REGULAR ARTICLE

Polymorphism, population structure, and multivariate relationships among secondary traits in open-pollinated corn heterotic groups

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ABSTRACT

Plant, ear and kernel traits directly or indirectly associated with grain yield in corn (*Zea mays* L.) have been suggested as "secondary" traits to select for larger grain yield, especially in open-pollinated corn varieties and their hybrids. Polymorphism, population structure, and multivariate relationships among 34 secondary traits and their impact on grain yield were quantified in 46 open-pollinated varietal hybrids within eight maternal heterotic groups. Large levels of polymorphism and population differentiation especially for reproductive traits, and above-average values for diversity indices, frequency of desirable trait variants, and population differentiation were found for almost all secondary traits. Maternal heterotic groups were identified as potential sources of desirable variants of single or multiple traits appropriate for adaptation to short-growing seasons, low-input farming and adverse environmental condition.

Key Words: *Zea mays; polymorphism; diversity; open-pollinated corn; secondary traits.*

INTRODUCTION

Open-pollinated corn (*Zea mays* L.) varieties of the Corn Belt Dent race were developed in the early 19th century by the hybridization of two highly differentiated races: the Northern Flints and the Southern Dents, followed by mass selection (Doebley et al., 1988). Due to their higher yield, open-pollinated varieties became the standard on the farm for almost 100 years. Inbred lines derived from those open-pollinated populations were then used in producing the first vigorous and high yielding hybrids in the early 1900s. For example, Reid Yellow Dent population, presumably due to its extensive allelic diversity

(Smith et al., 1985), contributed disproportionately (~50%) to pedigrees of modern corn hybrids (Troyer, 1999).

Open-pollinated varieties constitute a sizable part of the 20,000 corn accessions conserved in Old World gene banks (Ortiz et al., 2010), however, their original genetic base in the U.S. (~800 varieties) was reduced over time and many of these varieties are already extinct. Potentially, a genetic bottleneck of U.S. corn occurred when widely adapted and popular open-pollinated varieties were selected for early inbred development (Ho et al., 2005).

The single-cross hybrids of the 1990s evolved from open-pollinated varieties of the 1930s. This evolution was accompanied by an increase in the rate of hybrid improvement and in area of adaptation but also resulted in a loss of allelic diversity. For example, Ho et al. (2005) found that a diverse set of inbred lines displayed only 56% of alleles found in the Corn Belt Dents. Nevertheless, the use of open-pollinated varieties as genetic resources to develop corn tolerant to drought (Monneveux et al., 2006), low inputs (Kamara et al., 2003b) and superior protein quality (Reeves and Cassady, 2002) were among the most important achievements of corn breeding research during the last 50 years.

The limited diversity of current corn germplasm can lead to genetic vulnerability to biotic and abiotic stresses, and may limit future gains from selection (Ortiz et al., 2010). However, due to lack of agronomic evaluation, only about 10% of the estimated 250-300 corn landraces of the Americas are currently being utilized for the development of new inbred lines (Taller and Bernardo, 2004). Open-pollinated varieties, as well as landraces and synthetic populations, may be useful in improving corn yield in the Northern Corn Belt (Taller and Bernardo, 2004). Hence, the current interest in commercializing outstanding populations and population hybrids in some agricultural sectors of the U.S. and other corn-growing countries around the world. This interest is demonstrated by increased research efforts on open-pollinated varieties, their hybrids, and landrace corn under organic and other low-input farming in North America (Carena, 2005; Kutka and Smith, 2007), Europe (Vas Patto et al., 2008), Africa (Kamara et al., 2004), Latin America (Ortiz et al., 2008), and China (Song, 1999).

In-depth analyses of genetic relationships and levels of population differentiation of open-pollinated varieties and landraces can generate valuable information to help minimize the risk of genetic uniformity and vulnerability of corn to biotic and abiotic stresses and should lead to enhanced utilization for the improvement of corn especially in developing countries (Ortiz et al., 2010). Open-pollinated varieties are largely untapped genetic resources, if classified into well-defined or new heterotic groups, they can help ensure long-term breeding and selection gains. If open-pollinated varieties and their hybrids were better characterized, and there was a clearer understanding of the diversity structure of "secondary" traits associated directly or indirectly with grain yield, it would be possible to better target their utilization in corn improvement (Ortiz et al., 2008; 2010).

Farmers and public plant breeders will continue to improve open-pollinated varieties due to increasing demand for low-cost seed, better nutritional quality, wider adaptability, and larger diversity as compared with corn hybrids (Song, 1999); however, it is unlikely that open-pollinated varieties or their hybrids will be economically competitive with modern corn hybrids unless new high-yielding open-pollinated hybrid populations are made available to farmers (Carena, 2005).

Ho et al. (2005) emphasized the value of ancestral open-pollinated population of the US corn as a resource to broaden the genetic base of modern corn and to ensure long-term gains in corn breeding; whereas, Monneveux et al. (2008) suggested using secondary traits as a viable alternative to improving yield (*per se*) of open-pollinated varieties. The secondary traits are easy to observe and measure, genetically variable and highly heritable, and stable over the measurement period. The objectives of this study on 46 open-pollinated varietal hybrids grouped into eight maternal heterotic groups and evaluated under four

environments (i.e., location-years) were to (1) estimate levels of polymorphic diversity and population structure among 34 secondary traits (*senso* Monneveux et al., 2008) measured on plants, ears and kernels, and elucidate their multivariate relationships with grain yield, and (2) identify which maternal heterotic groups are potential sources of desirable variants of single or multiple traits.

MATERIALS AND METHODS

Three field experiments were conducted during 2004-2005 in three locations across the Northern Corn Belt (in Morris, Minnesota 45º 41´ N, 95º 48´ W, elevation 370 m; Brookings, South Dakota 44º 20´ N, 96º 47´ W, elevation 490 m, and in Colfax, Wisconsin 45º 00´ N, 91º 43´ W, elevation 300 m). Forty-six open-pollinated varietal hybrids derived from crosses between 11 maternal and 10 male corn heterotic groups were used in these experiments. In a preliminary multivariate analysis of variance (MANOVA) using adjusted trait means (see statistical analyses below), differences between maternal heterotic groups for all phenotypic traits and grain yield were highly significant, whereas differences between male heterotic groups were negligible and non-significant (Table 1). Therefore, the maternal heterotic groups were used as classificatory categorical source of variation in subsequent statistical analyses. The full description and pedigrees of these heterotic groups are available from the USDA's Plant Introduction Germplasm site (www.ars-grin.gov) and a brief description of the genetic material for the purpose of this study is available elsewhere (Jaradat et al., 2010). All field experiments were laid out in a randomized complete block design with three replicates in Morris, Minnesota, and two replicates in each of Brookings, South Dakota, and Colfax, Wisconsin. Each plot consisted of four rows 6.25 m long and 0.7 m between rows and 0.20 m among plants within rows. Management practices (i.e., seedbed preparation, seeding rate, sowing date, fertilizer rates and time of application, and weed control) were performed according to local standards for each location. The inner two rows in each plot were trimmed to a length of 5.25 m before combine harvesting, and grain yield was adjusted to 155 g kg^{-1} of moisture.

Table 1. Variation and test of significance based on the **P** matrix for 34 plant, ear and kernel secondary traits and grain yield (per plant and per hectare) among eight maternal heterotic groups (HGs) and among 46 open-pollinated varietal corn hybrids within maternal heterotic groups [OPVhs(HG)] evaluated under four environments.

Effect	Test statistics	P matrix based on	
		Secondary traits	Grain yield
Between maternal HG	Wilks' λ	0.001	0.001
	F	3	13670
	Effect d.f.	176	16
	Error d.f.	848	90
	Probability	0.0001	0.0001
Between OPVhs within HG	Wilks' λ	0.098	0.001
	F	4	20
	Effect d.f.	704	76
	Error d.f.	2640	90
	Probability	0.050	0.0001

PLANT SAMPLING AND MEASUREMENTS

Details of plant sampling and measurements are available elsewhere (Jaradat et al., 2010). A brief description is presented for the purpose of this study. Five plants per plot,

replicate, location and year, with a total of 50 plants per open-pollinated varietal hybrid, were sampled at physiological maturity from the two inner rows in each open-pollinated varietal hybrid, cut at the soil surface and photographed with ear(s) attached for further phenotypic analyses, then ears(s) were digitally photographed after being detached and their husks were removed. Morphological quantitative traits were measured on skeletal images as described by Foroutan-pour et al. (2000). Stalk lodging at the plot level was recorded under typical lodging-conducive conditions in Brookings, South Dakota, on a scale of 1 (0% lodged plants) to 5 (100% lodged plants). Root damage caused by the Western rootworm larva (*Diabrotica virgifera virgifera* LeConte) was scored on roots of three plants plot[-1] taken at random from each plot and replicate and expressed as scores ranging from 1 (no damage) to 6 (severe damage) (Hills and Peters, 1971).

STATISTICAL ANALYSES

Grain yield (Mg ha^{-1} and g plant[-1]) was adjusted to 155 g kg^{-1} grain moisture at harvest for each location-year combination (i.e., environment). In order to satisfy assumptions of uni- and multi-variate analyses of variance, all variables were subjected to the Levene test of homogeneity of variances and to the Shapiro-Wilk W test for normality, then the appropriate data transformation was carried out (Zar, 1996). Transformed data was back-transformed for reporting. Due to the large number of open-pollinated varieties and land constraints on the layout of the experimental plots, trait means were adjusted for spatial variability using the regular grid option in the spatial model of the Residual Error Maximum Likelihood (REML), with open-pollinated varieties as a fixed factor and environments and replicates as random factors (Smith et al., 2005; Payne et al., 2006). The adjusted mean and standard deviation (S.D.) calculated for each of the quantitative traits in each environment were used to categorize each trait into three discrete groups [i.e., (small) ≤ mean -1.0 S.D., (medium) > mean-1.0 S.D.< mean+ 1.0 S.D., and (large) ≥ mean+1.0 S.D.] according to Zar, (1996). A polymorphic diversity index (Zhang and Allard, 1986) was calculated for each heterotic group, open-pollinated varietal hybrid, and trait based on the relative phenotypic frequencies for each categorical trait as

$I = - \Sigma\, p_i \ln p_i$ for i = 1, 2 and 3,

where p_i is the relative frequency in the *i*th category of the *j*th trait and was used as a measure of phenotypic diversity. Total genetic diversity (H_T), and its components [i.e., within (H_S), and among (D_{ST}) populations] were calculated for heterotic groups and open-pollinated hybrids using frequencies of all categorical traits, then a population differentiation coefficient [i.e., the proportion of H_T found within populations (G_{ST})] was calculated as D_{ST}/H_T or alternatively as 1- (H_S/H_T) (Hamrick and Godt, 1989; Yeh et al., 2000).

Mean square error variances of each individual analysis by environment were found to be homogeneous based on Bartlett's χ2 test conducted before statistical analyses were carried out across environments. The variance components for open-pollinated varietal hybrids within a heterotic group pooled across all heterotic groups [$\sigma^2_{OPVh(HG)}$], environments [σ^2_E] and the interaction between open-pollinated varietal hybrids within heterotic groups and the environment [$\sigma^2_{OPVh(HG)*E}$] were estimated using the restricted maximum likelihood method (REML) (Smith et al., 2005; Payne et al., 2006). The phenotypic variance of an open-pollinated varietal hybrid mean was estimated as:

$[\sigma^2_P] = [\sigma^2_{OPVh(HG)}]+[\sigma^2_{OPVh(HG)*E}]/e+[\sigma^2_{Error}]/er;$

where e is the number of environments and r is the number of replicates in each of the e environments. The Principal Components Analysis (PCA) option in the Non-linear Iterative Partial Least Squares (NIPALS) module (StatSoft Inc., 2010b) was performed on mean values of each trait and heterotic group to identify latent variables (i.e., PCs) that accounted for most of the variance in the whole data set, and identify which traits are closely associated with which heterotic groups. A Partial Least Squares (PLS) regression model was developed to estimate grain yield (Mg ha^{-1}) as a function of open-pollinated heterotic groups, their

population parameters (i.e., *I*, *f* and G_{ST}), and plant, ear, and kernel traits. Calibration PCs and PLS models were developed using 75% of the whole data set, then the remaining 25% of the data were used to validate those models. Relevant modules in STATISTICA 9.1 (StatSoft Inc., 2010a) and GenStat 10.1 (Payne et al., 2006) were used in performing the statistical analyses, unless otherwise indicated.

RESULTS

Variation and test of significance based on the phenotypic (**P**) matrix for plant, ear and kernel traits, and grain yield per plant, among maternal heterotic groups and among open-pollinated varietal hybrids within heterotic groups are presented in Table 1. The nested MANOVA indicated large significant effects among heterotic groups and among open-pollinated varietal hybrids within heterotic groups for phenotypic traits and for grain yield per plant. Furthermore, large differences were observed in the **P** matrix structure, including large differences in the value, but not the sign, of correlation coefficients among traits within different open-pollinated varietal hybrids (data not presented). The test statistics (i.e., Wilks' λ) suggested that there were larger differences in secondary traits between heterotic groups (*P* = 0.0001) as compared to differences between open-pollinated varietal hybrids within heterotic groups (*P* = 0.05). Although Wilks' λs for grain yield analysis were highly significant and similar in magnitude for both effects (Table 1), the *F*-value for heterotic groups was much larger than the F-value for open-pollinated varietal hybrids within heterotic groups.

MULTIVARIATE RELATIONSHIPS

Loadings (i.e., simple correlations between variables and components) of heterotic groups, their population parameters (i.e. *I*, *f* and G_{ST}), and plant, ear, and kernel traits on the first two principal components (PCs) and variation accounted for by these PCs are presented as a bi-plot in Fig. 1. The first and second PCs in the validation model accounted for 0.42 and 0.17 of total variation in heterotic groups, population parameters, and quantitative traits combined. The first PC separated the heterotic groups into two; each was associated with a number of plant, ear and kernel traits. The first group consisted of four heterotic groups (BS, HPAL C#1, Nokomis Gold, and TEPR-EC6), had larger-than-average grain yield per plant, and was associated with a number of ear and kernel traits contributing to this larger grain yield. The second group consisted of the remaining four heterotic groups (Lancaster, Leaming, Minnesota 13, and Northwestern Dent), had smaller-than-average grain yield per plant as compared with the first group, and was associated with a number of traits, some of which (e.g., apical sterility, kernel moisture at harvest, kernel rows per ear) showed strong negative (*r* < -0.5; *P* < 0.05) loadings on PC1.

Population differentiation and frequency of the desirable trait variant, unlike the polymorphic diversity index, had large positive and negative loadings on PC2, respectively. Bi-variate correlations between *f* and *I* (*r* = 0.22), and between *I* and G_{ST} (*r* = 0.20) were positive and significant (*P* < 0.01), but not between *f* and G_{ST}. Nevertheless, all three population parameters had large positive loadings on PC1 and were associated with large grain yield per plant. Most heterotic groups had large positive or negative loadings on PC1 (*r* > |0.40|), except TEPR-EC6 and Leaming. However, most phenotypic traits had smaller loadings (*r* < |0.50|) except plant and tassel fractal dimensions, kernels per plant, kernels and kernel rows per ear, ear diameter and length, kernel moisture content at harvest, and apical sterility of the ear.

POPULATION STRUCTURE OF OPEN-POLLINATED VARIETAL HYBRIDS

Polymorphism, based on all traits, was 100% for each heterotic group (Table 2). When averaged across maternal heterotic groups, *I*, H_T, H_S, and G_{ST} were 0.88, 0.59, 0.19 and 0.68, respectively. Polymorphic diversity indices for heterotic groups were large and less variable when compared with their estimates for the four environments. Diversity within heterotic

groups (i.e., H_S) was relatively small and ranged from 0.12 to 0.27; it was relatively much smaller, and ranged from 0.08 in Wisconsin to 0.16 in Minnesota, for the four environments. Consequently, larger differences in population differentiation (G_{ST}) were found between heterotic groups (0.58 - 0.80) as compared to those found between environments (0.38 - 0.58). Population differentiation estimates were smallest for Nokomis Gold (0.53) and Minnesota 13 (0.58), intermediate for Lancaster, Leaming and TEPR-EC6 (0.61-0.67), and largest for BS-, HPAL C#1 and Northwestern Dent (0.70-0.80).

   Polymorphism ranged from 58.3 to 87.9% for the four environments. Relatively larger I estimates were found for the Minnesota (2004 and 2005) environments as compared to the South Dakota (2005) or Wisconsin (2004) environments. The same trend was observed for total diversity, but not for population differentiation.
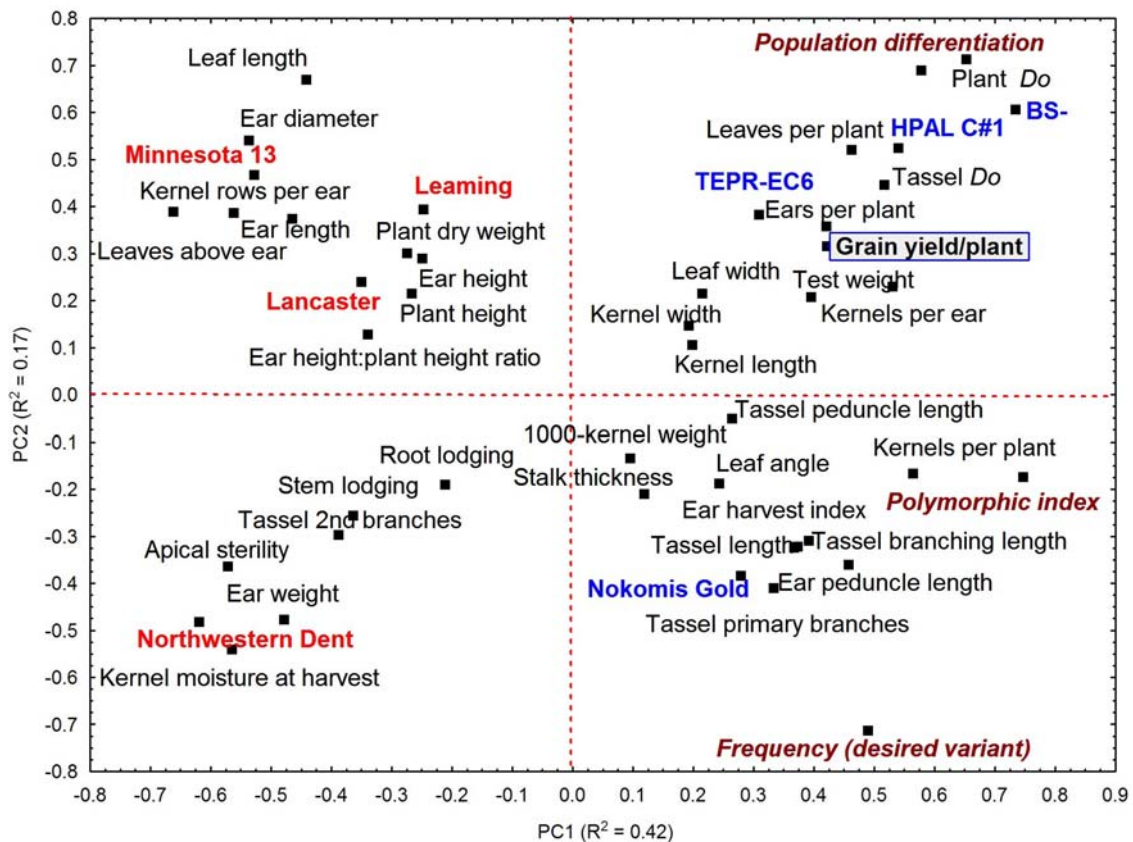

Figure 1. Loadings of maternal open-pollinated corn heterotic groups, their population parameters, and plant, ear, and kernel traits on the first two principal components (PC) and variation accounted for by these PCs.

POLYMORPHISM AND POPULATION DIFFERENTIATION

   Level of significance for four sources of variation (i.e., environment, heterotic groups, open-pollinated varietal hybrids within heterotic groups, and their interaction) indicated that most traits displayed significant differences due to variation among heterotic groups, whereas the least number of traits displayed significant differences due to variation among environments or due to the interaction between open-pollinated varietal hybrids within heterotic groups and the environment (Table 3). The traits that displayed significant differences due to environments ($P = 0.02$; kernel moisture content at harvest) also displayed significant differences due to the interaction of open-pollinated varietal hybrids within heterotic groups with the environment; whereas the traits that displayed marginal ($P = 0.09$; stalk thickness, kernels per plant, and ear weight), or no significant differences due to

environment (most traits, except grain yield per plant, and plant dry weight) showed no significant differences due to interaction of open-pollinated varietal hybrids within heterotic groups with the environment.

Estimates of polymorphic diversity index for individual traits ranged from 0.56 for ear leaf angle to > 0.80 for 70% of all traits; however, the five traits measured on individual kernels were less polymorphic than traits measured on ears or plants. Considerable population differentiation (G_{ST}) was found for many plant, ear, and kernel traits and the pattern of population structure differed greatly from one trait to another. Very few traits expressed small population differentiation (e.g., ear height:plant height ratio, ears per plant); whereas, most traits (80%) had G_{ST} values > 0.50. Kernel, ear, and plant traits, in this order, expressed decreasing level of population differentiation with the respective G_{ST} mean values of 0.60, 0.57, and 0.55.

Table 2. Polymorphic diversity indices (I ± S.D.) and genetic diversity analyses (total diversity, HT (mean±S.D.); diversity among maternal groups, H_S, (mean±S.D.); and level of differentiation, GST) based on 35 plant, ear and kernel traits measured on 46 open-pollinated varietal hybrids (OPVhs) in eight maternal heterotic groups (HG) and averaged over four environments.

Grouping	Polymorphism %	Diversity Index	Genetic diversity components		
		I	H_T	H_S	G_{ST}
Maternal HG					
BS-	100	0.86 (0.04)	0.61 (0.001)	0.17 (0.012)	0.7
HPAL C#1	100	0.96 (0.10)	0.62 (0.002)	0.18 (0.011)	0.79
Lancaster	100	0.85 (0.18)	0.55 (0.007)	0.21 (0.006)	0.61
Leaming	100	0.89 (0.07)	0.62 (0.001)	0.21 (0.016)	0.66
Minnesota 13	100	0.87 (0.06)	0.63 (0.003)	0.27 (0.010)	0.58
Nokomis Gold	100	0.86 (0.10)	0.58 (0.002)	0.27 (0.023)	0.53
Northwestern Dent	100	0.83 (0.17)	0.52 (0.006)	0.13 (0.006)	0.75
TEPR-EC6	100	0.95 (0.07)	0.60 (0.002)	0.12 (0.011)	0.8
Environments					
Morris, MN (2004)	78.8	0.44 (0.27)	0.29 (0.035)	0.16 (0.012)	0.44
Morris, MN (2005)	87.9	0.42 (0.25)	0.24 (0.026)	0.15 (0.010)	0.38
Brookings, SD (2005)	81.8	0.31 (0.24)	0.19 (0.027)	0.08 (0.011)	0.58
Colfax, WI (2004)	58.3	0.39 (0.22)	0.17 (0.019)	0.08 (0.009)	0.53

SOURCES OF DESIRABLE VARIANTS

Approximately 33% of the 280 estimates based on 35 traits and eight heterotic groups (Table 4) displayed above-average values for phenotypic diversity indices (*I*), frequency of desirable variant of a trait (f) and level of population differentiation (G_{ST}). Most of these traits have non-significant variance component due to the interaction of open-pollinated varietal hybrids within heterotic groups with the environment (Table 3). Three heterotic groups (i.e., HPAL C#1, BS-, and TEPR-EC6, in decreasing order) displayed the largest number of desirable trait variants (20, 16 and 13, respectively) having above-average values of all three population parameters; Nokomis Gold (6 traits), and Leaming (7 traits) displayed the smallest; whereas Minnesota 13 (9 traits), Lancaster (10 traits) and Northwestern Dent (11 traits) displayed intermediate number of desirable trait variants. Four of the 21 plant traits (ear height:plant height ratio, tassel secondary branching, ear leaf angle and average ear leaf length), one ear trait (ear diameter), and one kernel trait (percent kernel moisture at harvest)

failed to show desirable trait variants having above-average values for all three population parameters; whereas, seven plant traits (grain yield per plant, tassel peduncle length, tassel branching length, tassel primary branches, and tassel fractal dimension), and two ear traits (ear peduncle length and kernels per plant) had ≥ 50% desirable trait variants having above-average values for all three population parameters.

In addition to the relatively large differences between heterotic groups in the level of population differentiation (G_{ST}), there were differences in number of traits having all their diversity partitioned within populations (i.e., G_{ST} = 1). Only 15 out of the 280 G_{ST} estimates equaled unity. HPAL C#1 had the largest number of traits having all their diversity partitioned within populations (4), followed by Leaming (3), BS-, Minnesota 13, and Northwestern Dent (each with 2), Lancaster and TEPR-EC6 (each with 1) and Nokomis Gold with none. Five of these traits were plant traits (grain weight per plant, ear height, tassel length, tassel peduncle length, and average ear leaf width), four were ear traits (ear peduncle length, kernel rows per ear, kernels per ear, and kernels per plant), and one was a kernel trait (1000-kernel weight).
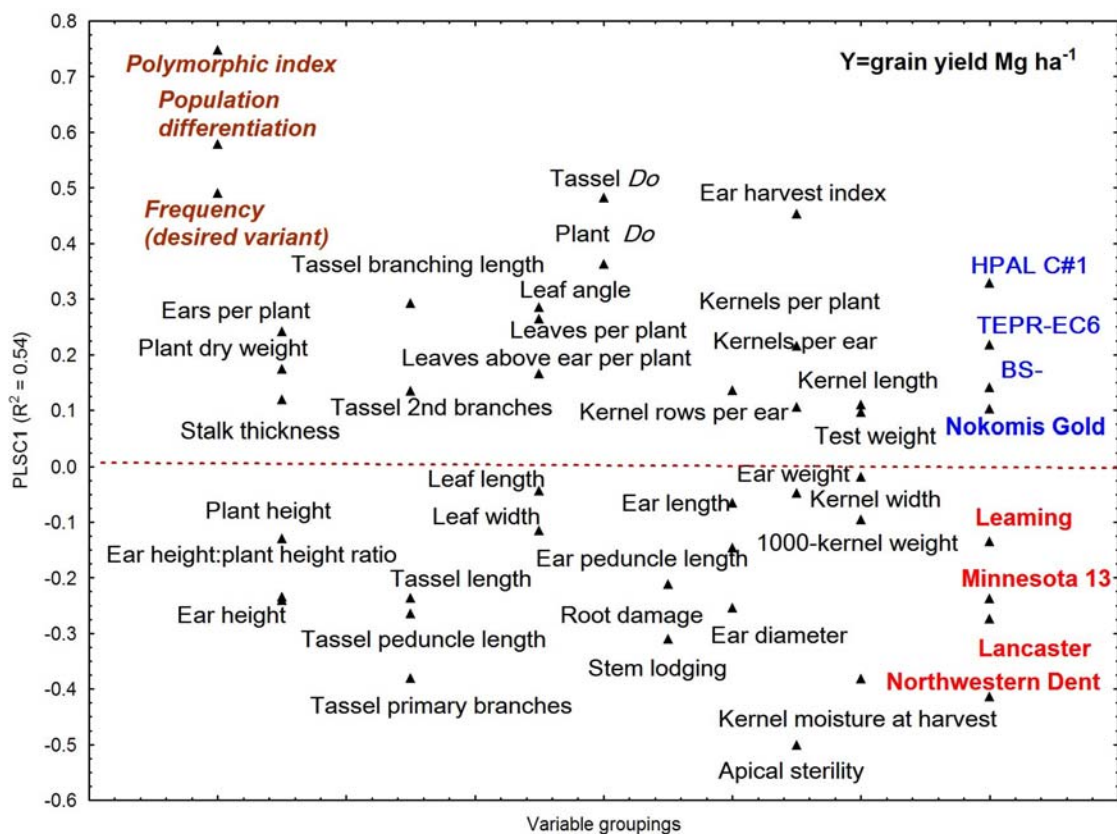
Figure 2. Grain yield (Mg ha⁻¹) as a function of maternal open-pollinated corn heterotic groups, their population parameters, and plant, ear, and kernel traits, and their loadings on the first partial least squares validation regression component (PLSC1).

MODELING GRAIN YIELD

Grain yield per hectare (Mg ha⁻¹), averaged over four environments, as a function of heterotic groups, their population parameters, and plant, ear, and kernel traits along with their loadings (i.e., correlation with the principal component) on the first partial least squares regression component (PLSC1) are presented in Fig. 2. The first PLSC of the validation model accounted for 0.54 of total variation in grain yield per hectare, whereas the second PLSC accounted for 0.18 of this variation (not presented). The whole set of variables was separated into eight groupings to easily visualize their associations, interactions, and loadings on

PLSC1. The heterotic groups were separated into two groups with the largest difference in loadings on PLSC1 was between HPAL C#1 and Northwestern Dent. The first group (HPAL C#1, TEPR-EC6, BS-, and Nokomis Gold, in decreasing order) loaded positively on PLSC1 with above-average grain yields, whereas the second group (Leaming, Minnesota 13, Lancaster, and Northwestern Dent, in increasing order) loaded negatively on PLSC1 with below-average grain yields.

All three population parameters (i.e., I, f and G_{ST}) had the largest positive loadings ($r > 0.50$) on PLSC1; whereas most plant, ear and kernel traits had smaller loadings ($r = \pm0.4$), with the exception of the positive loadings of ear harvest index ($r = 0.48$) and the plant fractal dimension ($r = 0.45$), and the negative loading of apical sterility ($r = -0.52$). Moreover, a few traits (e.g., ear height, plant dry weight, ear leaf length, ear length and ear weight) displayed very small loadings on PLSC1; however, these traits contributed to explaining the 18% variance in grain yield accounted for by the second PLS component (data not presented).

DISCUSSION

The limited diversity of current corn germplasm can lead to genetic vulnerability to biotic and abiotic stresses and it may limit future gains from selection; therefore, open-pollinated varieties, in addition to landraces and synthetic populations, may be useful in improving corn in the Northern Corn Belt (Taller and Bernardo, 2004), and elsewhere in developed (Tollenaar and Lee, 2002) and developing countries (Kamara et al., 2003a). Many heterotic groups proved to harbor large levels of "functional" variation for most secondary traits, a prerequisite initially sought for breeding open-pollinated varieties; the diversity of which was maintained during the last ~ 50 years at levels much larger than those of modern corn hybrids (Ho et al., 2005). Today, only a few corn breeders or farmers, especially in the US, have experience with the formation of synthetics or composites for release as high-yielding open-pollinated varieties (Kutka and Smith, 2007). Therefore, this and similar germplasm pools of potentially high-yielding open-pollinated varieties and their hybrids are useful to broaden the genetic bas available to farmers and for the production of high quality human food (Prasanna et al., 2001) and animal feed (Scott et al., 2008).

MULTIVARIATE RELATIONSHIPS

The bi-plot in Fig. 1 displayed the level of association among traits and between traits, population parameters, and heterotic groups. The first two PCs accounted for 59% of total validation variance; however, it took 10 additional PCs to account for 85% of total variance in the whole data set (data not presented); this reflects the wide variation between heterotic groups and the level of (dis)-association between traits and heterotic groups (Tollenar and Lee, 2002). Those traits close to the origin of the bi-plot, such as kernel length and width, may have little variability across heterotic groups or may not fit well into two dimensions. Other traits, such as kernels per ear (with positive loadings on both PCs) and 1000-kernel weight, with positive loading on PC1 and negative loading on PC2, both positively contributed to grain yield per plant, a phenomenon not regularly encountered in grain crops (Monneveux et al., 2008).

The bi-plot, also, illustrated the covariation and correlation among traits when averaged across environments and heterotic groups (Pressoir and Berthaud, 2004). The largest covariation values are between those traits loading positively and negatively on PC1 (accounted for 42% of total variation). Strong and positive simple linear correlations ($r = 0.22$ to 0.83; $P < 0.05$) were found between most traits and grain yield per plant across environments and heterotic groups (Jaradat et al., 2010). Elucidating the mechanisms underlying these relationships, when combined with a knowledge of available phenotypic diversity may allow us to elaborate new screening and breeding strategies and capture alleles that confer desired variants of specific traits or trait combinations of valuable "functional" utility.

Table 3. Level of significance of variance due to environments (E), maternal open-pollinated heterotic groups (HGs), open-pollinated varietal hybrids (OPVhs) within maternal heterotic groups OPVhs(HG), and their interacton [OPVhs(HG)xE]; and population statistics (polymorphic diversity index (*l*), and population differentiation (G_{ST}) estimated for 35 traits measured on 46 OPVs in eight maternal HGs.

Traits	Level of significance for *z* (random factor), or *F* (fixed factor) statistics				Population statistics	
	E	HGs	OPVhs(HG)	OPVh(HG) x E	*I*	G_{ST}
Plant architecture						
Grain yield/plant	0.150	0.001	0.006	0.050	0.89	0.58
Plant dry weight	0.210	0.001	0.500	0.050	0.98	0.48
Plant height	0.110	0.001	0.890	0.215	0.94	0.52
Ear height	0.110	0.001	0.020	0.435	0.91	0.62
Ear height:plant height ratio	0.153	0.050	0.010	0.091	0.97	0.17
Ears per plant	0.212	0.062	0.050	0.188	0.75	0.25
Stalk thickness	0.091	0.050	0.072	0.536	0.85	0.55
Tassel length	0.125	0.001	0.166	0.621	0.89	0.74
Tassel peduncle length	0.154	0.001	0.332	0.377	0.98	0.67
Tassel branching	0.151	0.001	0.044	0.425	0.87	0.63
Tassel 1st branch	0.150	0.001	0.185	0.860	0.92	0.6
Tassel 2nd branches	0.153	0.012	0.127	0.590	0.82	0.23
Leaves per plant	0.120	0.001	0.480	0.521	0.98	0.72
Leaves above ear	0.154	0.022	0.261	0.711	0.97	0.59
Ear leaf angle	0.211	0.081	0.199	0.273	0.56	0.62
Ear leaf length	0.152	0.001	0.050	0.050	0.88	0.6
Ear leaf width	0.155	0.001	0.050	0.522	0.92	0.65
Plant fractal dimension, *Do*	0.157	0.001	0.043	0.180	0.99	0.68
Tassel fractal dimension, *Do*	0.152	0.001	0.582	0.277	0.98	0.54
Stem lodging *		0.001	0.050		0.85	0.57
Root damage *		0.012	0.020		0.73	0.54
Ear traits						
Ear length	0.153	0.001	0.177	0.375	0.97	0.66
Ear peduncle length	0.150	0.001	0.034	0.522	0.97	0.49
Ear diameter	0.120	0.001	0.386	0.313	0.69	0.72
Kernel rows/ear	0.121	0.001	0.032	0.262	0.89	0.63
Apical sterility	0.155	0.174	0.390	0.014	0.89	0.32
Kernels per ear	0.126	0.001	0.002	0.155	0.9	0.68
Kernels per plant	0.091	0.011	0.051	0.190	0.75	0.49
Ear weight	0.090	0.050	0.062	0.322	0.91	0.6
Ear harvest index	0.158	0.082	0.090	0.282	0.87	0.56
Kernel traits						
Test weight	0.200	0.080	0.081	0.445	0.76	0.65
1000-kernel weight	0.156	0.001	0.092	0.178	0.79	0.61
Kernel moisture at harvest	0.021	0.082	0.129	0.050	0.65	0.64
Kernel length	0.122	0.001	0.050	0.120	0.77	0.56
Kernel width	0.120	0.001	0.060	0.192	0.76	0.53

* in Brookings, SD, only.

Table 4. Phenotypic diversity index (*I*), frequency of desirable variant (*f*), and population differentiation (G_{ST}) for each of 35 plant, ear and kernel traits measured on 46 open-pollinated varietal hybrids in eight maternal heterotic groups (Four heterotic groups with positive loadings on PC1, see Figure 1) and four environments (Values in bold italics are above the mean for all three parameters).

Trait	Desirable variant	BS-			HPAL C#1			Nokomis Gold			TEPR-EC6		
		I	*f*	G_{ST}	*I*	*f*	G_{ST}	*I*	*f*	G_{ST}	*I*	*f*	G_{ST}
Plant architecture													
Grain yield/plant	Large	*0.96*	*0.35*	*1.00*	*0.88*	*0.35*	*1.00*	0.67	0.00	0.75	0.92	0.25	0.08
Plant dry weight	Large	*0.85*	*0.30*	*0.82*	*0.92*	*0.35*	*0.85*	0.65	0.15	0.55	0.80	0.20	0.65
Plant height	>Medium	*0.98*	*0.30*	*0.70*	0.69	0.25	0.68	0.94	0.10	0.79	0.87	0.25	0.82
Ear height	Low	0.95	0.25	0.75	0.92	0.25	0.75	*0.69*	*0.55*	*0.84*	0.91	0.25	0.82
Ear height:plant height ratio	Small	0.92	0.50	0.38	0.69	0.25	0.45	0.67	0.60	0.25	0.88	0.20	0.67
Ears per plant	>1	*0.95*	*0.35*	*0.86*	*0.87*	*0.40*	*0.85*	0.65	0.20	0.36	*0.92*	*0.40*	*0.82*
Stalk thickness	Thick	*0.90*	*0.55*	*0.80*	*0.79*	*0.45*	*0.82*	0.75	0.20	0.65	0.89	0.45	0.49
Tassel length	Short	*0.95*	*0.50*	*0.72*	*0.93*	*0.50*	*0.87*	*0.98*	*0.35*	*0.81*	0.94	0.20	0.87
Tassel peduncle length	Short	*0.98*	*0.50*	*0.81*	*0.89*	*0.50*	*1.00*	*0.95*	*0.50*	*0.92*	*0.95*	*0.50*	*1.00*
Tassel branches length	Short	*0.84*	*0.60*	*0.78*	*0.92*	*0.50*	*0.82*	0.82	0.70	0.57	*0.82*	*0.40*	*0.75*
Tassel 1st branches	Short	*0.93*	*0.50*	*0.78*	*0.9*	*0.50*	*0.75*	0.81	0.70	0.57	*0.89*	*0.40*	*0.80*
Tassel 2nd branches	Short	0.82	0.25	0.82	0.67	0.00	0.56	0.56	0.00	0.57	0.95	0.00	0.43
Leaves per plant	Large	0.95	0.25	0.82	*0.68*	*0.50*	*0.77*	0.94	0.25	0.94	*0.97*	*0.50*	*0.85*
Leaves above ear	Large	0.82	0.25	0.75	0.67	0.25	0.48	0.69	0.00	0.83	*0.89*	*0.50*	*0.78*
Ear leaf angle	Narrow	0.75	0.00	0.5	0.65	0.00	0.85	0.55	0.00	0.49	0.75	0.00	0.48
Ear leaf length	Long	0.87	0.20	0.69	0.69	0.25	0.80	0.85	0.05	0.70	0.94	0.25	0.81
Ear leaf width	Wide	0.72	0.25	0.87	*0.9*	*0.30*	*0.87*	0.82	0.05	0.61	0.69	0.25	0.81
Plant fractal dimension, *Do*	Large	0.89	0.25	0.53	*0.92*	*0.30*	*0.87*	0.73	0.15	0.70	*0.87*	*0.40*	*0.79*
Tassel fractal dimension, *Do*	Large	0.92	0.25	0.62	*0.87*	*0.35*	*0.83*	*0.98*	*0.35*	*0.92*	*0.82*	*0.45*	*0.82*
Stem lodging	Low	0.85	0.15	0.85	*0.88*	*0.30*	*0.80*	0.85	0.15	0.81	*0.92*	*0.35*	*1.00*
Root damage	Low	0.92	0.20	0.80	*0.69*	*0.40*	*0.84*	0.89	0.25	0.76	*0.87*	*0.30*	*0.82*
Ear traits													
Ear length	Long	*0.93*	*0.30*	*0.81*	0.90	0.25	0.54	0.67	0.00	0.75	0.89	0.25	0.82
Ear peduncle length	Short	0.82	0.60	0.64	*0.89*	*0.50*	*1.00*	*0.81*	*0.70*	*0.81*	0.91	0.40	0.61
Ear diameter	Wide	0.65	0.00	0.37	0.87	0.00	0.67	0.61	0.00	0.80	0.88	0.00	0.54
Kernel rows per ear	Med	*0.86*	*0.30*	*0.74*	0.79	0.25	0.55	0.67	0.25	0.87	0.89	0.25	0.87
Apical sterility	Small	0.82	0.45	0.32	0.52	0.55	0.45	*0.95*	*0.55*	*0.87*	0.94	0.25	0.87
Kernels per ear	Large	0.90	0.25	0.28	*0.91*	*0.35*	*1.00*	0.90	0.10	0.56	0.95	0.25	0.80
Kernels per plant	Large	*0.95*	*0.35*	*0.80*	*0.86*	*0.40*	*0.95*	0.75	0.00	0.60	*0.87*	*0.40*	*0.88*
Ear weight	Large	*0.84*	*0.55*	*0.72*	0.69	0.45	0.82	0.76	0.05	0.75	*0.82*	*0.45*	*0.77*
Ear harvest index	Large	*0.93*	*0.85*	*0.83*	0.92	0.50	0.65	0.75	0.15	0.82	0.89	0.30	0.56
Kernel traits													
Test weight	Large	0.92	0.25	0.92	*0.89*	*0.35*	*0.86*	0.86	0.25	0.79	0.97	0.25	0.85
1000-kernel weight	Large	*0.92*	*0.30*	*1.00*	*0.88*	*0.30*	*0.79*	0.86	0.05	0.85	0.88	0.25	0.79
Kernel moisture at harvest	≤15.5	0.43	0.00	0.95	0.65	0.00	0.85	0.62	0.00	0.65	0.69	0.00	0.64
Kernel length	Large	0.87	0.25	0.43	*0.89*	*0.35*	*0.80*	0.94	0.10	0.79	*0.89*	*0.40*	*0.79*
Kernel width	Large	*0.82*	*0.35*	*0.78*	0.91	0.25	0.81	0.84	0.05	0.70	0.94	0.20	0.80

Table 4. (Continued) Phenotypic diversity index (*I*), frequency of desirable variant (*f*), and population differentiation (*G_{ST}*) for each of 35 plant, ear and kernel traits measured on 46 open-pollinated varietal hybrids in eight maternal heterotic groups (Four heterotic groups with negative loadings on PC1, see Figure 1) and four environments (Values in bold italics are above the mean for all three parameters).

Trait	Desirable variant	Maternal heterotic group, HG											
		Lancaster			Leaming			Minnesota 13			Northwestern Dent		
		I	f	G_{ST}	I	f	G_{ST}	I	f	G_{ST}	I	f	G_{ST}
Plant architecture													
Grain yield/plant	Large	*0.89*	*0.35*	*0.76*	0.85	0.25	0.34	0.69	0.00	0.25	*0.92*	*0.30*	*0.80*
Plant dry weight	Large	0.85	0.15	0.81	*0.79*	*0.30*	*0.78*	0.72	0.05	0.40	0.85	0.15	0.85
Plant height	>Medium	0.94	0.25	0.75	0.84	0.25	0.57	0.93	0.20	0.77	*0.89*	*0.35*	*0.87*
Ear height	Low	*0.85*	*0.5*	*0.74*	*0.92*	*0.35*	*1*	0.69	0.00	0.68	*0.82*	*0.60*	*0.61*
Ear height:plant height ratio	Small	0.85	0.35	0.37	0.72	0.15	0.37	0.67	0.00	0.25	0.85	0.55	0.07
Ears per plant	>1	0.63	0.25	0.42	0.75	0.15	0.45	0.53	0.00	0.35	0.75	0.50	0.28
Stalk thickness	Thick	0.91	0.35	0.42	0.75	0.25	0.86	0.82	0.05	0.45	0.8	0.45	0.32
Tassel length	Short	*0.92*	*0.50*	*0.85*	0.96	0.25	0.48	*0.95*	*0.04*	*0.82*	*0.92*	*0.50*	*1.00*
Tassel peduncle length	Short	*0.87*	*0.50*	*0.87*	0.98	0.05	0.85	*0.94*	*0.05*	*1.00*	*0.87*	*0.50*	*1.00*
Tassel branches length	Short	0.91	0.25	0.72	0.95	0.25	0.53	*0.84*	*0.55*	*0.70*	0.82	0.60	0.56
Tassel 1st branches	Short	*0.88*	*0.50*	*0.87*	0.92	0.25	0.33	*0.84*	*0.05*	*0.70*	0.89	0.60	0.55
Tassel 2nd branches	Short	0.89	0.10	0.45	0.87	0.10	0.31	0.52	0.01	0.24	0.92	0.10	0.15
Leaves per plant	Large	0.94	0.25	0.38	0.95	0.25	0.82	0.91	0.25	0.52	*0.91*	*0.30*	*0.77*
Leaves above ear	Large	0.95	0.25	0.82	0.98	0.20	0.52	0.69	0.00	0.43	0.82	0.05	0.62
Ear leaf angle	Narrow	0.65	0.05	0.73	0.67	0.10	0.92	0.85	0.00	0.65	0.64	0.05	0.54
Ear leaf length	Long	0.82	0.05	0.82	0.84	0.25	0.87	0.92	0.25	0.57	0.97	0.15	0.66
Ear leaf width	Wide	*0.89*	*0.30*	*0.85*	*0.93*	*0.35*	*1.00*	0.69	0.00	0.74	0.82	0.05	0.62
Plant fractal dimension, *Do*	Large	0.95	0.25	0.92	0.82	0.25	0.49	0.79	0.05	0.39	*0.93*	*0.30*	*0.87*
Tassel fractal dimension, *Do*	Large	0.97	0.25	0.95	0.95	0.30	0.76	0.93	0.25	0.57	*0.98*	*0.30*	*0.83*
Stem lodging	Low	0.72	0.05	0.80	0.85	0.15	0.81	0.85	0.25	0.52	*0.79*	*0.30*	*0.83*
Root damage	Low	0.69	0.00	0.75	0.89	0.25	0.76	0.96	0.25	0.54	0.85	0.25	1.00
Ear traits													
Ear length	Long	0.89	0.25	0.79	0.89	0.20	0.35	0.67	0.00	0.65	0.83	0.05	0.60
Ear peduncle length	Short	*0.94*	*0.40*	*0.85*	*0.92*	*0.40*	*0.76*	*0.78*	*0.55*	*0.84*	0.92	0.55	0.29
Ear diameter	Wide	0.69	0.00	0.69	0.82	0.00	0.55	0.67	0.00	0.55	0.69	0.25	0.56
Kernel rows per ear	Med	0.87	0.25	0.81	*0.87*	*0.35*	*1.00*	*0.69*	*0.35*	*0.82*	0.82	0.05	0.62
Apical sterility	Small	0.82	0.60	0.46	0.72	0.40	0.56	*0.90*	*0.50*	*0.82*	0.92	0.45	0.56
Kernels per ear	Large	0.88	0.25	0.95	0.85	0.25	0.35	*0.92*	*0.30*	*1.00*	0.89	0.25	0.65
Kernels per plant	Large	*0.95*	*0.40*	*1.00*	0.74	0.15	0.39	0.65	0.25	0.55	*0.90*	*0.40*	*0.76*
Ear weight	Large	0.89	0.35	0.65	*0.84*	*0.50*	*0.73*	0.82	0.10	0.46	0.89	0.15	0.65
Ear harvest index	Large	*0.94*	*0.40*	*0.72*	*0.93*	*0.45*	*0.82*	0.72	0.25	0.50	0.92	0.55	0.35
Kernel traits													
Test weight	Large	0.89	0.25	0.78	0.92	0.25	0.56	*0.85*	*0.35*	*0.87*	0.91	0.15	0.85
1000-kernel weight	Large	*0.92*	*0.30*	*0.89*	0.9	0.25	0.59	0.90	0.20	0.43	0.96	0.20	0.86
Kernel moisture at harvest	≤15.5	0.72	0.00	0.52	0.54	0.00	0.63	0.48	0.00	0.49	0.73	0.00	0.76
Kernel length	Large	0.87	0.25	0.38	0.85	0.25	0.66	0.89	0.25	0.66	*0.92*	*0.35*	*0.80*
Kernel width	Large	0.87	0.1	0.74	0.79	0.25	0.87	0.87	0.25	0.57	0.92	0.25	0.45

POPULATION STRUCTURE

The population differentiation coefficient (G_{ST} ranged from 0.53 to 0.80 for heterotic groups; Table 2; and from 0.17 to 0.74 for single traits; Table 3) is a powerful indicator of different histories and the consequent different allocation of genetic variation among and within heterotic groups. Also, it is an indicator of the level of available phenotypic variation that can be used to improve open-pollinated varietal hybrids. Values of G_{ST} can range from zero to one; low values indicating that little variation is proportioned within heterotic group or within open-pollinated varieties; whereas, large values indicate that a large amount of variation is found between heterotic groups or between open-pollinated varietal hybrids (Hamrick and Godt, 1989). The observed patterns of G_{ST} suggest that historical association is probably the main factor in shaping population structure for the heterotic groups (Lia et al., 2009), and may be interpreted as a result of ongoing gene flow, the consequence of historical association or a combination of both. Phenotypic reproductive traits displayed large G_{ST} values as compared to other traits; they are usually closely associated with grain yield per plant (Monneveux et al., 2008); and are expected, at least theoretically (Tollenaar and Wu, 1999), to be positively associated with better grain yield stability.

The majority of traits, especially the reproductive ones with large heritability (Jaradat et al., 2010; Ortiz et al., 2010) and small, or no-interaction with the environment in this germplasm pool, exhibited large polymorphic diversity indices (Table 3), and can be considered as components of a selection index (Ortiz et al., 2008). Additionally, as an indicator of phenotypic variation, there were more statistically significant quantitative differences in phenotypic traits between heterotic groups as compared to differences among open-pollinated varietal hybrids within heterotic groups, and the variance component between heterotic groups was more important than the variance components among open-pollinated varietal hybrids within heterotic groups; whereas the variance component due to the interaction between open-pollinated varietal hybrids within heterotic groups with the environment was negligible for most traits as was the case for populations within a corn landrace (Ortiz et al., 2008).

SOURCES OF DESIRABLE VARIANTS

The matrix in Table 4 furnishes the basic information for identifying heterotic groups with unique single or multiple trait combinations, or for identifying blocks of traits having above-average values for f, I and G_{ST} (33% of the whole data set). The eight heterotic groups were separated into two sub-groups based on their loadings on PC1 (Fig. 1). Unique and large blocks of traits having above-average values for all three population parameters can be found in BS-, HPAL C#1, and, to a lesser extent, in Northwestern Dent and TEPR-EC6. Of special interest are those traits having large portion of their H_T found within populations (i.e., G_{ST} close to 1) as an indicator of large level of population differentiation. Only two of such traits (i.e., short tassel peduncle length and large number of kernels per ear) were simultaneously encountered in two heterotic groups (i.e., HPAL C#1 and Minnesota 13).

The level of joint variation expressed in Table 4 also indicated that open-pollinated varietal hybrids, typical of heterogeneous and heterozygous open-pollinated populations (Lucchin et al., 2003) are not uniform, and are not as uniform as single-cross hybrids (Carena 2005); therefore, open-pollinated varietal hybrids might have the added advantage of plasticity. Desirable variants of a few traits of interest to farmers in regions with short-growing season, such as large number of leaves per plant, narrow ear leaf angle (Duvick and Cassman, 1999), and fast dry down at maturity (Soengas et al., 2003) or low kernel moisture content at harvest (Barata and Carena, 2006), although polymorphic, did not display above-average values for all three population parameters in any heterotic group.

MODELING GRAIN YIELD

Notwithstanding the large diversity found in these open-pollinated varietal hybrids, the PLSC1 of the validation model accounted for slightly more than half of the total variation in grain yield per hectare (GY ha^{-1}) and separated the heterotic groups and all 35 traits into almost two equal parts (Fig. 2). All three population parameters (i.e., f, I and G_{ST}) had large and positive impact on GY as they reflect the positive impact of most direct and indirect yield components on GY (Kamara et al., 2003a).

Plant and tassel fractal dimensions (Do) positively impacted GY. This impact is usually more pronounced in dicots than in monocots (Foroutan-pour et al., 2000). Plant Do reflects stalk and leaf characteristics. Total number of leaves per plant and those develop above the ear, but not ear leaf dimensions, contributed positively to GY (Table 2; Fig. 2). The short growing season, especially of the Minnesota environment in this study, may not allow open-pollinated varietal hybrid plants to develop the maximum number of leaves necessary for the optimum use of the limited growing period. Tassel Do reflects the size, dry weight, and branching of the tassel, all of which were reported (Uribelarrea et al., 2002; Monneveux et al., 2005) to correlate significantly with yield components and with GY. Tassel size is heritable (Monneveux et al., 2005) and a small tassel with many secondary branches (Uribelarrea et al., 2002) positively correlates with GY. Reduction in tassel size, when combined with increased branching, leads to pollen being shed as tassel differentiates and may lead to larger number of kernels per ear and a small apical sterility. Large scores for root damage and stalk lodging were associated positively with plant and ear height, and negatively with stalk thickness, and contributed to lower GY. Low root damage and stalk lodging are considered important agronomic characters in selection for improved open-pollinated varieties (Kamara et al., 2003a; Melani and Carena, 2005) because reduced root damage and stalk lodging should improve agronomic performance (Duvick and Cassman, 1999).

Grain yield in corn was reported to be more strongly associated with kernel number per ear than with number of ears per plant or with kernels per plant (Monneveux et al., 2005); however, in this study, ear length and kernel rows per ear were positively associated with GY. Large ears, especially at anthesis (Monneveux et al., 2005), constitute strong sinks that would result in larger number of kernels per ear or per unit area if number of kernels per plant and 1000-kernel weight do not exhibit a strong negative relationship. This trade-off can be minimized by selection for increased post-silking biomass production, longer leaf area duration and increased post-silking light interception (D'Andrea et al., 2008). Large levels of variation were found in this study for number of kernels per ear and number of ears per plant; however, depending on source-sink relationships, larger number of ears per plant, as a trait typically found in open-pollinated varieties and their hybrids, may become a better alternative sink than larger average size of individual ears. The later may lead to increased competition between neighboring grains and to increased abortion if the source became limiting (Monneveux et al., 2008).

Kernel moisture at harvest was one of a few traits significantly impacted by the environment. All open-pollinated varietal hybrids had kernel moisture content > 15.5% at harvest and there were significant differences among open-pollinated varietal hybrids within heterotic groups, mainly due to interaction with the environment (Table 3). Kernel moisture at harvest is considered as important as grain yield for areas with short growing season, such as the Northern Corn Belt (Barata and Carena, 2006). Fast dry down at maturity (Soengas et al., 2003) or low kernel moisture content at harvest (Barata and Carena, 2006) can stabilize yield by partially evading drought hazards, and will help reduce potential drying cost.

CONCLUSIONS

Heterotic groups of open-pollinated corn varieties and their hybrids gained increased interest among organic and low-input farmers due to their stable yields, broad adaptation,

low-input requirements, quality traits and tolerance to adverse conditions. Polymorphism, population structure, and multivariate relationships among 34 secondary traits and their impact on grain yield were quantified in 46 open-pollinated varietal hybrids within eight maternal heterotic groups. Large levels of polymorphism and population differentiation especially for reproductive traits, and above-average values for diversity indices, frequency of desirable trait variants, and population differentiation were found for almost all secondary traits. Maternal heterotic groups were identified as potential sources of desirable variants of single or multiple traits appropriate for adaptation to short-growing seasons, low-input farming and, possibly, adverse environmental condition. The information on the variability available in these open-pollinated varietal hybrids is of value in pursuing breeding and selection objectives for organic and low-input farming and to help stabilize yield through increased diversity on the farm.

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