Rapid estimation of broad sense heritability of farmer-managed maize populations in the Central Valleys of Oaxaca, Mexico, and implications for improvement

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Summary

A method for rapid estimation of broad sense heritability (H) was applied in farmers' maize fields in two communities in Oaxaca, Mexico. Plant and ear traits were documented and H estimates compared with narrow sense heritability (h^2) from family analysis and published estimates. Absolute values of H estimates were larger than h^2 estimates from this study and the literature. Relative ranking by trait was the same as in the literature, though not the same as rankings of h^2 estimates generated in this study. With an understanding of its limitations, this rapid, economical estimation procedure could provide useful initial information especially for collaborative crop improvement work between researchers and farmers or farming communities on-farm, a plant breeding context for which little empirical information is available.

Introduction

There is increasing interest in farmer-managed crop varieties (FVs, also called landraces) for both genetic resource conservation (Qualset et al., 1997), and crop improvement for low-resource agricultural systems (Ceccarelli et al., 1998; Weltzien & Fischbeck, 1990). Indeed these two interests converge in the discussion of whether in situ conservation will only persist if FVs are improved for local use (Brown & Young, 2000).

Research for local crop improvement, especially for low-resource farmers, is increasingly incorporated into collaborative or participatory plant breeding (CPB or PPB) (CGIAR, 1997; Cleveland & Soleri, 2002; McGuire et al., 1999; Witcombe et al., 1996). CPB implies interaction between farmer-breeders and formally trained plant breeders (hereafter, farmers and breeders, respectively) in crop improvement for local use (Eyzaguirre & Iwanaga, 1996), and includes close attention to adaptation to local biophysical and sociocultural factors. One form of CPB will be based on revisions of existing local selection methods to improve low resource farmers' own crop populations (McGuire et al., 1999). This approach can be economical, and has the potential to improve selection response because a) the target and selection environments are the same, and b) it uses material with a history of selection under local conditions (Ceccarelli et al., 1998). This is the CPB context emphasized in this paper.

CPB will require innovations addressing the demands of interdisciplinary (social and natural sciences) and intercultural (farmers and researchers) collaboration, and of plant improvement often in variable, stress-prone environments. Due to widespread occurrence of qualitative G × E interactions, the contri-

bution of specific ecological adaptation to population performance is being investigated by plant breeders working in a range of environments (e.g., Cooper, 1999; Cooper & Byth, 1996). Implicit in addressing forms of local adaptation is decentralization of plant improvement (Ceccarelli et al., 1996; Witcombe, 1998), in many cases requiring additional methodological changes relevant to smaller target areas. Some CPB improvements may have limited geographic coverage and the cost of assessment and improvement methodologies will require evaluation in light of these circumstances. Researchers may need to reconsider the amount and precision of information required for CPB, and look for innovative, economical sources of information and ways of using it.

While a small but growing literature exists on the genetic structure of FVs under farmer management (e.g., Louette et al., 1997; Louette & Smale, 2000), much remains to be understood concerning the genetic consequences of the interaction of growing environments and farmers' practices. Indeed, environments, plant populations, selection criteria and methods in CPB could all differ sufficiently from those of more conventional breeding experiences to make generalizations based on those experiences about heritability of traits and expectations for response to selection inadvisable (Smith et al., 1990). Exploitation of local adaptation depends on consideration of these differences, including estimation of heritabilities that are locally relevant and reflect the selection strategies used.

This research was undertaken as part of a larger interdisciplinary study (Cleveland et al., 2000; Soleri et al., 2000; Soleri & Cleveland, 2001) exploring methodologies potentially useful for CPB, particularly mass selection on-farm. We report estimations of broad sense heritabilities (H) on-farm in populations of farmer-managed maize (*Zea mays* L.) FVs from two communities in Oaxaca, Mexico. Where possible, these are compared with published estimates for similar traits and with estimates of narrow sense heritability (h^2) from experimental plots in this study. These estimates and other information generated by this study may have utility in the creation of simple, multiple trait selection tools for CPB.

Materials and methods

This study investigated populations of maize grown by traditionally based farming households in the Cent-

ral Valleys of Oaxaca, Mexico. Communities in this area are predominantly either indigenous Zapotec, or Mestizo or a mix of these two (INEGI, 1993: 35). While off-farm work is increasingly important in this region, including temporary migration within Mexico and to the USA (Stephen, 1994; M.W. Rees, personal communication August 1997), subsistence agriculture predominates and maize production is the foundation of most rural households' economy (INEGI, 1993). Ninety five percent of the area's agricultural production occurs during the summer season (May-November), with maize accounting for 87% of that (Dilley, 1993). Eighty eight percent of summer maize production in the Central Valleys is rainfed and vulnerable to variation in initiation of the summer rainy season and the *canicula* or mid-season drought, resulting in maize crop failures one year in four (Dilley, 1993).

Materials

On-farm and experimental plot studies were used for estimating broad and narrow sense heritabilities, respectively. The on-farm sites and sources of the maize populations studied were two communities (referred to here by pseudonyms); Santa Maria with more favorable and San Antonio with relatively less favorable growing conditions (Table 1).

This study used the most commonly sown variety in these communities, known as '*blanco criollo*,' a variety dominated by the maize race typical of this region, *Bolita* (Aragón Cuevas, 1989). Populations of this variety grown by four households in Santa Maria and three in San Antonio were studied. Data were collected on-farm in 1996 and 1997, and five of these populations were included in the 1997 experimental plots.

Seed for each on-farm field was that maintained by the household whose field it was and is referred to here as a population, a household's seedlot (Louette et al., 1997) and the resulting plants of one variety grown in one year. While data were collected on-farm for two consecutive years, it was not assumed that consecutive plantings of a variety grown by one household would have the same genetic variation or structure, thus they are identified as different populations.

Data were collected for traits a) with known heritabilities and/or components of variation in maize (Hallauer & Miranda, 1988) (ear and plant height, ear dimensions), b) of agronomic importance in the local growing environment identified by breeders working

Table 1. Characteristics of study communities in the Central Valleys of Oaxaca, Mexico

| Characteristic	Santa Maria	San Antonio
Elevation (masl)[a]	1490	1780
Average annual precipitation (mm)[b]	685	468
Predominant soil characteristics[c]	alluvial, sandy clay	piedmont, gravel
District average maize yield (t h^{-1})[a]	0.76	0.45
Average sowing rate (seed h^{-1})[d]	47,000	40,000
Population size (1995)[a,e]	2800	2533
Predominant ethnic/linguistic group[f]	Mestizo/Spanish	Zapotec/Zapotec

[a] INEGI 1996.
[b] Dilley 1993.
[c] Kirkby 1973.
[d] Based on field observations, Soleri 1996–1997.
[e] 1998 estimates for both communities = 3000, M.W. Rees personal communication 1998.
[f] INEGI 1993.
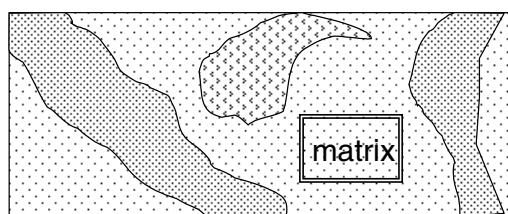
Typical, variable farmer's field

Figure 1. Placement of matrix for on-farm, rapid estimation of broad sense heritability in a single year and location.

in the region, (anthesis-silking interval, ear leaf dimensions, primary tassel branch number) (F. Aragón C., F. Castillo, GO. Edmeades, personal communications 1996; Paterniani, 1990), and c) of interest to local farmers (stover production [plant height × stalk diameter], days to anthesis, ear size [length, diameter] and weight, grain yield, 100 kernel weight). Traits of interest to farmers were identified through participant observation, informal discussions and interviews with farming households early in the summer of 1996.

Methods on farm

We used a method for estimating broad-sense heritability in a single season in an extant plant stand (Smith et al., 1998). Planting dates for the on-farm fields were determined by each household and ranged from mid-May through late June in both years (1996 and 1997). None of these fields received irrigation. At each on-farm site a matrix of 480–500 contiguous, approximately equidistantly spaced plants was identified within a farmer-sown and managed field (Figure 1). Matrix dimensions included 10 × 50, 22 × 22 and 20 × 25 hills, depending upon individual field dimensions.

This method assumes random distribution of genetic variation (V_G) within a field and therefore the contributions of V_G and nonrandom environmental variance (V_E) to variances of subplot means (V_X) (subplot = group of contiguous plants within the matrix, with x = number of plants in the subplot) are expected to change at different rates as × changes. Considered alone the contribution of nonrandomly distributed V_E is defined by the regression coefficient b (heterogeneity coefficient) of Smith's Law (Smith, 1936):

$$V_X = V_1/x^b$$

with V_1 being the total phenotypic variance in the field estimated with x = 1 (Smith et al., 1998). This is combined with the contribution of randomly distributed V_G in the H estimation method applied in this research (Smith et al., 1998)

$$V_X = (V_1\alpha/x^b) + (V_1[1-\alpha])/x$$

where α is V_E and $1-\alpha$ is V_G. Distinguishing V_E from V_G assumes the former is predominantly nonrandom, resulting in a similarity between neighbors in the form of covariance. Severe, abrupt environmental changes violate this assumption, as do small scale patches (Usnasis, 1972). Consequently, using visual observations in the first month after sowing, on-farm matrices were intentionally placed in within field locations displaying relative internal homogeneity, avoiding inclusion of two or more visually-obvious, environmental patches (see Figure 1). For every matrix the relative

contributions of V_G and V_E to V_X for each trait were calculated using iterative, non linear estimation for 12 subplot sizes.

All data were collected on the same individual plants, one selected at random from each hill within the matrix and tagged before anthesis. Because local planting design always includes multiple kernels per hill, data were initially screened, and if necessary, adjusted for the covariate plants per hill (LeClerg et al., 1962). Anthesis-silking interval (ASI) and days to anthesis were determined by observations every other day from first pollen shed to first emergence of silks; plant morphological traits (ear height, plant height, stalk diameter, ear leaf dimensions, tassel branch number) were recorded post-anthesis; ear traits were measured post harvest on air dried ears.

Analysis of data collected on-farm was performed using PLANTVAR and BASICNL, programs written for SAS (SAS Institute, 1989) for use with this method (Smith et al., 1998). Population H estimates were accompanied by 95% confidence intervals of the non linear estimation of α and b (not reported here) and used to calculate population and community (average) H estimates. These estimates assume subsequent selection would be biparental and on an individual plant basis.

Experimental plots

Half sib family analysis of components of variance in five of the farmer-maintained populations was conducted in 1997 at two sites that were typical, irrigated farmers' fields in two communities in the study area, one adjoining Santa Maria, the other 35 km north of Santa Maria in the same valley. At both sites fields were located in the high alluvial zone with sandy clay soils (Kirkby, 1973). Sowing rate was 47,600 seeds h^{-1} with one field planted 8 July, the other 10 July, 1997. Irrigation was applied as needed and fertilization and pest control were as recommended by the local office of the national agricultural research institute. One hundred half sib families were sown in 5m ear-row plots for each of the five populations. Each plot contained eight hills with two kernels sown $hill^{-1}$. A modified randomized block design (Eckebil et al., 1977; Yates, 1936) with blocks within replications was used, each block containing ten randomly selected families from each of the five populations and with two replications at each location.

All data were collected on a maximum of ten plants per family plot. Traits documented post an-

thesis were ear and total plant heights and stalk diameter. Ear length, diameter and weight, and kernel row number were measured immediately post-harvest with grain moisture recorded simultaneously for a bulked, balanced, one kernel-row sample from all documented ears in each family plot in each block using a DICKEY-john HM moisture gauge.

Analysis was conducted using a mixed model analysis of variance (SAS version 6.12) with all effects considered random (Littell et al., 1996). Plants per hill and grain moisture were the covariates in this experiment, the latter for ear weight only. Population narrow sense heritabilities (h^2) on an individual plant basis were calculated as

$$h^2 = \frac{4\,(V_{FAMILY})}{(V_{FAMILY}+V_{LOC}+V_{REP}+V_{BLOCK}+V_{PPH}+V_{MOIST}+V_{ERROR})^*}$$

* variances due to effect of family, location, replication, block, plants per hill, grain moisture, and error, respectively.
(equation 54, Nyquist, 1991: 278).

Results and discussion

On-farm findings regarding specific traits

To improve the utility of the H estimates (Table 2) we discuss those together with other descriptive statistics from the on-farm data. In the context of CPB where the efficiency of obtaining local data will be critical, even coarse, descriptive statistics such as these can be informative.

Decisions regarding the development of selection strategies require an estimation of total phenotypic variance (V_P) in addition to heritability. Intrapopulation coefficients of variation (CVs) estimated from data collected in the on-farm matrices indicate V_P, and when combined with H estimates, provide insights into populations' selection potential. Similarly, correlations among traits (Table 3) are an important consideration in the development of selection strategies (Hallauer & Miranda, 1988: 150ff). Indeed, a suite of traits is of interest to the maize farmers we worked with (Soleri et al., 2000). Below we outline how H, CVs and phenotypic correlations from the on-farm data can be used to identify promising selection criteria for CPB.

Table 2. Summary of mean broad sense heritability (H) estimates, trait mean and mean within population coefficient of variation (CV) across all populations for 13 traits in maize: both communities combined

Trait (number of populations)	Mean H estimate ± SE[a]	Trait mean across populations ± SE	Mean within population CV (%) of trait
Ear height (cm) (n = 11)	0.74 ± 0.05	95.1 ± 6.1	22.3
Plant height (cm) (n = 8)	0.65 ± 0.04	225.0 ± 10.6	13.3
Stalk diameter (cm) (n = 11)	0.67 ± 0.05	1.9 ± 0.1	16.5
Ear leaf width (cm) (n = 9)	0.65 ± 0.07	8.1 ± 0.3	16.4
Ear leaf length (cm) (n = 8)	0.65 ± 0.07	82.5 ± 3.3	13.8
1° tassel branches (count) (n = 8)	0.71 ± 0.06	11.6 ± 1.0	36.3
Days to anthesis (days) (n = 6)	0.65 ± 0.09	64.7 ± 3.5	5.6
ASI[b] (days) (n = 4)[c]	0.48 ± 0.18	3.9 ± 1.2	102.7
Ear length (cm) (n = 10)	0.63 ± 0.07	11.4 ± 0.4	19.9
Ear diameter (m) (n = 9)	0.55 ± 0.11	42.4 ± 0.1	10.8
Grain yield (gm) (n = 12)	0.47 ± 0.08	70.5 ± 4.5	45.7
100 kernel weight (gm) (n = 8)	0.61 ± 0.11	38.7 ± 1.3	21.4

[a] Standard error of the mean across populations.
[b] ASI = anthesis-silking interval.
[c] Estimates only available from San Antonio populations.

Table 3. Examples of coefficients of phenotypic correlation: mean of all populations combined (n maximum = 12)[a]. Reproductive phenology and post harvest traits in maize[b]

Traits	Days to anthesis	ASI[e]	Ear length	Ear diameter	Grain yield	100 kernel weight
Ear height	[c]	–0.28	0.41	0.14	0.32	0.17
Plant height	[c]	–0.35	0.42	0.29	0.42	0.13
Stalk diameter	[c]	ns	0.40	0.20	0.41	0.28
Ear leaf width	[c]	–0.16	0.47	0.25	0.37	0.26
Ear leaf length	[c]	–0.04	0.45	0.24	0.30	0.24
1° tassel branches	[d]	–0.10	0.27	0.19	0.22	ns
Days to anthesis	–	–0.24	[d]	[d]	[d]	[d]
ASI[e]	–	–	–0.25	–0.29	–0.31	–0.09
Ear length	–	–	–	0.46	0.68	0.32
Ear diameter	–	–	–	–	0.58	0.40
Grain yield	–	–	–	–	–	0.43

[a] Significant at $p \leq 0.05$ for individual location means (n = 2) and across locations mean unless otherwise indicated.
[b] Calculations based on 812–3938 individual plants.
[c] Santa Maria location mean significant and negative; San Antonio location mean significant and positive.
[d] Santa Maria location mean significant and negative; San Antonio location mean not significant.
[e] ASI = anthesis-silking interval.
ns = not significant.

Ear height

H of height to the first-developed ear was consistent with expectations based on the estimation method and values in the literature (Table 2) (e.g., Bolaños & Edmeades, 1996; Fountain & Hallauer, 1996; Hallauer & Miranda, 1988). CVs for the two communities were similar, suggesting heritable genetic variation is present for this trait that may serve as a proxy for total plant height as demonstrated by the high phenotypic correlation (0.70) between the two traits. Some farmers expressed a desire for shorter plants to avoid lodging or increase harvest index. This desire is not universal however, as stover is valued in these communities, and in poor years may be the only product harvested. Depending on farmers' goals, the ease of measurement with minimal experimental error makes ear height a trait with potential for change through on-farm CPB in these populations.

Plant height

For CPB projects needing to minimize investments in developing selection strategies, few field visits will be possible, and traits subject to degeneration in the field are to be avoided. One of these is total plant height as the central spikes of tassels are easily broken off. Due to low CV, lower relative H (Table 2), high phenotypic correlation with ear height, and potential for experimental error, plant height seems a poor trait for selection.

Stalk diameter

In these populations stalk diameter had a high phenotypic correlation (>0.91) with stover yield. With an overall mean H of 0.67 and variation present (Table 2), stalk diameter could be a trait for achieving gain from selection. Phenotypic correlations between stalk diameter and other plant morphology (not shown) and post harvest traits were positive and significant (Table 3). Based on these, selection for large stalk diameter and increased stover production would be possible, but improvement would likely occur through selection for larger plant and ear phenotypes.

Ear leaf dimensions

Ear leaf length and maximum width were measured because of the association between ear leaf area and N uptake (Lafitte & Edmeades, 1994), considered important in this region (Aragón Cuevas, 1996). H estimates and CVs for both ear leaf dimensions were similar and consistent across communities. Phenotypic correlations between these traits and grain yield were significant and agreed in sign with other traits associated with grain yield in these environments. For this reason, and because ear leaf dimensions are not of direct interest to farmers, other traits such as ear height and ear dimensions are preferable mass selection criteria. Those traits would select for yield while maintaining selection pressure for larger ear leaf size and associated benefits for N uptake.

Primary tassel branch number

The number of primary tassel branches was documented to test whether a negative correlation existed between this trait and grain production, especially under drought stress (Paterniani, 1990). To the contrary, a small but significant positive phenotypic correlation was observed between tassel branches and grain yield, and a significant negative correlation with ASI (Table 3). Comparing phenotypic and genetic correlations between tassel branch number and grain yield

under severe drought stress, Bolaños & Edmeades (1996) found them opposite in sign with genetic correlation being positive, suggesting substantial environmental correlation for this trait (Falconer & Mackay, 1996: 313). H estimates, population means and CVs were similar between communities. Despite this and the ease of data collection, the lack of other studies and the conflicting findings here and elsewhere should discourage use of primary tassel branch number in selection.

Days to anthesis

Across populations in which H was estimable (n = 6), days to initiation of anthesis had the lowest mean CV of any trait (Table 2). This, and the range of individual population means recorded (50–78 days), suggest that there has been and continues to be substantial selection pressure exerted on this trait. As cycle duration is a fundamental distinguishing characteristic used by local farmers, selection may have reduced genetic diversity for this trait. Should a new duration class be desired, new genetic variation may have to be introduced into individual populations, although the range of population means suggests sufficient variation may be present locally from other FV populations. This possibility is reflected in farmers' seed acquisition strategy in San Antonio where reduced duration is a primary objective when new seed stocks are sought. Louette et al. (1997) also found cycle length to be a primary distinguishing characteristic among varieties of farmer-managed maize in Jalisco, Mexico. The relatively high H estimate for this trait (Table 2) supports the finding in other studies that environmental variation has a relatively small effect on days to anthesis (Bolaños & Edmeades, 1996). Despite similar H estimates from each community, phenotypic correlations between this trait and others relating to plant size and yield differed between communities (Table 3), with five of 11 correlations being significant but opposite in sign, and another five being significant and negative in Santa Maria but not significant in San Antonio. The consistency of the correlations in Santa Maria and their contrast with San Antonio may result from specific ecological adaptation to each growing environment and distinct community level selection strategies, both considerations for CPB. Although laborious to document, this trait's importance and high H value make it a desirable selection criterion.

ASI

In a study of drought stress in tropical maize populations, the interval between initiation of anthesis and silking (ASI) was negatively and significantly correlated with grain yield under drought, and ASI heritability was not reduced by increased drought stress (Bolaños & Edmeades, 1996). The relationship between ASI and grain yield under drought was also observed by Paterniani (1990) and reduced ASI is a trait increasingly sought in the development of drought tolerant maize populations (Chapman & Edmeades, 1999). However, ASI poses challenges for data collection, especially in CPB; it is labor intensive, the potential for experimental error can be high, with full expression occurring only under moderate to severe drought, complicating characterization. ASI can show enormous variation primarily due to differences in initiation of silking as seen in the Oaxaca data (Table 2). The extent and pattern of the variation documented for ASI in this study prohibited calculation of H for most populations. For the four San Antonio populations where it was calculable, average H was relatively low and CV was over 100% (Table 2). Significant negative phenotypic correlation coefficients for ASI and ear dimensions and grain yield (Table 3), support the hypothesis that reduced ASI may contribute to improved yield under drought stress. The difference between individual ASI as measured in this study and ASI between 50% anthesis and silking in a plot as this trait is typically measured may also warrant consideration if days to anthesis has much intrapopulation V_P. For methodological and practical reasons ASI seems a poor trait to address in on-farm selection.

Ear length

Ear length is a primary component of farmers' definition of 'good ears' for planting seed. Mean H and population means were similar between locations, and variation was present (Table 2). Long ears were associated with larger plants (greater ear height, larger stalk diameters, longer and wider ear leaves) having shorter ASIs and larger ear diameters. Given this information, its ease of measurement and its importance to farmers, ear length seems an appropriate selection criterion.

Ear diameter

Ear diameter is also a trait used by many farmers when selecting planting seed, though apparently not as important as ear length (Soleri et al., 2000). Correlations between ear diameter and other traits related to plant size and harvest were generally comparable to those of ear length (Table 3), but H and CVs were lower (Table 2). Based on farmers' preferences and the findings of this research, ear length would be a more appropriate selection criterion than ear diameter.

Grain yield

Grain yield is of great interest to farmers, with medium to low heritability reported in the literature (Hallauer and Miranda, 1988). Differences between communities in population mean grain yield per ear (66.6 gm in Santa Maria and 75.9 gm in San Antonio) are not reflected in mean ear dimensions or 100 kernel weights, and may be the result of lower grain filling in Santa Maria, experimental error, or both. In the on-farm context, the potential for experimental error from grain loss is substantial and can confound identification of genotypes with superior grain yield, especially under drought stress. Similarly, CVs are high for this trait, perhaps in part reflecting experimental error. Yet, the CV for 100 kernel weight suggests that some of the variation in grain yield is in fact the result of phenotypic differences. Still, the low H estimates and potential for experimental error make this a problematic selection criterion. Bolaños & Edmeades (1996) reported high (>0.76) genetic and phenotypic correlations between grain yield and ears per plant (prolificacy) under severe water stress, yet unlike grain yield, H for prolificacy increased under drought stress. Thus selection for prolificacy (e.g., Chapman and Edmeades, 1999), and other traits discussed above, seems a more appropriate approach to on farm improvement of grain yield.

100 kernel weight

Weight of 100 randomly selected kernels from an ear permits rough comparison of kernel size and density between individuals. Farming households in the Central Valleys of Oaxaca use a similar comparison when selecting or buying planting seed, with weight per volume and per individual kernel receiving attention (Soleri & Cleveland, unpublished data). Assuming careful execution including random sampling of well-dried kernels, elimination of those effected by pest infestation, and accurate counting, 100 kernel weight is less vulnerable to experimental error than grain yield and may address these farmers' interests in grain size and density. Still, in the context of CPB this advantage must be weighed against the time required to document this trait. Given this consideration, and the variation documented here, 100 kernel weight may

Table 4. Summary of traits appropriate and inappropriate for local maize selection based on data obtained with the on-farm rapid H estimation method

Traits appropriate for on-farm selection across communities	Rationale
Ear height	$H > 0.70$; variation present (CV = 22%); easy to measure; minimal experimental error; significant positive phenotypic correlation with other traits important to farmers, indirect selection for ↓ lodging, ↑ harvest index, or ↑ stover production
Ear length	$H > 0.60$; variation present (CV = 19%), easy to measure; minimal experimental error; significant positive phenotypic correlation with other traits important to farmers
Stalk diameter	$H > 0.60$; variation present (CV = 19%); easy to measure; minimal experimental error; significant positive phenotypic correlation with traits important to farmers
100 kernel weight	$H \geqq 0.60$; variation present (CV = 21%); easy to measure; experimental error easy to control; significant positive phenotypic correlation with traits important to farmers. However, time consuming.
Traits inappropriate for on-farm selection across communities	**Rationale**
Primary tassel branches	Inconclusive evidence of relationship to important traits
Plant height	Susceptibility to damage
ASI	Laborious, correct characterization difficult
Grain yield	High potential for experimental error on farm
Trait suggesting ecological specificity and distinct selection strategy by community	**Rationale**
Days to anthesis	$H > 0.60$, introduction of V_G required (CV = 5.6), phenotypic correlations with important yield and plant size traits consistently opposite in sign and predominantly significant between communities; community preferences.

be most appropriate as a secondary selection criteria, applied to genotypes first selected for other traits.

Overall, these data suggest a basic, multiple trait selection tool including ear height, days to anthesis (after introduction of variation into populations) and ear length (Table 4). Depending on population size and selection intensity, 100 kernel weight and perhaps stalk diameter may be included. Though not documented in this study, prolificacy would also be a valuable trait for inclusion.

Credibility of the on-farm estimates

This research is the first application on-farm of a methodology to rapidly estimate H using data from randomly sown individual plants in farmers' fields (Smith et al., 1998). One way to assess the credibility of these estimates is through comparison with heritabilities obtained for the same traits using typical estimation methods. While heritability estimates are specific to the genetic and environmental populations on which they are calculated (Falconer & Mackay, 1996; Nyquist, 1991), average estimates by species

Table 5. Classification of maize trait heritabilities in the literature and H estimates from Oaxaca study using classes defined by Hallauer & Miranda

Trait (n populations in Oaxaca study)	Class of trait average h^2 in Hallauer & Miranda[a]	Oaxaca on farm (biased H)[b]			Bolaños & Edmeades[d] (unbiased H)			Fountain & Hallauer[e] (h^2 plot mean)		
		Trait mean H	Trait mean H rank	Class of trait H[c]	Trait mean H	Trait mean H rank	Class of trait H[c]	Trait mean H	Trait mean H rank	Class of trait H[c]
Ear height (11)	HI	0.74	1	VH	0.70	3	HI	0.62	1	HI
1° tassel branch number (8)	nc	0.71	2	VH	0.79	2	VH	–	–	–
Stalk diameter (11)	nc	0.67	3	HI	–	–	–	–	–	–
Plant height (8)	HI	0.65	5.5	HI	0.80	1	VH	0.56	3	HI
Days to anthesis (6)	HI	0.65	5.5	HI				0.68	2	HI
Ear leaf width (9)	nc	0.65	5.5	HI	–	–	–	–	–	–
Ear leaf length (9)	nc	0.65	5.5	HI	–	–	–	–	–	–
Ear length (10)	M	0.63	8	HI	–	–	–	0.24	4	M
100 kernel weight (8)	nc	0.61	9	HI	–	–	–	–	–	–
Ear diameter (9)	M	0.55	10	HI	–	–	–	0.40	5	M
ASI[f] (4)	nc	0.48	11	M	0.60	4	HI	–	–	–
Grain yield (12)	L	0.47	12	M	0.59	5	HI	0.24	6	L

[a] Mean of components of variation from experiments conducted using mating designs I, II, and III and 'a few' F_2 populations (Hallauer & Miranda 1988: 116). See below.
[b] Biased H, assuming biparental control (Smith et al., 1998).
[c] Classes established by Hallauer & Miranda 1988: 118. VH = very high = $h^2 > 0.70$, HI = high = $0.50 < h^2 < 0.70$, M = medium = $0.30 < h^2 < 0.50$, L = low = $h^2 < 0.30$, nc = not classified, – = trait not reported.
[d] Mean for S1–3 progenies of six tropical maize populations grown under no-, intermediate-, and severe-water stress (Bolaños & Edmeades, 1996).
[e] Mean for three broad-based synthetic populations (Fountain & Hallauer, 1996).
[f] ASI = anthesis-silking interval.

and trait are used as general references by breeders and were used as an initial comparison in this study.

Given the different types of estimates and the effects of specific populations and environments, a comparison of relative heritability rankings has greater utility than one of absolute values. In recognition of this, several authors suggest a species-specific ranking of traits into classes of low, medium, high and very high heritability (class names assigned by us) (Hallauer & Miranda, 1988; Jensen, 1988; Nyquist, 1991). For maize, Hallauer & Miranda (1988: 118) have grouped h^2 estimates calculated on a plot means basis as follows: $h^2 > 0.70$ very high (VH), $0.50 < h^2 < 0.70$ high (HI), $0.30 < h^2 < 0.50$ medium (M), $h^2 < 0.30$ low (L). Using those same class values here, H estimates produced by this and other studies are in general agreement with the classes suggested by Hallauer & Miranda (Table 5), as is their relative rank within each data set.

The h^2 estimates produced by the half sib analysis of five of these populations in experimental plots were also intended to help evaluate the credibility of

the on-farm H estimates. Because of severe conditions during the 1997 season and subsequent losses (39% of plants lost) from those experimental plots, the results are based on fewer individual plants than originally intended. Still, the points to note regarding these data (Table 6) are: first, there is an expected pattern of H estimates being greater than h^2 estimates for the same trait, with the exception of ear height. This exception may be the result of large V_E in some on-farm environments. But it is more likely due to two of the population h^2 estimates for this trait being > 1.00 because of the small size of certain covariates (e.g., location) in the analysis, and thus ultimately attributable to experimental error in that data set. Second, the difference between the class assignments of H and h^2 estimates is greater for post harvest traits than plant morphology traits, typically a two class difference for the former as compared with one class for the latter, with the same exception as noted above. Third, the rank correlation coefficient between populations for the two estimation methods for these traits was insignificant. This may indicate the contribution of

Table 6. Average on-farm H estimates and h^2 estimates calculated from half sib family analysis of the same maize populations and trait rankings[a]

Ear height		Plant height		Stalk diameter		Ear diameter		Ear length		Ear weight	
H	h^2	H	h^2	H	h^2	H	h^2	H	h^2	H	h^2
0.70 ± 0.07 (4)	0.83 ± 0.09 (1)	0.65 ± 0.09 (6)	0.51 ± 0.07 (3)	0.73 ± 0.03 (3)	0.60 ± 0.12 (2)	0.80 ± 0.08 (1)	0.36 ± 0.13 (5)	0.73 ± 0.09 (2)	0.41 ± 0.07 (4)	0.68 ± 0.08 (5)	0.19 ± 0.02 (6)

Trait average H and h^2 ± SE
(rank among all traits for that method of estimation)

Class of heritability estimate according to Hallauer & Miranda (1988)[b]

HI	VH	HI	HI	VH	HI	VH	M	VH	M	HI	L

[a] h^2 estimates included only for analyses with family components of variation having z-scores with $P = 0.05$. For these calculations populations with h^2 estimates ≤ 1.00 reported as 1.00 (n = 3).
[b] Classes established by Hallauer & Miranda (1988): 118. VH = very high = h$^2 > 0.70$, HI = high = $0.50 < h^2 < 0.70$, M = medium = $0.30 < h^2 < 0.50$, L = low = h$^2 < 0.30$.

$V_{G \times E}$ to V_G in H as estimated on farm, producing crossovers in trait ranks that are not present when $V_{G \times E}$ is accounted for in a replicated, multi-location experimental design. However, the role of $V_{G \times E}$ deserves consideration as well because of the contrast between soil types, fertility and water availability between experimental plots and farmers' typical rain-fed fields, despite their proximity. Finding the balance between investment in experimental work and accurately depicting the target environment is a challenge researchers are increasingly aware of (e.g., see Ceccarelli, 1989; Rattunde & Witcombe, 1993). It seems that the compromises made in finding that balance can be consequential, and in this case suggest ecological specificity may be a greater concern than geographic proximity. Finally, comparison of these data through rank correlations requires the use of absolute values for both H and h^2, excluding the use of classes that are more appropriate for the H estimates generated on-farm. As a result, small differences in heritability values creates differences in rank that would not occur in class based comparisons.

When Smith et al. (1998) tested the method for rapid estimation of H with an herbaceous short-lived perennial, all estimates fell within the 90% confidence interval for ANOVA-based H estimates. The data presented here do not offer such a clear test of the methodology, and were not intended to do so. Aside from the h^2 estimates from our experimental plots, when the on-farm H estimates are ordered by rank, there is agreement with many of the rankings resulting from other methods of estimation. It is not possible to determine if the exceptions to this represent actual differences due to materials and locations or errors due to methodology. Our experience and results from other studies suggests to us that discrepancies between on-farm H and h^2 estimates from the progeny analysis are likely due to inaccuracies in the latter not the former. While the on-farm estimates may lack the precision expected from more conventional methods, it may be that implementing conventional studies even in experimental plots in the CPB context runs the greater risk of inaccuracy. These data suggest the on-farm method can provide useful insights regarding broad classes of H on-farm but not absolute H values – accuracy but imprecision (see Sokal & Rohlf, 1995: 13), and should therefore be used with a clear recognition of its limitations (Smith et al., 1998). The best use of the estimates is as a rapid orientation to approximate, relative classes of H, recalling that precise values for class delineation are arbitrary.

Application to developing selection strategies

The utility of heritability estimates depends on how they were generated and how they will be used. There are four issues of particular relevance to both the estimation methodology and the application context reported here; genotype × environment variance, selection unit, broad v. narrow sense heritabilities, and the cost and state of knowledge regarding heritability estimates.

Genotype × environment variance
Inclusion of $V_{G \times E}$ in the numerator of heritability calculations, in single location estimates such as the on-farm ones reported here, tends to bias the estimate

upward (Nyquist, 1991: 286). The extent to which this bias is either real or prohibitive depends on the population of environments addressed, existing knowledge, resources for improving estimates through field trials and research and selection designs. If applying mass selection on-farm, then the population of spatial environments will be those in which the genetic population is being grown and selected, and where the estimates are made. As such, the presence of genotype × location variation will not affect estimate utility. However genotype × year variation will introduce bias, as in more conventional evaluations that do not include multi-year trials.

Selection unit

Estimating response to mass selection in which the individual is the selection unit requires heritabilities calculated on an individual basis (Falconer & Mackay, 1996; Nyquist, 1991: 312). Total phenotypic variance can be reduced in calculations based on family means through experimental design (Nyquist, 1991: 257), accordingly increasing h^2 estimates. This is not possible with calculations of V_P on an individual basis unless investigating a single genotype (F_1, clone, inbred line) . For this reason, heritabilities calculated on an individual basis will be lower than heritabilities calculated on a family basis, and response to selection will reflect this. The on-farm methodology used here produces H estimates that assume a) all pollen sources are included within the matrix, and b) individual selection with biparental control. If neither assumption is met these estimates may inflate expected gain from selection up to a maximum of 50% over what could be achieved with mass selection without pre-flowering selection and roguing in open-pollinated populations (Simmonds, 1979: 139).

Broad v. narrow sense heritabilities

Although h^2 estimates are of greatest value for predicting response to selection in cross-pollinating species, in the absence of anything else H estimates are useful because they represent the upper limit possible for h^2 (Nyquist, 1991: 285). For yield, Hallauer & Miranda (1988: 117) estimate an average of 61.2 and 38.8% of V_G can be attributed to V_A and V_D (variance due to dominance interactions), respectively, assuming no variance due to epistasis or linkage. They conclude that although the relative contribution of V_A may vary, overall the largest proportion of V_G can be attributed to V_A for most traits, four times more on average than V_D. On the other hand, theory suggests that

fitness-related traits and/or those subjected to strong selection over time (e.g., days to anthesis in the Oaxaca maize populations), the proportion of V_A may be substantially reduced (Silvertown & Doust, 1993: 21).

For the reasons outlined above we anticipated the on-farm H estimates to be approximately 20% larger than comparable h^2 estimates from the half sib analyses (and perhaps more than this for traits like days to anthesis), as was borne out by our findings for plant height and stalk diameter (Table 6). For post harvest traits, H estimates were from 45–72% larger than corresponding h^2 estimates suggesting a large contribution by $V_{G \times E}$ to these trait phenotypes, and/or variation introduced by exposure to more environmental factors for traits documented later in the season.

Cost and state of knowledge

Typically, heritability estimates in plants are obtained through the evaluation in field trials of progenies or clones of known genetic relationship from populations of interest (Nyquist, 1991). In addition to consideration of relevance to selection units, often the time and expense involved in producing such estimates cannot be justified. In CPB there may be many crop populations and subenvironments targeted in a region, making estimation of heritabilities for each population via conventional methods prohibitive. Still, it would be useful to have some empirical evidence on which to develop CPB strategies for crop improvement, especially if those strategies make demands on farming households' limited resources.

As an example, Table 7 compares the cost of the two methods used in this study; H estimation on-farm and h^2 estimation via analysis of half sib families, each for a single population. These are conservative estimates using only one location for the experimental trial and do not include non labor costs such as land, water, machinery, and other inputs necessary for researcher-run field trials. In addition to the rapidity and relative economy of the on-farm method, it also has the advantage of evaluating the crop population in farmers' selection environment and management conditions. The idea is not to shift costs of research onto farmers (see Smale et al., 1998), these are working fields, sown regardless of research agendas. Application of this method has a minimal impact on fields, although even this should be compensated for as it was in this study.

Table 7. Comparison of approximate cost in labor and time for on-farm H estimates and h^2 estimates from a half sib trial, both for one maize population only[a]

Task	On-farm H estimation[b] (workers × # days)	Half sib trial[c] (workers × # days)
Planting	0	6 PDs[d] (6 × 1 day)
Field maintenance (preparation, cultivation, weeding, irrigation)	0	15 PDs (1 × 15 days)
Data collection on 3 traits	4 PDs (4 × 1 day)	16 PDs (4 × 4 days)
Data entry	0.5 PDs (1 × 0.5 days)	2 PDs (1 × 2 days)
Data analysis	0.5 PDs (1 × 0.5 days)	0.5 PDs (1 × 0.5 days)
Approximate cost in PDs	5 PDs	39.5 PDs
Approximate time elapsed from first investment until analysis complete	2 days	∼ 70 days for post anthesis plant morphological traits

[a] Based on time and labor use in Oaxaca study.
[b] Assuming one matrix of 500 plants.
[c] Assuming one location, 1 population, 100 families/population, 10 plants/family, 2 replications.
[d] PD = person day of labor.

Conclusion

Much of the research and breeding activities undertaken for CPB have been based on theory and the available empirical evidence developed under conditions quite different than those present in farmers' fields or have made limited use of theory (e.g., Rice et al., 1998; Smale et al., 1998). Breeders' contributions to collaboration will be more effective if they have sufficient information on which to apply the insights of genetics and statistical analysis. Given the environmental, genetic and sociocultural variability present in many low resource agricultural systems, the application of deductive reasoning and generalization are a necessity. Still, the differences between some CPB situations and ones typical of more conventional breeding contexts suggest local empirical evidence and the possibility for inductive reasoning would be valuable. Yet the cost of such local evaluations may be high in situations with great spatial and temporal diversity, posing a dilemma. The H estimations reported here, and other descriptive statistics generated simultaneously, can provide locally specific, useful information that, while limited, still exceeds that available otherwise.

Locally specific information is useful for identifying distinctions, and determining when generalization is appropriate. Here, estimates of H and population means and CVs between communities were, for the most part, similar and appear adequately represented by their combined summary data. Cross-pollination and extensive seed flow networks could contribute to similarities among genetic populations in this area (Smale et al., 1998). We hypothesize that the similarity in H values despite the different growing environments suggests that intrafield and inter year V_E may contribute to V_E within communities being as great as that between. Despite the apparent similarities of maize populations from the two communities based on these data, the contrasting phenotypic correlations for a few important traits (Table 3) as well as the different selection goals of farming households in each (e.g., for cycle duration, see Soleri & Cleveland, 2001; Soleri et al., 2000), imply that evidence of ecological and social specificity should be sought before changing local selection strategies (Simmonds, 1979).

As a method based on single site and season data, the results of the on-farm H estimations must be used with caution. This approach will provide initial heritability information relevant to the genetic populations and their response to the repeatable elements in the population of environments in which they are grown, but not the nonrepeatable elements of those same environments (e.g., precipitation). The difference between the narrow-sense heritabilities estimated in this research and the lack of response to selection for some of those same traits observed elsewhere (Soleri et al., 2000) likely reflects the effect of a large component of V_E in farmers' crop populations grown on-farm, resulting in very low heritabilities for many traits. Therefore, relatively large on-farm H estimates may also be deceptive in that they were estimated in a small and relatively homogeneous area of each field,
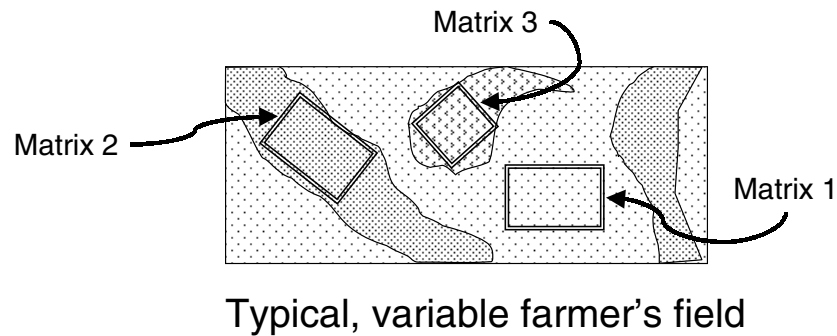
Figure 2. Recommendations for placement of matrices for on-farm, rapid estimation of broad sense heritability in a single year and location.

and thus may more accurately represent the level of H possible with field stratification (Gardner, 1961). Even within such small areas V_E can vary as was borne out for ear height H estimates (0.64, 0.71) from two matrices approximately 40 meters apart within one field in the same season. Averaging H estimates made on several within field matrices, placed to account for gross intrafield V_E (Figure 2) may provide a more accurate H value for that population-environment combination and will be explored in the future.

As one of the most studied crop species in the world, heritability averages for many maize traits are available (e.g., Hallauer & Miranda, 1988). However this is not the case for many other crop species important to low resource farmers. Even for well-studied species, H estimates are rarely available for farmers' growing conditions or genetic populations. In these cases, with adjustments made for predominantly autogamous or clonally propagated species, on-farm estimates of H can be a valuable – and often the only – initial descriptor of the population available.

Regarding development of new methodologies for assessing population genetic parameters in situ of non domesticated plant species Ritland (1989: 198) commented that 'the loss of rigor from abandoning artificial experiments is offset by the gain in realism.' Whether the loss is indeed 'offset' will depend on how the findings are used. Applied carefully, the H estimates discussed in this study are a useful improvement over a complete lack of information, especially when they can be obtained at such a low cost in time and resources. Although less precise, in the CPB context the on-farm method is more economical and may be more accurate than more conventional methods, while also providing other useful information. The possibility of merging the focus of both farmers' and plant breeders' knowledge on the same local plant breeding context and material would seem a useful step toward realizing the potential of CPB.

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