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Genetic changes from introgression of highland Mexican germ plasm into a Corn Belt Dent population of maize

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Summary. A backcross population (NZS1) of maize (*Zea mays* L.) was produced by crossing a highland Mexican population with the elite Corn Belt Dent synthetic AS3, and then by backcrossing to AS3. S_1 lines, S_2 lines, and S_2 testcrosses with an elite tester were used to compare the means, correlations, genetic variances, and predicted gains from selection of NZS1 and AS3 for grain yield, grain moisture at harvest, root and stalk lodging in a cool, temperate environment in New Zealand. The S_1 and S_2 lines from NZS1 had lower mean grain yields, higher levels of root lodging and higher mean grain moistures than the S_1 and S_2 lines from AS3. Mean grain yields of testcrosses of NZS1 and AS3 were similar, but NZS1 testcrosses had higher levels of root lodging. Genotypic variances estimated from S_1 and S_2 lines were larger for grain yield and root lodging for NZS1, smaller for grain moisture, and similar for stalk lodging. Predicted gains from selection for grain yield using intrapopulation methods based on the additive-genetic variance were larger for NZS1, but predicted gains for testcross selection were similar for the two populations. Lines with high combining ability for grain yield and acceptable grain moisture in combination with the tester occurred in NZS1. Because of the higher additive-genetic variance and the occurrence of lines with high combining ability for grain yield, we concluded that populations including highland Mexican germ plasm should be valuable for recurrent selection programs in New Zealand and in other cool, temperate regions.

Key words: Maize – Introgression – Genetic variances – Highland Mexican germ plasm

Introduction

The incorporation of germ plasm from tropical populations of maize (*Zea mays* L.) into populations adapted to temperate regions has been suggested as a method for increasing the germ plasm base of temperate maize (Lonnquist 1974; Brown 1977). For temperate regions with warm summers, tropical races of lowland or mid-altitude origin have been emphasized (Stuber 1978; Goodman 1985), but in temperate regions with cool summers, such as New Zealand, tropical races of highland origin could be a better choice (Eagles 1986).

The value of a population for improvement by recurrent selection and as a source of inbred lines depends on the mean performance of the population and on the genetic variability in the population for traits of economic importance. Eagles and Hardacre (1989) developed a population (NZS1) by crossing a highland Mexican population with an elite synthetic of Corn Belt Dent origin (AS3) and then backcrossing to the Corn Belt Dent synthetic. In New Zealand, NZS1 produced a lower mean grain yield than AS3, but in crosses with an unrelated Corn Belt Dent population, NZS1 and AS3 had similar combining abilities for grain yield. Grain moisture levels of NZS1 and AS3 were similar, but NZS1 had a higher level of root lodging (Eagles and Hardacre 1989).

The objective of this study was to compare the genetic variability in NZS1 and AS3 for four traits of economic importance: grain yield, grain moisture at harvest, root lodging, and stalk lodging. Comparisons were made in S_1, S_2, and S_2 testcross generations. Information from this study can be used to assess the value of including highland Mexican germ plasm in foundation populations for improving maize in cool, temperate regions.

Materials and methods

The populations used in these experiments were NZS1 and AS3. NZS1 had the pedigree Criollo de Toluca × $AS3^2$, where Criollo de Toluca is a landrace population of the Conico race from the highlands of Mexico and AS3 is an elite synthetic of Corn Belt Dent origin. The version of AS3 used for these experiments was AS-3(HT)C3 (Peterson et al. 1976). Although NZS1 is strictly a

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composite (Hallauer and Miranda 1981), both NZS1 and AS3 will be referred to as synthetics.

The initial cross to develop NZS1 was made between 19 plants of Criollo de Toluca and 80 plants of AS3. Pollen bulks were collected from AS3 and applied to the silks of Criollo de Toluca over several days. The backcross was made from 95 paired crosses, with Criollo de Toluca × AS3 as the female parent and AS3 as the male parent. After backcrossing, NZS1 was random-mated for two generations. Further details of the construction were given by Eagles and Hardacre (1989).

S_1 lines

Approximately 800 plants each of NZS1 and AS3 were grown at Palmerston North during the 1983–1984 season. Self-pollinations were made in each synthetic, with 372 plants selfed in NZS1 and 277 selfed in AS3. At maturity, ears from 180 plants were selected from each synthetic. Selection was practiced for seed set, freedom from ear rots, and freedom from root and stalk lodging.

The 180 S_1 lines from each synthetic were randomly divided into three sets, each containing 60 lines. The lines were then grown in three adjacent experiments at Kairanga (near Palmerston North) in the 1984–1985 season. Each experiment contained 121 lines, one set each from NZS1 and AS3, plus one random line used to complete the lattice. The design for each experiment was an 11 × 11 simple lattice (Cochran and Cox 1957). No line was included in more than one experiment. The Kairanga location has a long, cool growing season (Eagles et al. 1989), and agronomic management was designed to produce high grain yields.

Each plot consisted of one row 3.75 m long with a row width of 0.75 m. Forty-two seeds were sown in each row. At the 4- to 5-leaf stage, each plot was thinned to 21 plants to give a population density of 71,000 plants/ha.

Root lodging was recorded immediately before harvest as the number of plants leaning more than about 15° from the vertical. Stalk lodging was recorded as the number of plants where the stalk had broken between the soil surface and the ear node. Both were expressed as the percentage of the total number of plants in each plot.

All ears were hand harvested from each plot for grain yield and grain moisture determination. The harvested ears were shelled using a Haban husker-sheller, and grain moisture at harvest was determined using an electronic moisture meter. Grain yield at 15% moisture was calculated from grain weight and grain moisture.

Selection among S_1 lines

Following usual maize breeding practice, lines with poor performance in the S_1 generation were not included in S_2 and testcross experiments (Hallauer and Miranda 1981). Lines were eliminated using a selection index of the form

$$I = GY - 0.25\,GM - RL - SL$$

where I was the selection index, GY, GM, RL, and SL were mean grain yield, grain moisture, root lodging, and stalk lodging, respectively, expressed in standard units, e.g., $GY = G/\hat{\sigma}_p$, where G was mean grain yield and $\hat{\sigma}_p$ was an estimate of the phenotypic standard deviation for mean grain yield. Estimates of the phenotypic standard deviations were obtained from analyses of variance conducted individually for the two synthetics.

The 16 lines with the highest index were selected from each synthetic in each experiment, producing 48 selected lines for NZS1 and 48 selected lines for AS3.

S_2 lines and testcrosses

S_1 lines from NZS1 and AS3 were grown in a crossing nursery in the 1984–1985 season. Up to three plants in each line were simultaneously self-pollinated and crossed to the tester A665 × CM105. A665 has the pedigree ND203 × A635^4, where A635 has the pedigree ND203 × B14^3, and CM105 has the pedigree V3 × B14^2 (Henderson 1984), so both A665 and CM105 are derivatives of B14. Checks were produced by crossing the tester with A659 and Mo17Ht. A659 is an inbred line derived from AS3, and Mo17Ht has been widely used in the USA (Henderson 1984; Darrah and Zuber 1986). The hybrid (A665 × CM105) Mo17Ht was known to produce high grain yields in New Zealand (H. A. Eagles, unpublished data).

One S_2 line and its testcross were selected from each of the 48 selected lines from NZS1 and from AS3. Selection within an S_1 line was practiced for seed set, freedom from ear rots, and freedom from root and stalk lodging. The 96 resulting S_2 lines, plus 4 lines used to complete the lattice, were grown at Kairanga during the 1985–1986 season. The experimental design was a 10 × 10 triple lattice (Cochran and Cox 1957). Plot techniques were the same as those used with the S_1 lines the previous season, and the same traits were evaluated.

Testcrosses of the selected S_2 lines were grown at Kairanga and Pukekohe in the 1985–1986 season and at Kairanga in the 1986–1987 season. The climate at Pukekohe has been described previously (Eagles et al. 1989). The experimental design was a 10 × 10 triple lattice, with the testcrosses of A659 and Mo17Ht entered twice. Plot techniques were the same as those used for the S_1 and S_2 lines, except that ears from the end plants of each plot were removed before the plots were harvested. The same traits were evaluated.

To identify superior lines for comparison with A659 and Mo17Ht, selection was practiced using data from the S_2 line and testcross experiments. Index values were calculated independently for the S_2 line and testcross experiments, using the method described for the S_1 generation. A combined index was then calculated for each S_2 line by adding the two values. Lines were selected using the combined index, but consideration was also given to seed quality and ear rot data from a crossing nursery grown at Palmerston North during the 1986–1987 season.

Statistical analyses

All experiments were analyzed using methods appropriate for both lattice and randomized complete block designs (Cochran and Cox 1957). There were no gains in efficiency from the lattice designs, so results are presented for analyses from randomized complete block designs.

For S_1 lines, S_2 lines, and testcrosses, variance components and their standard errors were calculated by methods described by Hallauer and Miranda (1981). Analyses of variance were conducted separately for NZS1 and AS3. For S_1 lines, differences among experiments were small, so sums of squares were pooled across experiments.

To compare NZS1 and AS3 for predicted effects of selection for individual traits, predicted gains from selection were calculated for grain yield, grain moisture, and root and stalk lodging for both synthetics in the S_1, S_2, and testcross generations. Predicted gains from selection were calculated from $k\hat{\sigma}_g^2(\hat{\sigma}_p)^{-1}$, where k is the theoretical standardized selection differential, $\hat{\sigma}_g^2$ is an estimate of the genotypic variance and $\hat{\sigma}_p$ is an estimate of the phenotypic standard deviation (Hallauer and Miranda 1981). For predicting gains, k was set equal to 1, which is equivalent to selecting approximately 38% of the population. For S_1 or S_2 line selection, predicted gains were appropriate for improvements in population means using recombination of S_1

Table 1. Mean grain yield (Mg ha^{-1}), grain moisture (%), root lodging (%), and stalk lodging (%) for 180 S_1 lines each of NZS1 and AS3 grown in 1984–85, for 48 S_2 lines of each synthetic grown in 1985–86, and for 48 S_2 testcrosses of each synthetic grown in three environments during 1985–86 and 1986–87

Generation	Grain yield		Grain moisture		Root lodging		Stalk lodging	
	NZS1	AS3	NZS1	AS3	NZS1	AS3	NZS1	AS3
S_1	8.36	8.70**	25.1	24.2**	6.3	0.8**	25.4	21.6**
S_2	6.13	7.25**	27.9	26.3**	25.7	8.9**	4.6	2.2**
Testcross	11.39	11.45	23.9	23.4**	10.6	7.9**	3.1	2.7

** NZS1 and AS3 significantly different at the 1% level

Table 2. Estimates of genotypic variance (σ_g^2) and their standard errors for grain yield, grain moisture, root lodging, and stalk lodging for 180 S_1 lines each of NZS1 and AS3 grown in 1984–85 and for 48 S_2 lines of each synthetic grown in 1985–86

Generation	Synthetic	Grain yield	Grain moisture	Root lodging	Stalk lodging
S_1	NZS1	2.86±0.38	5.22±0.64	102.7± 13.6	256.1±38.1
	AS3	1.72±0.23	5.84±0.68	2.0± 0.7	236.7±35.7
S_2	NZS1	4.15±0.91	7.36±1.65	559.6±126.4	23.3± 6.2
	AS3	2.80±0.64	10.48±2.21	201.6± 46.8	21.1± 4.9

or S_2 lines, but recognizing that these predictions could be biased in the presence of dominance. For testcross selection, the predicted gains were appropriate for improvement of the mean combining ability with A665 × CM105 using recombination of selected S_2 lines.

Results and discussion

Means

The S_1 lines from NZS1 produced a lower mean grain yield, a higher mean grain moisture, and higher mean root and stalk lodging than the S_1 lines from AS3 (Table 1). Similar results were obtained with the S_2 generation in the following season but with a higher level of root lodging and a lower level of stalk lodging (Table 1).

Mean grain yields of the testcrosses of NZS1 and AS3 were very similar, but grain moisture and root lodging were significantly greater in NZS1 (Table 1). However, the grain moisture difference was small and of little practical significance.

The reduced grain yield of NZS1 compared to AS3 in the S_1 and S_2 generations and the almost identical grain yield in the crosses with an unrelated tester agree with previous results from the S_0 generation (Eagles and Hardacre 1989). These results are probably due to differences in the frequencies of nuclear genes. However, the cytoplasm of NZS1 is from Criollo de Toluca and cytoplasmic effects provide an alternative explanation (Eagles and Hardacre 1989).

The increased root lodging of NZS1 also agrees with previous results and supports the conclusion that root lodging could be a major limitation to the use of NZS1 as a source of commercially acceptable inbred lines (Eagles and Hardacre 1989).

Variances and correlations

For grain yield in the S_1 and S_2 generations, estimates of genotypic variances were greater for NZS1 than for AS3 (Table 2). The increased genotypic variance in the population including tropical germ plasm agrees with previous results from the Corn Belt of the USA (Goodman 1965; Albrecht and Dudley 1987). Crossa and Gardner (1987) obtained a similar result for a population containing 50% exotic germ plasm, but not for a population containing 25% exotic germ plasm; however, the exotic germ plasm used in their study included a Chinese variety which could have been of temperate origin.

For grain yield in testcrosses, estimates of genotypic variances were almost identical for AS3 and NZS1, but the estimate of the genotype × environment interaction variance was larger for NZS1 (Table 3). The larger genotype × environment interaction variance for NZS1 could be due to the high level of root lodging for this synthetic (Table 1), combined with differences in root lodging in the three environments where the testcrosses were grown (5.8%, 20.9%, and 0.5% root lodging).

The correlation between S_2 and testcross line means for grain yield was lower for NZS1 compared to AS3 (Table 4). This reduced correlation was not due solely to increased standard deviations in the denominator of the correlation coefficient, but also to a reduction in the

Table 3. Estimates of genotypic variance (σ_g^2) and genotype × environment interaction variance (σ_{ge}^2) and their standard errors for grain yield, grain moisture, root lodging, and stalk lodging for 48 S_2 testcrosses each of NZS1 and AS3 grown in three environments

Variance	Synthetic	Grain yield	Grain moisture	Root lodging	Stalk lodging
σ_g^2	NZS1	0.23 ± 0.08	1.54 ± 0.36	52.2 ± 18.6	4.3 ± 2.2
	AS3	0.22 ± 0.08	2.15 ± 0.47	14.7 ± 8.4	2.7 ± 1.8
σ_{ge}^2	NZS1	0.24 ± 0.08	0.19 ± 0.09	79.0 ± 15.9	5.4 ± 2.7
	AS3	0.14 ± 0.08	0.19 ± 0.08	43.8 ± 10.4	6.7 ± 2.5

Table 4. Correlations between S_2 line per se and testcross performance for 48 lines each of NZS1 and AS3 for four characters

Synthetic	Grain yield	Grain moisture	Root lodging	Stalk lodging
NZS1	0.23	0.49**	0.64**	0.48**
AS3	0.39**	0.63**	0.55**	0.24

** Significantly different from zero at the 1% level

estimate of the covariance between S_2 line and testcross means from 0.42 for AS3 to 0.31 for NZS1.

AS3 was made from eight selected inbred lines and it underwent three cycles of recurrent selection for high grain yield (Peterson et al. 1976) before it was used to develop NZS1. Therefore, frequencies of favorable alleles in AS3 were expected to be high. The introgression of unfavorable alleles into such a population will reduce the frequency of favorable alleles to intermediate levels, concurrently increasing genotypic variances and reducing means (Falconer 1960). This was the result observed for comparisons between AS3 and NZS1 in the S_1 and S_2 generations and, for variances, the differences should be independent of cytoplasmic effects. This suggests that the majority of alleles introgressed from Criollo de Toluca into AS3 to develop NZS1 were unfavorable for high grain yields, but it does not preclude the possibility that some favorable alleles were introduced.

The genetical interpretation of differences between AS3 and NZS1 for genotypic variances among testcrosses is complicated by differences between the synthetics for genotype × environment interaction variances. However, similar testcross means and variances for AS3 and NZS1 suggest that unfavorable alleles from Criollo de Toluca were masked by favorable dominant alleles in the tester. This type of masking effect also provides an explanation for the difference between the synthetics for the correlation between S_2 line and testcross means (Smith 1986).

For grain moisture, estimates of genotypic variances were smaller for NZS1 than for AS3 in all generations (Tables 2 and 3). This result was unexpected because Criollo de Toluca is later maturing than AS3 (H. A. Eagles, unpublished data), and Albrecht and Dudley (1987) obtained increased genotypic variances for this trait for populations containing tropical germ plasm.

For root lodging, estimates of genotypic variances were much larger for NZS1 than for AS3 (Tables 2 and 3). The correlation between S_2 and testcross generations was high for root lodging for both NZS1 and AS3 (Table 4). The testcrosses and S_2 lines were grown in different experiments, and only one of the three evaluation environments used for the testcrosses was the same as the one used for the S_2 lines. Therefore, these correlations were largely genotypic, and their high values indicate that root lodging is highly heritable in the New Zealand environment, and that effective selection for hybrid performance can be made among partially inbred lines. A high heritability for root lodging agrees with experiences in the Corn Belt of the USA (Kevern and Hallauer 1983). However, the causes of root lodging could be different because rootworms (*Diabrotica* species), a major cause of root lodging in the Corn Belt, do not occur in New Zealand. Root lodging in New Zealand is caused primarily by fungi, especially *Rhizoctonia solani* (Fowler 1985).

For stalk lodging, genotypic variances were similar for NZS1 and AS3 (Tables 2 and 3), suggesting that both synthetics should respond similarly to selection. However, the correlation between S_2 and testcross performance was higher for NZS1 (Table 4), suggesting that selection among partially inbred lines for hybrid performance would be more effective for NZS1.

Correlations between traits were not high in NZS1 and AS3 (Table 5) and should not greatly impede the simultaneous improvement of grain yield, grain moisture, root lodging, and stalk lodging.

Selected line performance

The value of a population in regions dominated by hybrid cultivars depends on the ability of the population to produce inbred lines with superior combining ability for traits of economic importance. One method of evaluating a population for this purpose is to compare the testcross performance of selected lines from the population with the hybrid performance of established inbred lines

Table 5. Phenotypic correlations between characters for the S_1, S_2, and testcross generations of NZS1 and AS3

Characters	S_1 lines		S_2 lines		Testcrosses	
	NZS1	AS3	NZS1	AS3	NZS1	AS3
Yield, moisture	0.10	0.01	−0.29*	−0.14	−0.01	0.22
Yield, root lodging	0.04	0.24**	−0.25	−0.11	0.14	−0.14
Yield, stalk lodging	0.26**	0.04	−0.02	0.16	−0.07	−0.19
Moisture, root lodging	0.10	0.12	0.24	0.13	0.18	−0.13
Moisture, stalk lodging	−0.08	0.04	0.09	−0.17	0.07	−0.08
Root lodging, stalk lodging	−0.26**	0.02	−0.34*	−0.14	0.13	0.15

*,** Significantly different from zero at the 5% and 1% levels, respectively

Table 6. Mean grain yields (Mg ha^{-1}), grain moistures (%), root lodging (%), and stalk lodging (%) for testcrosses of five selected S_2 lines from both NZS1 and AS3 and for two inbred lines crossed to the same tester[a]

Line	Grain yield	Grain moisture	Root lodging	Stalk lodging
NZS1-70	11.9	21.0	10.2	1.6
NZS1-71	11.7	23.7	2.7	1.6
NZS1-101	12.6	24.4	9.0	1.6
NZS1-123	12.4	23.5	10.6	2.6
NZS1-141	13.0	24.2	3.7	0.5
AS3-45	11.7	23.0	0.4	1.6
AS3-79	12.3	23.1	8.5	0.0
AS3-86	12.2	26.2	1.6	1.1
AS3-94	12.1	24.6	5.8	0.5
AS3-108	12.2	23.2	1.1	0.0
A659	11.0	21.8	9.8	0.8
Mo17Ht	12.0	25.5	1.1	0.5
LSD ($p=0.05$)[b]	1.1	1.2	15.1	6.5
LSD ($p=0.05$)[c]	1.0	1.0	13.1	5.6

[a] Tester was A665 × CM105

[b] For comparisons excluding A659 and Mo17Ht; calculated using lines × environments interaction mean square for error

[c] For comparisons including A659 and Mo17Ht; calculated using lines × environments interaction mean square for error

crossed to the same tester. The testcrosses of five lines selected from NZS1 and five selected from AS3 were compared to hybrids of A659 and Mo17Ht (Table 6). The lines were selected using data on grain yield, grain moisture, root and stalk lodging from both the S_2 line and testcross experiments.

One line, NZS1-141, produced a testcross with a significantly higher grain yield and a significantly lower grain moisture than the hybrid of Mo17Ht. Other lines produced testcrosses with similar grain yields and significantly lower grain moistures (Table 6). As an S_2 line, NZS1-141 produced a higher grain yield than any S_2 line from AS3 (data not presented). One line from AS3 produced a testcross with a mean grain yield equal to that of NZS1-141, but that line was not selected because of excessive root lodging (data not presented).

The identification of NZS1-141 supports the opinion of Eagles et al. (1989) that populations containing highland Mexican germ plasm can produce inbred lines with high combining ability for grain yield and acceptable combining ability for grain moisture in cool, temperate areas, such as New Zealand.

Predicted gains from selection

Using either S_1 or S_2 line selection, predicted gains for selection for increased grain yield or reduced root lodging were much higher for NZS1 than for AS3 (Table 7). For grain moisture, predicted gains were similar for NZS1 and AS3 using S_1 selection, but slightly higher for AS3 using S_2 line selection. Predicted gains for selection for reduced stalk lodging were similar for NZS1 and AS3 using all methods.

Genotypic variances estimated from S_1 and S_2 generations, and used to calculate predicted gains, were inflated by genotype × environment interaction variances (Hallauer and Miranda 1981). Therefore, predicted gains from S_1 or S_2 line selection were inflated by an unknown amount. For grain yield, the covariances between S_1 and S_2 line means for grain yield were 1.33 for NZS1 and 0.63 for AS3. These covariances are predominantly a function of the additive-genetic variance, although they include terms with dominance effects (Cockerham 1983). Because the S_1 and S_2 generations were grown in different seasons, the covariances are largely unbiased by genotype × environment interaction. However, these covariances are biased by selection in the S_1 generation (Falconer 1960). Because the actual standardized selection differentials used for selection in the S_1 generation were similar and of low magnitude (0.54 for NZS1 and 0.50 for AS3), the size of the bias should be similar for NZS1 and AS3. Using these covariances as estimates of the additive-genetic variance, predicted gains can be calculated (Hallauer and Miranda 1981; Cockerham 1983). These predicted gains were 0.71 and 0.91 Mg ha^{-1} for the S_1

Table 7. Predicted gains from selection per unit selection intensity ($k = 1$) for grain yield (Mg ha^{-1}), grain moisture (%), root lodging (%), and stalk lodging (%) for S_1, S_2 and S_2 testcross generations of NZS1 and AS3

Generation	Grain yield		Grain moisture		Root lodging		Stalk lodging	
	NZS1	AS3	NZS1	AS3	NZS1	AS3	NZS1	AS3
S_1	1.52	1.17	2.1	2.3	9.1	0.9	13.7	13.1
S_2	1.96	1.57	2.6	3.2	22.4	13.3	4.2	4.3
Testcross	0.37	0.35	1.2	1.4	5.6	2.4	1.4	0.9

and S_2 generations of NZS1, respectively, and 0.43 and 0.55 Mg ha^{-1} for the S_1 and S_2 generations of AS3, respectively. Due to selection between the S_1 and S_2 generations, predicted gains calculated using covariances probably underestimated the true values. Nevertheless, the two methods of estimating predicted gain concur with the fact that gains from intrapopulation selection methods based on additive-genetic variances should be substantially greater for NZS1 than for AS3.

The predicted gains from selection for reduced root and stalk lodging were undoubtedly biased because of the skewed distributions associated with these traits (data not presented). Nevertheless, the genotypic variances and correlations between S_2 and testcross performance were large enough to indicate that rapid progress should be possible by selecting for reduced levels of both types of lodging, especially in NZS1.

For grain yield, predicted gains using S_1 or S_2 line selection were much higher than predicted gains using testcross selection (Table 7). Predicted gains using S_1 or S_2 line selection are appropriate for estimating improvements in mean performance of the synthetics per se, while predicted gains using testcross selection are appropriate for estimating improved combining ability with the tester (A665 × CM105). The tester used in these experiments is a cross between elite, related lines that probably contain a high frequency of favorable dominant alleles. Improvements in combining ability, and correlated improvements in mean performance of populations, could be slow with such a tester (Hallauer and Miranda 1981; Smith 1986), therefore, for improving mean grain yield of NZS1 and AS3 per se, S_1 or S_2 line selection should produce more rapid progress. However, the ultimate use of lines from these synthetics is to produce hybrids in combination with elite inbred lines, so combining ability with such lines must be considered.

Selection against poorly adapted genotypes in early cycles of selection of NZS1 will probably reduce genotypic variances and reduce long-term responses to selection for grain yield (Moll and Smith 1981). Therefore, the value of NZS1 as a foundation population for recurrent selection could be overestimated. Nevertheless, the much greater genotypic variances in NZS1 and the occurrence of lines with high combining ability for grain yield and acceptable grain moisture in combination with an elite tester suggest that populations including highland Mexican germ plasm should be valuable for commencing recurrent selection programs in New Zealand and other cool, temperate regions.

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