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Estimation of Genetic Variance in Corn from F₁ Performance with and without Pedigree Relationships among Inbred Lines

C. M. Bromley,* L. D. Van Vleck, B. E. Johnson, and O. S. Smith

ABSTRACT

Estimates of genetic variance are needed for ranking of inbred lines for selection and for prediction of response to selection. The objectives of this study were to determine whether including relationships among inbred lines affects estimates of genetic variance and whether random association among inbred lines mated together affects estimates. Genetic variance was estimated with different models with restricted maximum likelihood for eight traits from matings of inbred lines from two heterotic groups (Iowa Stiff Stalk Synthetic, SSS, and unrelated to SSS, NSSS) of corn (*Zea mays* L.). For each comparison relationships among one or both of the inbred lines were either considered or ignored. With relationships ignored, variance due to inbred line effects was reduced on average by 33% for SSS inbred lines and 18% for NSSS inbred lines. Estimates were also reduced for variance of SSS inbred lines by 11 to 41% when calculations were done with effects of NSSS inbred lines considered to be fixed and 6 to 31% for variance of NSSS inbred lines with SSS inbred lines considered fixed. The increase in variance with relationships among inbred lines considered indicates that potential gain from selection would be greater than predicted from estimates of variance due to line effects calculated ignoring relationships among lines. Estimates of inbred line variance within a heterotic group were usually smaller when lines in the other group were considered fixed. This result suggests that variance due to line effects can be inflated due to association of inbred lines between heterotic groups.

SETS OF CROSSES AMONG INBRED LINES (e.g., Comstock and Robinson, 1948) are often used in corn to estimate components of genetic variance. Although with the original factorial mating design of Comstock and Robinson (1948) the parent inbred lines were assumed to be random, in applied corn breeding available inbred lines are selected and usually related within heterotic group. Thus, analyses should consider relationships among inbred lines (e.g., Bernardo, 1994). Animal geneticists regularly use genetic relationship matrices when estimating genetic components of variance. Hudson and Van Vleck (1982) and Dong and Van Vleck (1989) noted that ignoring existing relationships usually resulted in a reduction in estimates of genetic variance. The first objective of this study was to determine if estimates of genetic variances were the same when relationships among inbred lines were included or ignored.

Henderson (1973) suggested that associations between one random factor and another random factor

can inflate variances of random factors such as genetic variances. Meyer (1982) and Van Vleck (1985) used models for estimating genetic variances that considered effects of previously selected older sires that have large numbers of progeny to be fixed effects and effects of young sires with only progeny for an initial progeny proof to be random effects. National dairy and beef cattle (*Bos indicus* and *Bos taurus*) genetic evaluations routinely consider herd-year-season (contemporary) effects to be fixed effects rather than random effects to account for any association of contemporary effects with effects of sires. The second objective of this study was to determine whether random association of inbred lines in crosses between inbred lines of different heterotic groups affects estimates of genetic variance. Therefore, two additional sets of analyses were done, one set with the effects of inbred lines from one heterotic group modeled as fixed effects and the second set with the effects of inbred lines from the other heterotic group modeled as fixed effects.

MATERIALS AND METHODS

Traits

Phenotypic measurements were recorded for eight traits (Table 1) from progeny obtained by crossing seven different sets of four inbred lines per set from SSS at random with seven sets of four NSSS inbred lines, resulting in 16 single crosses per set. The NSSS inbred lines are a mixture of different base populations. The sets were grown across twenty locations and 2 yr (1991, 1992), although no traits were measured for all plots (Table 1).

Brittle snap was not originally intended to be measured in this study but interest in this trait developed at one location. Two additional locations were grown with the intent to measure artificial brittle breakage. Natural storm pressure occurred before scheduled artificial breakage, causing expression in both plantings and resulting in the information analyzed. Measurements from these locations were analyzed separately for brittle breakage and excluded in analyses of the other traits. Observations were percentages of plants snapped at or below the ear node.

Plant and ear heights were averages of five plants per plot measured to the nearest 15.5-cm increments from the soil surface to tip of tassel or ear node, respectively. Root and stalk lodging were measured as the percentages of unlodged plants in a plot. Days to pollen shed were recorded as growing degree units (gdu) from planting until 50% of the plants were shedding. Yield was recorded as pounds of grain and converted to metric tons per hectare at 155 g H₂O kg⁻¹. Seedling vigor was subjectively scored from one (low) to nine (high). Number of plots, overall means, and standard deviations are reported in Table 1.

Abbreviations: gdu, growing degree units; MTDFREML, multiple trait derivative free restricted maximum likelihood; NSSS, unrelated to SSS; SSS, Iowa Stiff Stalk Synthetic.

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Table 1. Number of observations (plots) per trait and overall means and standard deviation

Trait	No. of plots	No. of environments	Mean	Standard deviation
Seedling vigor (score)	1532	7	8.61	1.69
Brittle snap (%)	663	3	71.97	22.84
Plant height (cm)	2635	12	288.06	31.80
Ear height (cm)	2413	11	121.59	18.95
Yield (t ha ⁻¹)	3692	17	10.54	2.32
Days to pollen shed (gdu)	1540	7	141.15	5.38
Plants not root lodged (%)	1090	5	86.61	17.73
Stalks not lodged (%)	2135	10	93.35	11.44

Statistical Analyses

Analyses for each trait were based on the model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad [1]$$

where \mathbf{y} is the vector of observations for that trait; $\boldsymbol{\beta}$ is the vector of fixed effects associated with records in \mathbf{y} by design matrix, \mathbf{X} (fixed effects were year by location combination, and with some models, effects of parental inbred lines of one or the other heterotic group were designated as fixed); \mathbf{u} is the vector of random effects associated with records in \mathbf{y} by design matrix, \mathbf{Z} (random effects were effects of parental inbred lines not specified as fixed), with $\mathbf{u} = (\mathbf{u}_{\text{SSS}}' \mathbf{u}_{\text{NSSS}})'$ when effects of inbred lines in both parental groups were considered random; and \mathbf{e} is the vector of random residual effects.

The first and second moments are

$$\mathbf{E}(\mathbf{y}) = \mathbf{X}\boldsymbol{\beta} \quad [2]$$

and

$$\mathbf{G} = \mathbf{V} \begin{bmatrix} \mathbf{u}_{\text{SSS}} \\ \mathbf{u}_{\text{NSSS}} \end{bmatrix} = \begin{pmatrix} \mathbf{A}_{\text{SSS}}\sigma_{\text{SSS}}^2/4 & 0 \\ 0 & \mathbf{A}_{\text{NSSS}}\sigma_{\text{NSSS}}^2/4 \end{pmatrix} \quad [3]$$

and

$$\mathbf{R} = \mathbf{V}(\mathbf{e}) = \mathbf{I}_N\sigma^2 \quad [4]$$

where \mathbf{A}_{SSS} and \mathbf{A}_{NSSS} are matrices of Wright's numerator relationships among SSS and NSSS inbred lines, respectively. The variances, σ_{SSS}^2 and σ_{NSSS}^2 , are variances of additive genetic effects in the initial populations of SSS inbred lines and NSSS inbred lines, respectively; \mathbf{I}_N is an identity matrix with N the number of observations, and σ^2 is the residual variance.

In these analyses, the convention of animal breeders was followed to use the numerator relationship matrix, \mathbf{A} , as a measure of genetic likeness among inbred lines. Plant breeders (e.g., Bernardo, 1994) typically have expressed \mathbf{G} in terms of coefficients of coancestry, which are one-half the numerator relationships. The coefficients of coancestry were calculated from pedigrees. Coefficients of coancestry among SSS inbred lines varied from 0.148 to 0.574, with a mean of 0.363, and among NSSS inbred lines varied from 0.048 to 0.509, with a mean of 0.246. Coefficients of coancestry between SSS and NSSS inbred lines varied from 0.005 to 0.081, with a mean of 0.023. For the analyses, the SSS inbred lines were considered unrelated to the NSSS inbred lines. With a sire and dam model corresponding with fully inbred lines in heterotic groups SSS and NSSS, the sire and dam components of variance in the absence of maternal effects estimate one-half of additive genetic variance (Henderson, 1977).

Initially a component of variance for SSS \times NSSS interaction was included in the model, but this component was small for all traits (average of total variance was .008) and had no effect on patterns seen from these analyses and are not reported.

For the first objective, effects of inbred lines within each

heterotic group were considered random and related. This model was compared with a similar model with pedigree information excluded. For the second objective, two additional sets of analyses were done. First, calculations were done as if inbred lines in the first heterotic group (SSS) were fixed with relationships within the second heterotic group (NSSS) either considered or ignored. Second, calculations were done as if inbred lines in the second heterotic group (NSSS) were fixed with relationships within the first heterotic group (SSS) either considered or ignored. The modeling of one set of inbred line effects as fixed removes those effects from the model for the usual quadratics computed to estimate components of variance due to line effects of the other heterotic group that might inflate components of variance (e.g., Henderson, 1973, 1985). The modeling of one set of effects as fixed removes those effects from expectations of the usual quadratics computed to estimate components of variance of line effects within the other heterotic group (Van Vleck, 1985).

Estimates of variance components due to line effects were obtained with a derivative-free restricted maximum likelihood program (multiple trait derivative free restricted maximum likelihood, MTDFREML; Boldman et al., 1995). The MTDFREML package is a set of programs that use numerator relationships and a derivative-free algorithm to obtain restricted maximum likelihood estimates of variance and covariance components. These programs can be used to obtain solutions for fixed effects, breeding values and other random effects, as well as sampling variances of solutions to MME and expected values of the solutions. Fixed effects, covariates, and other random effects can be specified separately for each trait.

The matrix of numerator relationships among the SSS inbred lines and among the NSSS inbred lines was inverted with a separate program and written to files usually written by a program in the MTDFREML package that calculates elements of the inverse of the numerator relationship matrix from a list of animals with sires and dams following rules of Quaas (1976). Inbred lines in the first heterotic group were treated as first-animal genetic effects and inbred lines in the second heterotic group were treated as second-animal genetic effects (typically maternal effects in animal models). Thus, estimates of line variances for both heterotic groups were easily obtained with no reprogramming of the package.

With the derivative-free algorithm, convergence for variance and covariance component estimation occurs when the global maximum of the log likelihood function is found. The simplex (polytope) method described by Nelder and Mead (1965) is the procedure used to locate the minimum with respect to the variance components of negative two times the logarithm of the likelihood (Λ), which corresponds with the maximum of the logarithm of the likelihood. Minus twice the likelihood, $-2\Lambda = \text{constant} + \log|\mathbf{R}| + \log|\mathbf{G}| + \log|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y}$, with \mathbf{C} a full-rank portion of the coefficient matrix of the mixed model equations and $\log|\mathbf{G}| = \log|\mathbf{A}_{\text{SSS}}| + q_1 \log(\sigma_{\text{SSS}}^2) + \log|\mathbf{A}_{\text{NSSS}}| + q_2 \log(\sigma_{\text{NSSS}}^2)$, where q_1 is the order of \mathbf{A}_{SSS} (number of SSS inbred lines), q_2 is the order of \mathbf{A}_{NSSS} , σ_{SSS}^2 is the variance of effects due to SSS inbred lines, and σ_{NSSS}^2 is the variance of effects due to NSSS inbred lines, and $\mathbf{y}'\mathbf{P}\mathbf{y}$ is the generalized residual sum of squares (Harville, 1977; Smith and Graser, 1986; Meyer, 1989). For a single trait analysis, $\mathbf{y}'\mathbf{P}\mathbf{y}$ converges to $N - \text{rank}(\mathbf{X})$. The derivative-free method basically tries different \mathbf{R} and \mathbf{G} (e.g., σ^2 of $\mathbf{R} = \mathbf{I}_N\sigma^2$, σ_{SSS}^2 of \mathbf{A}_{SSS} , σ_{NSSS}^2 of \mathbf{A}_{NSSS}) until the combination that maximizes the log of the likelihood (i.e., minimizes negative two times the log of likelihood) is found for the data vector, \mathbf{y} . The simplex algorithm cannot guarantee convergence to a global maximum. The variance of the simplex, which is an intermediate convergence criterion, depends on the current simplex and

Table 2. Log likelihoods multiplied by negative two for analyses to estimate variance components due to line effects for eight traits of corn with relationships ignored or included and with effects of lines within heterotic group considered fixed or random effects.

Trait	Relationships: SSS effects†: NSSS effects‡:	Model characteristics					
		Ignored Random Random	Included Random Random	Ignored Random Fixed	Included Random Fixed	Ignored Fixed Random	Included Fixed Random
Seedling vigor (score)		627.24	621.97	662.66	661.80	673.89	671.04
Brittle snap (%)		4 327.01	4 319.60	4 149.72	4 149.84	4 164.92	4 160.75
Plant height (cm)		10 116.43	10 108.78	10 034.91	10 028.91	10 027.22	10 026.71
Ear height (cm)		8 290.68	8 278.45	8 223.20	8 215.00	8 215.69	8 211.76
Yield (t ha ⁻¹)		25 558.38	25 550.12	25 437.26	25 435.74	25 431.40	25 426.08
Days to pollen shed (gdu)§		5 200.95	5 188.91	5 124.61	5 123.01	5 126.76	5 119.24
Root lodging (%)		7 047.22	7 041.41	6 912.12	6 912.11	6 908.46	6 903.65
Stalk lodging (%)		11 008.26	11 003.38	10 934.50	10 933.96	10 936.87	10 932.85

† SSS is Iowa Stiff Stalk Synthetic.

‡ NSSS is unrelated to SSS.

§ gdu is growing degree units.

becomes small even if convergence is to a local minimum. The program is restarted with estimates at intermediate convergence as initial values until a global maximum is found (e.g., the log likelihood does not change to third decimal place after consecutive restarts).

RESULTS AND DISCUSSION

Including or Ignoring Relationships

For the comparisons with effects of inbred lines within both heterotic groups considered random, the likelihood improved ($-2\log L$ decreased) for all eight traits after pedigree relationships were included, indicating a better fit to the data (Table 2). The changes in -2Δ were generally small between including relationships and ignoring relationships.

When effects of inbred lines of the NSSS heterotic group were considered as fixed for the second set of comparisons, the likelihood improved slightly for all traits except brittle snap after pedigree information was included. Similarly, when effects of SSS inbred lines were considered as fixed, the likelihood improved for all eight traits after pedigree information was included.

Estimates of variance due to effects of inbred lines increased after pedigree information was included in all analyses, except for one pair of analyses for which the

estimates were equal (Tables 3 and 4). With both sets of inbred lines considered random (Table 3), the ratio of estimates of σ_{SSS}^2 ignoring and considering relationships ranged from 0.51 to 0.87, with an average of 0.67 (Table 3). With effects of inbred lines of the NSSS heterotic group considered fixed and SSS inbred lines as random (Table 4), the ratios of estimates of σ_{SSS}^2 ignoring and including relationships ranged from 0.59 to 0.89, with an average of 0.68.

For all traits except days to pollen shed, estimates of σ_{NSSS}^2 also increased after pedigree information was included (Table 4). With effects of inbred lines in the SSS heterotic group also considered as random, the ratios of estimates of σ_{NSSS}^2 ranged from 0.62 to 1.00, with an average of 0.82 (Table 4). When effects of inbred lines of the SSS heterotic group were considered as fixed in the second set of comparisons (Table 4), the ratio of estimates of σ_{NSSS}^2 ignoring and including relationships ranged from 0.69 to 0.94, also with an average of 0.82.

These results show that failure to consider relationships among inbred lines may result in decreased estimates of genetic variance. These decreases are substantially greater than those observed in animal studies (e.g., Dong and Van Vleck, 1989). The average relationships in this study are much larger than those in the animal studies. In addition, the sires in the study of dairy cattle

Table 3. Estimates of components of variance due to effects of lines in the Iowa Stiff Stalk Synthetic (SSS) heterotic group with relationships among lines in the heterotic group included (Models 1b and 2b) and with relationships ignored (Models 1a and 2a) and with effects of unrelated to SSS (NSSS) lines considered as random (Models 1a and 1b) or as fixed (Models 2a and 2b) effects.

Trait	Relationships: SSS effects: NSSS effects:	Model 1a	Model 1b	Ratio†	Model 2a	Model 2b	Ratio‡
		Ignored Random Random	Included Random Random		Ignored Random Fixed	Included Random Fixed	
Seedling vigor (score)		2.94	5.82	0.51	3.91	6.16	0.64
Brittle snap (%)		39.87	64.81	0.62	37.32	62.84	0.59
Plant height (cm)		21.10	24.71	0.85	14.26	18.07	0.79
Ear height (cm)		13.35	15.36	0.87	11.61	13.03	0.89
Yield (t ha ⁻¹)		0.053	0.082	0.66	0.051	0.080	0.63
Days to pollen shed (gdu)§		1.85	2.87	0.64	1.69	2.62	0.64
Root lodging (%)		19.88	33.28	0.60	17.18	28.82	0.60
Stalk lodging (%)		1.40	2.31	0.60	1.25	2.04	0.61
Average ratio				0.67			0.68

† Ratio of estimate of variance component from Model 1a to estimate of variance component from Model 1b.

‡ Ratio of estimate from Model 2a to estimate from Model 2b.

§ gdu is growing degree units.

Table 4. Estimates of components of variance due to effects of lines in the heterotic group unrelated to the Iowa Stiff Stalk Synthetic group (NSSS) with relationships among lines in the heterotic group included (Models 2a and 3b) and with relationships ignored (Models 1a and 3a) and with effects of Iowa Stiff Stalk Synthetic (SSS) lines considered as random (Models 1a and 1b) or as fixed (Models 3a and 3b) effects.

Trait	Relationships: SSS effects: NSSS effects:	Model 1a Ignored Random	Model 1b Included Random	Ratio†	Model 3a Ignored Fixed Random	Model 3b Included Fixed Random	Ratio‡
Seedling vigor (score)		7.63	8.53	0.90	7.27	9.46	0.77
Brittle snap (%)		95.77	109.74	0.87	81.45	99.98	0.81
Plant height (cm)		12.07	19.42	0.62	9.81	14.32	0.69
Ear height (cm)		8.77	11.74	0.75	8.00	10.00	0.80
Yield (t ha ⁻¹)		0.040	0.045	0.89	0.039	0.043	0.91
Days to pollen shed (gdu)§		2.10	2.10	1.00	1.88	1.99	0.94
Root lodging (%)		15.75	18.23	0.86	13.97	16.45	0.85
Stalk lodging (%)		1.65	2.03	0.81	1.43	1.74	0.82
Average ratio				0.82			0.82

† Ratio of estimate from Model 1a to estimate from Model 1b.

‡ Ratio of estimate from Model 3a to estimate from Model 3b.

§ gdu is growing degree units.

were not as inbred as the inbred lines in this study. The changes in estimates of genetic variance due to ignoring relationships will probably depend on the magnitude of the relationships. Further study would be needed to investigate cases between the extremes of unrelated inbred lines and highly related inbred lines.

Considering Lines as Fixed Effects

Estimates of σ_{SSS}^2 decreased for seven of eight traits when effects of NSSS inbred lines were considered fixed rather than random in the calculations (Table 3; Columns 1 vs. 4 with relationships among SSS inbred lines ignored and Columns 2 vs. 5 with relationships considered). Similarly, variances of effects of inbred lines in the NSSS heterotic group also decreased for all except one of eight traits when SSS inbred lines were considered fixed rather than random in the calculations with relationships ignored (Table 4; Columns 1 vs. 4) and for all eight traits with relationships considered (Table 4; Columns 2 vs. 5).

These analyses demonstrate that randomly mating inbred lines in a set does not ensure that the variances will be unaffected by the mating partner probably because of the limited number of mates in a mating set. A larger number of mates would tend to average out better and worse mates more completely. For most traits the difference was small between estimates when the effects of the other heterotic group were considered

fixed or random for the analysis. However, for plant height, the estimate of σ_{SSS}^2 was considerably larger, by 37% (24.71 vs. 18.07), and of σ_{NSSS}^2 by 36% (19.42 vs. 14.32) when both sets of line effects were considered random rather than when effects of the other heterotic group were considered fixed for the calculations.

Estimates of residual variance (Table 5) for all traits and all comparisons were nearly the same whether pedigree information was included or whether effects of inbred lines in one or the other heterotic group were considered as fixed.

CONCLUSIONS

The increase in variance due to line effects after including numerator relationships among the inbred lines indicates that potential gain from selection would be greater than predicted from estimates of variance due to line effects ignoring relationships among inbred lines. The results also suggest that associations of inbred lines from one heterotic group in a mating set may bias estimates of variance due to effects of inbred lines in the other heterotic group. Thus, estimates of gain from selection might be overestimated if such inflated variances were used to predict selection response. A larger study would be needed to answer the more important questions of whether ignoring relationships or considering effects of the mating partners to be fixed effects would

Table 5. Estimates of residual variances with relationships among lines in an heterotic group ignored or included in the analysis and with effects in the one or the other heterotic group considered as random or fixed effects.

Trait	Relationships: SSS effects: NSSS effects:	Model 1a Ignored Random	Model 1b Included Random	Model 2a Ignored Random Fixed	Model 2b Included Random Fixed	Model 3a Ignored Fixed Random	Model 3b Included Fixed Random
Seedling vigor (score)		97.01	96.94	96.98	97.00	96.96	96.98
Brittle snap (%)		205.28	205.24	205.29	205.37	205.37	205.28
Plant height (cm)		102.77	102.71	102.71	102.71	102.77	102.71
Ear height (cm)		68.13	66.26	66.26	66.26	66.26	66.26
Yield (t ha ⁻¹)		1.42	1.42	1.43	1.43	1.42	1.42
Days to pollen shed (gdu)§		9.64	9.64	9.64	9.64	9.63	9.63
Root lodging (%)		216.50	216.50	216.58	216.61	216.49	216.49
Stalk lodging (%)		61.42	61.39	61.40	61.42	61.45	61.40

† SSS is Iowa Stiff Stalk Synthetic.

‡ NSSS is unrelated to SSS.

§ gdu is growing degree units.

change the ranking of inbred lines for breeding value, especially when more inbred lines were included in the analyses.

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Plot Direction and Spacing Effects on Interplot Interference in Spring Wheat Cultivar Trials

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ABSTRACT

Interplot interference can distort treatment estimates when genotypes differ for height. Two field arrangements were examined to determine if interplot interference could be reduced. One arrangement compared north–south vs. east–west row direction at Saskatoon in 1995 and 1996. The other experiment investigated the effects of separating plots with a row of spring-planted winter wheat (*Triticum aestivum* L.) at Regina and Swift Current in 1995 and 1996. Interplot interference was evaluated with two spring wheat cultivars differing for height, Oslo (short) and Glenlea (tall). Interplot interference caused a 12% yield reduction in Oslo in the north–south rows, which was significantly greater than the 7% yield reduction in the east–west rows. The 7% yield reduction when spring-planted winter wheat separated the plots was significantly less than the 18% yield reduction when plots were adjacent. This study was conducted at fairly high latitudes and the conclusions should be restricted to higher latitudes. We conclude that spring wheat field trials with plots differing for height may have less interplot interference if rows are oriented east–west and separated with winter wheat.

CLARKE ET AL. (1998) demonstrated that interplot interference can be a source of yield distortion in field trials containing genotypes differing for height in the short growing season on the Canadian prairies. The

interrow and interplot spacing was 0.3 m and plot rows were oriented north–south. Spring-planted winter wheat has been used to separate plots and reduce interplot competition. May and Morrison (1986) concluded that as long as the separation method is not more competitive, the separation method should not alter yield selection. Barley (*Hordeum vulgare* L.) and spring wheat plots separated with spring-planted winter wheat were less competitive than when flanked by the same genotype or when a barley plot was flanked by wheat or a wheat plot flanked by barley (May and Morrison, 1986). However, increased space between plots may also increase heterogeneity within blocks (Spitters, 1979; Federer and Basford, 1991).

When row direction was indicated in studies that reported interplot interference in field trials, the row direction was generally north–south (Austin et al., 1977; Austin and Blackwell, 1980; Kempton and Lockwood, 1984; Kempton et al., 1986; Clarke et al., 1998). However, Kiesselbach (1919) and Jensen and Federer (1964) reported interplot interference in trials with east–west rows as well with north–south rows, and Fisher (1979) and Kempton et al. (1986) reported interplot interference when rows were east–west. Baker and Rosnagel (1988) reported significant interplot interference in three of four north–south tests, two with wheat and one with barley, and not in the four east–west tests. Baker and Meyer (1966) demonstrated that during the morning and late afternoon, north–south rows admitted more light than east–west rows. At Cambridge, Kempton et

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