/kernel	–0.28*	NS	–0.31**	NS	NS	–0.29**	NS
Starch	mg·g^{-1}	NS	NS	NS	NS	NS	NS	NS
	mg/kernel	0.33**	0.25*	0.26*	0.29**	NS	NS	NS
Protein	mg·g^{-1}	NS	ns	NS	NS	NS	NS	NS
	mg/kernel	0.24*	0.33**	0.40**	0.34**	0.32**	NS	NS
Lipids	mg·g^{-1}	NS	NS	0.23	0.24	NS	NS	NS
	mg/kernel	0.24**	0.25*	0.48**	0.51**	0.36**	NS	0.23*
Kernel physiological variables (Illinois, year 1)								
Kernel dry weight	mg/kernel	0.41**	0.34**	0.46**	0.45**	0.33**	NS	NS
Conductivity	μS·g^{-1}	–0.63**	–0.57**	–0.51**	–0.49**	NS	NS	–0.28*
Endosperm dry weight	mg/kernel	0.44**	0.41**	0.42**	0.50**	0.25*	NS	NS
Embryo dry weight	mg/kernel	0.39**	0.40**	0.40**	0.43**	NS	0.23*	NS

NS,*,**Nonsignificant or significant at $P < 0.01$ or 0.001, respectively.

gence. The *sugary enhancer1* mutation contributed by the IL731a parent was associated with a significant reduction in emergence. In contrast, alleles linked to umc160 and php200020 originating from IL731a were associated with enhanced emergence.

The two major chromosomal regions associated with emergence in the *sh2* population across 4 locations included umc131 on chromosome 2 and bnl9.08 on chromosome 8 (Table 5) and together accounted for 17.7% of the total variation (adjusted R^2) in this trait. Segregation at loci linked to php200689 on chromosome 1 also significantly influenced *sh2* emergence in Illinois and Wisconsin. Alleles that enhanced emergence originated from the Ia453 *sh2* parent, except for the IL451b allele of php200689.

Only one common region in the genomes of the two populations was found to contain a QTL that significantly influenced emergence. Two RFLP markers (umc160 and bnl9.08) that were significantly associated with emergence mapped to approximately the same position (8.057 and 8.062 cM) in the *se1* and the *sh2* populations, respectively. Additional mapping work is required to determine if this region is segregating for a gene or genes that can influence emergence in both *su1se1* and *sh2* sweet corn. Beneficial alleles associated with improved seedling emergence in the *sh2* population (linked to umc131, bnl9.08, and php200689) did not appear to be background specific since Yousef and Juvik (2002) found that they exerted similar effects when backcrossed into different sweet corn inbreds. The results for emergence were more consistent across environments than those for seedling growth rate.

In the *se1* population, two QTL were observed to affect seedling growth rates in Illinois, year-1 (php200581 and php200020 on chromosome 2 and 7) and Wisconsin (umc134 and umc60 on chromosome 2 and 3) while only one QTL linked to umc152 on chromosome 10 was detected across three environments (Table 4). Significant markers accounted for only 5.2%, 14.9% and 6.9% of the total variance (adjusted R^2) in this trait for Illinois, Wisconsin, and Israel, respectively. For the *sh2* population, two QTL linked to php20075b and npi570 were associated with seedling growth rate in Illinois (year-1) but no QTL common across all three environments were detected. Alleles elevating seedling growth rate were contributed by the Ia453 *sh2* parent. The genes responsible for variation in seedling growth rate in both the *se1* and *sh2* populations are apparently strongly influenced by the environment.

QTL ASSOCIATED WITH KERNEL CHEMICAL AND PHYSIOLOGICAL CHARACTERISTICS. Many different QTL influencing kernel chemical

Table 4. QTL detected by PLABQTL (LOD > 3.0) in the *se1* population.

QTL[z]	Marker	SI[y]	LOD[x]	R^{2w}	a[v]	d[u]
Field performance variables						
Seedling emergence (%)[t]						
Illinois, year 1						
2.186	se1 (1) [s]	180–187	8.6	19.0	–6.8	3.5
3.232	npi420 (1)	213–232	2.6	5.6	3.2	–0.2
8.057	umc160 (1)	51–69	6.0	12.2	4.6	2.0
				39.9 (28.3)[r]		
Illinois, year 2						
2.187	se1 (0)	178–187	2.5	6.0	–5.0	2.5
				6.0 (4.6)		
Israel						
2.187	se1 (0)	179–187	3.8	8.9	–7.0	–2.0
10.044	npi582 (9)	28–54	4.7	9.7	–5.3	7.6
				18.6 (12.7)		
Wisconsin						
2.187	se1 (0)	182–187	9.7	21.3	–9.5	4.4
8.061	umc160 (5)	47–73	4.0	8.3	5.1	3.9
				29.6 (24.5)		
Across 4 environments						
2.186	se1 (1)	181–187	11.2	24.1	–7.9	2.0
7.151	php200020 (1)	138–167	2.6	5.5	3.1	–0.5
8.057	umc160 (1)	48–73	5.1	10.5	4	1.9
				40.2 (29.8)		
Seedling growth rate (mm·d^{-1})						
Illinois, year 1						
2.162	php200581 (0)	126–163	3.6	7.5	0.7	0.7
7.151	php20020 (1)	141–165	3.2	6.8	0.4	0.0
				14.2 (5.2)		
Israel						
10.031	Umc152 (3)	16–47	3.8	8.1	–0.7	0.1
				8.1 (6.9)		
Wisconsin						
2.058	umc134 (2)	45–68	3.9	8.3	0.5	0.4
3.118	umc60 (2)	102–128	4.7	9.7	–0.6	0.1
				18.0 (14.9)		
Across 4 environments						
10.040	umc152 (6)	19–50	5.7	11.7	–0.6	0.2
				11.7 (7.4)		
Kernel chemical variables (Illinois, year 1)						
Fructose (mg·g^{-1})						
1.028	php200689 (1)	22–31	4.4	9.2	0.5	0.3
1.208	umc84 (9)	199–218	3.6	8.1	0.7	0.0
3.116	umc60 (0)	105–122	3.3	6.9	0.4	–0.2
				24.3 (11.4)		
Fructose (mg/kernel)						
1.029	php200689 (0)	23–35	3.9	8.1	0.1	0.0
3.117	umc60 (1)	105–123	3.8	8.0	0.1	0.0
				16.1 (9.5)		
Glucose (mg·g^{-1})						
2.099	umc5 (0)	93–100	4.7	9.7	2.0	–1.0
6.051	umc59 (4)	41–55	22.0	38.0	-3.0	–0.1
				47.7 (36.6)		
Glucose (mg/kernel)						
2.099	umc5 (0)	92–100	3.5	7.4	2.0	–1.0
4.025	umc31a (1)	12–37	3.0	6.9	0.1	–0.1
6.044	umc59 (4)	40–48	20.3	35.7	-0.4	0.0
				50.0 (37.2)		
Sucrose (mg·g^{-1})						
2.063	umc134 (7)	56–77	3.1	6.6	-5.3	3.2
2.185	se1 (2)	179–187	6.7	15.2	8.1	–4.7
3.098	umc50 (16)	87–111	6.3	12.8	6.3	–6.8
6.047	umc59 (1)	34–48	3.9	8.2	-4.3	1.8
				42.8 (34.3)		
Sucrose (mg/kernel)						
2.147	umc49 (12)	135–159	3.2	6.7	0.5	–1.1
2.186	se1 (1)	179–187	4.1	9.7	0.8	–0.6
3.092	umc50 (10)	66–102	5.8	11.9	0.8	–1.0
6.041	php200854 (2)	34–48	4.4	9.2	–0.7	–0.1
				37.5 (27.2)		
Maltose (mg·g^{-1})						
2.071	umc134 (0)	63–78	3.7	7.8	1.7	0.1
4.140	npi570 (4)	135–150	3.4	7.1	2.9	0.1
6.065	umc113b (1)	56–78	3.4	7.1	0.8	–2.0
7.025	umc116 (1)	20–26	4.2	14.7	1.6	–3.7
				36.7 (15.4)		
Maltose (mg/kernel)						
2.071	umc134 (0)	63–78	3.9	8.2	0.1	0.3
4.097	bnl7.65 (17)	79–114	3.4	7.2	–0.3	0.2
4.140	npi570 (4)	135–151	3.3	7.1	2.9	0.2
6.126	umc113b (1)	119–128	3.5	7.3	1.6	–3.7
				29.8 (13.0)		
Total sugars (mg·g^{-1})						
2.148	umc49 (13)	137–161	3.8	8.0	7.0	–8.4
2.185	se1 (2)	180–187	9.1	19.9	11.3	–6.8
3.068	npi276a (2)	66–115	3.9	8.1	6.6	–6.9
6.047	umc59 (1)	35–48	4.0	8.3	–5.6	0.6
9.115	npi209 (0)	98–115	3.1	6.6	4.7	–2.2
				50.9 (36.6)		
Total sugars (mg/kernel)						
2.035	umc34 (0)	24-36	3.4	9.1	1.1	0.0
2.061	umc134 (5)	56–68	4.6	9.7	–1.0	0.6
2.148	umc49 (13)	138-161	4.3	8.9	1.0	–1.1
2.184	se1 (3)	179–187	7.1	16.0	1.4	–0.9
3.091	umc50 (9)	66–102	5.4	11.1	0.9	–0.9
5.143	pnl5.71 (2)	133–153	4.3	9.0	–1.0	0.4
6.042	php200854 (3)	32–48	4.6	9.5	–0.8	–0.2
9.115	npi209 (0)	101–115	3.9	8.2	0.7	–0.2
				81.4 (37.2)		
Phytoglycogen (mg·g^{-1})						
6.049	umc59 (2)	47–58	8.1	16.1	33.3	–22.1
9.072	umc114 (2)	58–88	3.3	6.9	23.3	15.1
				23.0 (15.6)		
Phytoglycogen (mg/kernel)						
6.045	umc59 (3)	39–54	6.0	12.2	4.1	–3.6
				12.2 (11.5)		
Starch (mg·g^{-1})						
2.182	se1 (5)	175–187	3.3	7.7	–25.7	7.2
				7.7 (4.0)		
Starch (mg/kernel)						
7.048	umc110 (6)	34–66	3.3	7.0	4.2	–0.5
				7.0 (5.1)		
Protein (mg·g^{-1})						
3.116	umc60 (0)	99–117	4.7	9.6	–17.7	2.6
				9.6 (7.7)		
Protein (mg/kernel)						
7.092	npi235b (1)	76–93	3.5	7.4	2.8	2.4
8.043	npi260b (3)	40–52	5.5	11.4	2.7	1.5
				18.8 (11.3)		
Lipids (mg·g^{-1})						
8.041	npi260b (1)	40–52	3.5	7.5	6.2	4.1
9.092	umc114 (18)	77–105	3.2	6.8	6.9	12.6
				14.3 (11.1)		
Lipids (mg/kernel)						
8.043	npi260b (3)	40–53	5.0	10.5	1.2	0.7
				10.5 (8.3)		
Kernel physiological variables (Illinois, year 1)						
Kernel dry weight (mg)						
7.047	umc110 (7)	34–71	3.8	7.9	10.0	–2.9
8.046	npi260b (6)	40–57	4.6	9.8	8.4	4.8
				17.7 (10.9)		
Conductivity (μS·g^{-1})						
9.013	umc113a (10)	0-24	3.3	7.2	6.7	3.6
7.2 (6.2)						
Endosperm dry weight (mg)						
9.029	umc113a (6)	23–37	3.5	7.4	12.7	11.4
				7.4 (6.3)		
Embryo dry weight (mg)						
9.015	umc113a (7)	2–44	3.4	7.3	4.1	3.3
				7.3 (5.4)		

[z]QTL map location (chromosome number to the right of period, three digit number refers to distance in *cM* from first marker on that chromosome).
[y]Support intervals indicate a 1 LOD score drop off from maximum score.
[x]Log10 of the likelihood ratio, calculated from the F value in the multiple regression (Lander and Botstein, 1989).
[w]Phenotypic variation explained by QTL (%).
[v]Additive effect of QTL, $1/2(A_1A_1\text{-}A_2A_2)$.
[u]Dominance effect of QTL, $[(A_1A_2) - (A_1A_1 - A_2A_2)/2]$, A_1 allele is from W6786, A_2 allele is from IL731a.
[t]For seedling emergence, LOD > 2.5 was used as explained in the text.
[s]Values in parentheses are map distances in *cM*, between the listed interval marker and QTL.
[r]Adjusted R^2 values from PLABQTL output are in parenthesis next to full model R^2.

Table 5. QTL detected by PLABQTL (LOD > 3) in the *sh2* population.

QTL[z]	Marker	SI[y]	LOD[x]	R^{2w}	a[v]	d[u]
Field performance variable						
Seedling emergence (%)[t]						
Illinois, year 1						
1.067	php200689 (2) [s]	49–81	2.7	10.2	5.4	1.4
2.004	umc131 (4)	0–13	3.5	13.4	–6.3	2.3
7.034	umc116 (4)	5–39	2.7	10.2	–4.4	4.6
3.005	php20075b (0)	69–85	3.0	11.3	–4.1	5.4
8.069	php100040 (7)	56–85	3.1	11.5	–5.1	–5.0
				56.6 (32.0)[r]		
Illinois, year 2						
2.007	umc139 (6)	0–25	3.1	12.0	–4.4	–0.2
8.059	bnl9.08 (5)	54–69	3.9	14.1	–5.9	–1.3
				26.2 (13.0)		
Wisconsin						
1.065	php200689 (0)	49–78	2.6	10.4	4.3	1.5
2.005	umc131 (5)	0–13	3.3	13.4	–5.5	1.4
				23.8 (16.7)		
Across four environments						
2.005	umc131 (5)	0–13	3.6	13.8	–4.8	1.0
8.062	bnl 9.08 (8)	54–71	4.2	15.4	–5.5	–3.3
				29.1 (17.7)		
Seedling growth rate (mm·d^{-1})		14.9(8.3)				
Illinois, year 1						
3.005	php20075b (0)	0–10	3.9	15.1	-0.1	0.7
4.050	npi570 (1)	34–70	3.1	12.3	-0.5	0.1
				27.4 (18)		
Kernel chemical variables (Illinois, year 1)						
Fructose (mg·g^{-1})						
2.000	umc131 (0)	0–6	4.1	15.4	1.0	–0.2
				15.4(10.5)		
Fructose (mg/kernel)						
2.000	umc131 (0)	0–7	3.7	14.3	0.1	0.0
				14.3(10.8)		
Glucose (mg·g^{-1})						
2.000	umc131 (0)	0–4	6.8	24.4	1.3	–0.6
				24.4 (18.7)		
Glucose (mg/kernel)						
2.000	umc131 (0)	0–4	6.2	22.3	0.1	0.0
7.034	umc116 (4)	19–40	3.1	11.4	–0.1	–0.1
7.048	npi263 (1)	46–55	3.4	12.5	0.1	0.0
				46.2 (24.9)		
Maltose (mg·g^{-1})						
3.016	umc26a (1)	6–28	4.2	16.4	0.8	–0.2
8.138	umc30 (1)	129–141	3.4	13.6	–1.0	–0.2
				30.0 (10.8)		
Maltose (mg/kernel)						
3.016	umc26a (1)	7–29	4.3	16.8	0.1	0.0
8.138	umc30 (1)	130–139	3.5	13.9	–0.1	0.0
				30.7 (10.8)		
Total sugars (mg/kernel)						
3.017	umc26a (0)	8–18	3.3	12.3	7.0	–0.3
				12.3 (4.0)		
Phytoglycogen (mg·g^{-1})						
2.085	umc36 (0)	77–85	3.3	12.5	1.6	7.5
				12.5 (4.2)		
Phytoglycogen (mg/kernel)						
5.050	umc27 (2)	38–55	4.1	14.9	0.2	–0.3
				14.9 (8.3)		
Starch (mg·g^{-1})						
2.016	umc139 (4)	1–25	3.9	14.4	–36	3.5
10.000	umc146 (0)	0–7	4.2	15.3	–3.8	–41.6
				29.7 (22)		
Starch (mg/kernel)						
2.012	umc139 (1)	6–21	5.9	21.4	–4.4	0.7
10.000	umc146 (0)	0–11	3.0	11.0	0.2	–3.8
				32.4 (18.7)		
Kernel physiological variables (Illinois, year 1)						
Kernel dry weight (mg)						
2.010	umc139 (3)	2–19	3.4	12.9	–5.2	3.7
				12.9 (7.1)		
Endosperm dry weight (mg)						
8.088	php100040 (13)	63–102	3.7	14.5	–17	–1.8
				14.5 (4.9)		

[z]QTL map location (chromosome number to the right of period, three digit number refers to distance in *cM* from first marker on that chromosome).
[y]Support intervals indicate a 1 LOD score drop off from maximum score.
[x]Log10 of the likelihood ratio, calculated from the F value in the multiple regression (Lander and Botstein, 1989).
[w]Phenotypic variation explained by QTL (%).
[v]Additive effect of QTL, $1/2(A_1A_1 - A_2A_2)$.
[u]Dominance effect of QTL, $[(A_1A_2) - (A_1A_1 - A_2A_2)/2]$, A_1 allele is from Ia453, A_2 allele is from IL451.
[t]For seedling emergence, LOD >2.5 was used as explained in the text. [s]Values in parentheses are map distances in *cM*, between the listed interval marker and QTL.
[r]Adjusted R^2 values from PLABQTL are in parenthesis next to full model R^2.

composition were detected in the *se1* and *sh2* populations (Tables 4 and 5). In the *se1* population, a total of 13 and 16 unlinked regions were identified that influenced mature-dry kernel fructose, glucose, sucrose, or maltose on a mg·g^{-1} and mg/kernel basis, respectively. The s*e1* gene and the QTL linked to umc50 appeared to exert major influences on mature-dry kernel sucrose and total sugar content with 11.1% and 16.0% of the phenotypic variation for total sugars (mg/kernel) explained by the segregation of alleles at these markers, respectively (Table 4). In the *sh2* population smaller numbers of QTL were detected compared to that of *se1* population as might be anticipated considering the reduced marker coverage of the genome and the smaller population size. The marker umc131 on chromosome 2 in the *sh2* population was linked to a major QTL with significant effects on most mature-dry kernel sugars. Nearly all of the QTL for sugar content mapped to regions distinct in the genomes of the two populations.

The putative QTL affecting mature-dry kernel phytoglycogen, starch, protein, and lipids in the *se1* population are listed in Table 4. Three QTL regions in the *sh2* population were found to be associated with differences in the concentration and amount of phytoglycogen and starch (Table 5). While the *se1* locus was found to be associated with kernel starch content, the umc59 locus with kernel phytoglycogen, and umc60 with protein content in the *se1* population, no regions in either population were found to significantly influence all the major kernel chemical fractions. In the *se1* population, QTL alleles for increased phytoglycogen and lipids were contributed primarily by the IL731a parent and alleles for elevated starch primarily from W6786. In the *sh2* population alleles from IL451b primarily increased kernel phytoglycogen and protein, while alleles from Ia453 elevated starch and lipids. Other physiological factors significantly associated with seedling emergence were kernel leachate conductivity, endosperm dry weight, and embryo dry weight. These traits were significantly influenced by allelic variation at umc113a on chromosome 9 in *se1* population and php100040 on chromosome 8 in the *sh2* population.

QTL AFFECTING BOTH FIELD PARAMETERS AND KERNEL CHARACTERISTICS. QTL located in the chromosome regions around *se1* and umc160 from the *se1* population and umc131 from the *sh2* population appeared to be close to gene(s) that strongly influenced kernel chemical and physiological characteristics as well as field parameters. The umc36a locus is linked (12.3 cM) to the *se1* gene on the long arm of chromosome 2 in the *se1* population (Fig. 1) (Tadmor et al., 1995). The *se1* gene was observed to affect many different kernel characteristics and accounted for 24.1% of the total variation in emergence across the four environments and 19.9% of the variation in mature-dry kernel total sugar concentration (mg/g) in the *se1* population (Table 4). An important region in the *sh2* population was on chromosome 2 between the maker loci umc131 and umc139. This region accounted for 13% of the total variation in Illinois emergence and 21.4% of the variation in kernel starch content (mg/kernel) (Table 5).

For the purposes of cultivar improvement it is appropriate to

consider which of the loci identified in the two populations that are associated with enhanced emergence provide the greatest potential value in a breeding program to improve sweet corn stand establishment without undesirable effects on sweet corn eating quality. Table 6 lists six genomic regions identified in the *se1* and *sh2* populations that conferred the greatest and most consistent effect on seedling emergence. Mean emergence of $F_{2:3}$ families for each genotypic class at each of the loci in the *se1* population indicated that the *se1*/*se1* homozygous class was associated with a 29% reduction in emergence compared to the *Se1*/*Se1* homozygous class. When homozygous, the *se1* gene was found to increase fresh harvested (20 d after pollination) kernel total sugar content by 53% and taste panel perceived sweetness and overall liking (hedonic) by 67% and 17% respectively (Azanza et al., 1996b). While the improved eating quality conferred by *se1* has led to its widespread commercial use, it comes with the cost of reduced seedling emergence. Families homozygous for the IL731a allele in the region of umc160 and php200020 conferred a 22% and 11% respective increase in emergence when compared to the genotypic class homozygous in this region for the W6786 allele. In contrast to *se1* these alleles were associated with only minor reductions in fresh kernel sugar concentrations (8% for umc160 and 7% for php200020). The QTL associated with the umc160 locus appears to be valuable for improving emergence with only minor effects on fresh harvest eating quality, particularly since this region on chromosome 8 and possibly the same QTL exerted similar effects in the *sh2* population (bnl9.08).

In the *sh2* population families homozygous for the Ia453 allele in the region of bnl9.08 and umc131 conferred 62% and 52% respective increases in emergence when compared to the genotypic class homozygous in this region for the IL451b allele. While the Ia453 allele at umc131 was associated with significantly decreased mature-dry kernel sugar content and increased kernel starch neither this allele or the Ia453 allele at bnl9.08 significantly reduced fresh harvest kernel sweetness or sensory panel overall liking (Han, 1994). Families homozygous for the IL451b allele

Table 6. Major QTL effect on seedling emergence and kernel mature dry and fresh harvest characteristics in the $F_{2:3}$ *se1* and *sh2* populations; PG = phytoglycogen, C = conductivity, S = sweetness.

		Characteristic										
		Mature dry								Fresh harvest		
Genotype[z]	Seedling emergence (%)	Kernel wt ($mg \cdot g^{-1}$)	Total sugars ($mg \cdot g^{-1}$)	PG ($mg \cdot g^{-1}$)	Sucrose ($mg \cdot g^{-1}$)	Starch ($mg \cdot g^{-1}$)	C ($\mu S \cdot g^{-1}$)	Endosperm wt (mg)	Embryo wt (mg)	Total sugars ($mg \cdot g^{-1}$)	S[y]	Hedonic[y]
se1 population												
se1												
A_1A_1	62	119	41	380	36	222	24	96	23	228	6	6
A_1A_2	59	117	47	391	40	207	26	96	24	263	7	6
A_2A_2	48	116	67	392	53	174	33	93	25	349	10	7
%[x]	29*	3	63*	3	47*	28*	38*	3	9	53*	67*	17
umc160												
A_1A_1	51	111	53	394	44	191	28	92	22	295	8	6
A_1A_2	58	117	49	397	42	197	27	96	24	269	7	6
A_2A_2	62	124	49	368	41	222	25	99	25	273	7	6
%	22*	12*	8	7	7	16*	12	8	14	8*	14*	0
php200020												
A_1A_1	55	112	48	391	41	197	27	93	23	285	8	6
A_1A_2	57	116	53	381	44	202	27	95	23	280	8	6
A_2A_2	61	122	47	415	39	202	26	100	25	266	7	7
%	11*	9	2	6*	5	3	4	8	9	7*	14	17
sh2 population												
php200689												
A_1A_1	22	87	46	16	40	312	64	65	18	---	10	8
A_1A_2	30	91	45	14	39	317	59	70	19	---	10	7
A_2A_2	32	91	38	14	34	293	56	68	19	---	11	8
%	45*	5	21	14	18	6	14	5	6	---	10	0
umc131												
A_1A_1	35	93	37	15	34	342	56	70	19	---	10	8
A_1A_2	30	92	43	16	38	298	57	70	19	---	10	7
A_2A_2	23	86	51	13	43	296	65	65	18	---	10	8
%	52*	8*	38*	15	26*	16*	16	8	6	---	0	0
bnl9.08												
A_1A_1	34	91	44	13	39	306	54	68	19	---	11	9
A_1A_2	28	91	42	15	37	313	62	68	19	---	10	7
A_2A_2	21	85	45	16	40	310	63	66	17	---	10	8
%	62*	7	2	23	3	1	17	3	12	---	10	13

[z]A_1: allele from W6786, A_2: allele from IL731a in *se1* population; A_1: allele from Ia453, A_2: allele from IL451b in *sh2* population.
[y]Sweetness and hedonic traits were evaluated by sensory evaluation on a scale from 1 (lowest) to 15 (highest) (Azanza et al., 1996b, Han, 1994).
[x]Percent increase over low genotype class at each QTL.
*The three marker genotype class means were significantly different at $P < 0.05$.

in the region of php200689 on chromosome 1 displayed a mean increase of 45% in emergence when compared to the genotypic class homozygous in this region for the Ia453 allele without any effect on fresh eating quality. The beneficial alleles for each of these QTL show potential for use in sweet corn improvement programs.

The detection of QTL associated with effects on more than one trait in this study (Table 6) suggests either an individual QTL has a pleiotropic effect on more than one trait or that different QTL affecting different traits are clustered together in tightly linked groups (Paterson et al., 1991). Pleiotropic gene expression would explain some of the phenotypic correlations observed among the $F_{2:3}$ families. The alternative possibilities of QTL with pleiotropic effects or tightly linked QTL with effects on different traits could be better resolved in future studies with denser probe saturation in these regions. The presence of several marker loci in a given chromosome region has been suggested to be a powerful tool for elucidating the nature of the observed associations among traits and loci (Edwards et al., 1992). Those regions in which linked markers show progressive increase in marker effects (reflected as R^2 values) with decreasing recombination distance for different traits would be an indication of the presence of a single QTL with a pleiotropic effect on several traits. A significant pleiotropic effect of a QTL on two different traits may be due to the direct or indirect effect of an enzyme in a metabolic pathway that influences the expression of both kernel characteristics. The observation that segregation at the umc131 locus in the *sh2* population influences both kernel starch content and field emergence provides an additional piece of evidence suggesting a cause-effect relationship may exist between these variables. This region was also associated with significant effects on mature-dry kernel sugar content.

In conclusion, the evaluation of kernel characteristics and field parameters of the $F_{2:3}$ segregating generation in combination with RFLP analysis allowed for study at the genetic and biochemical level of the association between kernel traits and field parameters by testing the effect of specific chromosomal regions on several kernel properties. Results from correlations between variables indicated that mature-dry kernel leachate conductivity, embryo size, and kernel starch content are primarily associated with improved field performance and sweet corn seed quality. Combination of the sweet corn RFLP genetic maps and analysis of kernel characteristics allow for the identification of QTL controlling sweet corn emergence, seedling growth, and seed chemical composition. These data provide the necessary information to initiate marker-assisted selection for the genetic improvement of sweet corn seed quality. Marker-assisted selection using this information is being used to develop sweet corn germplasm with improved seed and eating quality (Yousef and Juvik, 2002).

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