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Full Length Research Paper

S_1 selection of local maize landraces for low soil nitrogen tolerance in Zambia

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Low soil nitrogen (N) limits maize production in Zambia. S_1 selection was used to select for tolerance to low N among ninety-six maize landraces during 2004 - 2007 in Zambia. The landraces were evaluated under low N, drought and optimal conditions; and selfed in a nursery, under optimal conditions. Data on grain yield (GY), number of ears per plant, leaf senescence and anthesis-silking interval were used to calculate selection indices. Fourteen S_1 lines, from each of the best four landraces under each environment and across all environments were evaluated under the three environments, and at the same time crossed to a tester. Twenty-two best S_1 lines under each environment and across were identified and also their testcrosses were evaluation under the three environments. Significant GCA effects for GY under low soil N were found; suggesting that population improvement under soil N stress was effective. Heritability for GY under low soil N conditions was low (0.38) implying that selection based on GY was ineffective. The r_G for GY under low soil N and optimal environments was moderate (0.458), suggesting that selection for GY in one environment was not as effective as in the other. Low soil N tolerant landraces were identified and should be used to breed for the low soil N conditions.

Key words: Maize, landrace, heritability, correlation, nitrogen, tolerance, stress.

INTRODUCTION

Although maize is the most important and widely grown food crop in Zambia, its grain yield (GY) is low under small-scale farmers condition. Average GY per district ranges between 0.58t ha^{-1} to 3.1t ha^{-1} among the small-scale farmers, who account for over 90% of the farming community in Zambia (CSO, 2006). According to Waddington and Heisey (1997), nitrogen (N) is the most severe and wide spread constraint to maize production as most farmers lack cash or credit to access fertilisers.

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Abbreviation: AD, Anthesis date; **ASI,** anthesis-silking interval; **EPP**, number of ears per plant; **GCA,** general combining ability effects; **GE**, genotype × environment interaction effects; **Gtext,** grain texture; **GY,** grain yield; **H^2,** broad sense heritability estimate; **LNTI,** low N tolerant index; **LR,** landrace; **Lroll,** leaf rolling; **Lsene,** leaf senescence; **r_G,** genetic correlation; **S_1,** line selfed first generation line; **SD,** silking date; **SI,** selection index; **TC,** testcross.

Removal of subsidies on fertilisers by the Zambian government further reduced the use of fertiliser in the country and the fertilizer: maize price ratio (number of kg maize required to purchase one kg fertiliser) increased from 0.9 in 1986 to 2.7 in 1993 (Mungoma and Mwambula, 1997) and to 2.6 in 2007. Nitrogen deficiency in maize production is also reported as a wide spread problem among small-scale farmers in the whole of southern Africa and elsewhere in tropical areas (Waddington and Heisey, 1997; Logrono and Lothrop, 1997; Loomis, 1997). Yield loss due to soil N deficiency is a generally wide spread problem in the tropics (Mduruma and Ngowi, 1997; Betran et al., 2003).

Nitrogen is an important element to maize production as it promotes vegetative growth, maximizes both kernel initiation and kernel set, it is also key in filling the kernel sink (Below, 1997). Nitrogen deficiency interferes with protein synthesis, induces leaf senescence and therefore, reduces the general growth of the maize plant (Bruns and Abel, 2003) thereby limiting yield. In Asia, N deficiency causes yield losses of 10 - 50% (Logrono and Lothrop, 1997). Santos et al. (1997) observed yield losses of 65.8% when an open pollinated variety that was developed under soils of high fertility was grown under low N conditions. Increased varietal tolerance to low soil N stress offers an effective partial solution to enhance maize production and food security among the resource poor small-scale farmers. Under this strategy, plants are able to tolerate deficiency of N by partitioning more N and carbohydrates to the ear. An appropriate breeding strategy can be used to develop genotypes that tolerate the stress and produce high grain yield under both low soil N and optimal conditions. Few scientists have recently explored this area because it has often been assumed that there is no interaction for GY between N levels and cultivars.

Lafitte et al. (1997) evaluated landraces (LRs) and improved varieties under low N and optimal conditions and found that LRs were superior in grain N concentration but not in GY at both soil N levels. This implied that LRs were slow in use N for developing grain irrespective of amount of available N. However, LRs appear to have traits with higher adaptive value in acquisition of much N even in soils that have low N. Probably this is so because they have been traditionally managed under soils of low fertility over generations. In developing varieties for low N environments, superior genotypes should be selected from germplasm well-adapted to such stress environments. Genetic variance for GY under low N environments is low (Banziger et al., 1997; Betran et al., 2003) and identification of genotypes which tolerate the stress on the basis of GY alone may not be effective. Local unimproved varieties (landraces) should be the preferred germplasm, because they may be able to contribute useful traits with adaptive value for stable GY production under low N conditions (Lafitte et al., 1997), provided other deleterious traits they carry do not affect their performance in other environments.

Selecting under high inputs increases genetic variance relative to environmental variance and thus increases heritability. This increases the chances of selecting superior genotypes and making breeding progress. It is, however, less effective if the variety is targeted for a low input environment such as that under low N conditions because genetic correlation for GY between the two environments may be low (Banziger et al., 1997). Use of selection environment that differs considerably from the target environment (Indirect selection) is usually not as effective as direct selection in the target environment (Falconer, 1981). To develop an appropriate breeding strategy in selecting genotypes that tolerate low N conditions, information on gene action is important. Below et al. (1997) reported that additive gene action in Corn Belt germplasm was important; while Betran et al. (2003) reported that non-additive gene action in tropical maize was important. However, these studies have collectively shown that many N use traits were under genetic control and that physiological processes limiting yield differed according to the level of N. Further research in this area is needed to improve strategies in breeding for low N tolerance.

General combining ability (GCA) is the mean performance of a line in all its crosses, expressed as a deviation from the mean of all crosses (Hallauer and Miranda, 1988). Information of GCA effects may be used to estimate gene action of traits. In statistical terms, GCA effects are main effects and indicate primarily additive gene action (Falconer, 1981). Effects of GCA can also be used to select superior genotypes under low N conditions. High GCA effects under low N reflect the presence of the desired low N tolerant alleles being sought. Vasal et al. (1992) crossed 88 inbred lines to four testers and used GCA and specific combining ability (SCA) effects to identify and form heterotic groups of maize with subtropical adaptation. Betran et al. (2003) reported low GCA effects for GY under low N conditions and that there was crossover type of interaction of GCA effects under low and optimal conditions. In this study GCA effects were used to identify populations where gains in tolerance to low N conditions were effective and appropriate for low N conditions.

Information on heritability of traits and their correlation with GY is important in predicting breeding progress for the low N environment. Banziger et al. (2000) found that information on GY, number of ears per plant (EPP), anthesis-silking interval (ASI) and leaf senescence (Lsene) were important in selecting superior genotypes under low N conditions. Therefore, these traits were measured in this study. Lafitte and Banziger (1997) found that selection under drought also improved tolerance to low N conditions by 3.4% per year. Tassel size (Tsize) and leaf rolling (Lroll) are often used in selecting genotypes that tolerate drought conditions (Edmeades et al. (1999). In maintaining there LRs farmer in Zambia used grain texture (Gtext) to select seed normally cultivated under low soil fertility. This study was carried out to determine: a) tolerance to low N conditions; b) genotype x environment interaction effects; c) heritability of GY and other traits and; d) correlations among traits in landraces of maize grown under low N conditions. The hypothesis tested in the study was that there is adequate genetic variation among maize LRs for low N tolerance that can be improved by selection.

MATERIALS AND METHODS

Germplasm

The germplasm for the research study was obtained from CIMMYT (Zimbabwe). These included 96 LRs originally collected from Zambia, four open pollinated varieties (OPVs) released in Zambia as checks (c) and a single cross hybrid (CML312/CML395) as a tester, whose parents are superior for tolerance to drought and low N stress. Check varieties used during 2005/06 and 2006/07 season were obtained from Seed Control and Certification Institute of Zambia (SCCI).

Table 1. Features of the experimental sites and the amount of rainfall received (mm) at the trial sites during the study period.

Trial site	Location of trial site			Amount of water during seasons (mm)		
	Latitude (South)	Longitude (East)	Altitude (m)	2004/05	2005/06	2006/07
Rain fed						
Chilanga	15.55˚	26.26˚	1227	640.8	910.5	568.0
Golden Valley	14.97˚	28.10˚	1148	825.5	905.1	1167.1
Kabwe	14.44˚	28.45˚	1172	730.1	871.3	1067.0
Nanga	15.86˚	27.76˚	1044	583.7	790.8	663.9
Irrigated				**Amount of irrigation water (mm)**		
Nanga	15.86˚	27.76˚	1044	640.0	640.0	-
Lusitu	16.13˚	28.83˚	480	-	-	640.0
Luangwa	15.10˚	30.18˚	373	-	-	640.0

Generation of Selfed first generation lines (S_1 lines)

During the first season (2004/05), all the 96 LRs and check OPVs were planted in a nursery at Chilanga under optimal (112kg N ha^{-1}, 44kg P ha^{-1} and 30kg K ha^{-1}) conditions. The entries were randomized without replication. The plot size per entry was two rows 5 m long, 0.75 m between rows and two plants per hill, spaced 0.5 m within the row (22 plants per row; total 44 plants per entry). At least 14 plants were selfed per entry. The nursery was maintained clean of weeds by hand weeding. Planting, self pollination and harvesting were done by hand. Each ear of the harvested S_1 line was stored separately. Fourteen S_1 lines (with at least 200 kernels per ear) for each of the 16 superior landraces were drawn at random.

Generation of testcrosses (TCs)

During the 2005/06 season, all the 224 S_1 lines were crossed to a single cross hybrid tester (CML312/CML395) in a nursery which was planted at Nanga under optimal conditions. The tester has alleles for tolerance to low N (also drought) and has been used in many hybrids in the SADC region. An isolation block was established which was more than 400 m from the nearest maize crop. Plot size was 2 rows, 5 m long, 0.75 m between rows and two plants per hill spaced 0.5 m within the row. The nursery was maintained clean of weeds by hand weeding. Two rows of a tester were planted after every 6 rows of the entries in one planting as anthesis of the S_1 lines fell within the range of days the tester will shed pollen The S_1 lines were de-tasseled before shedding pollen. Planting, de-tasseling and harvesting were done by hand. Seed harvested for each testcross (TC) was bulked into one family.

Experimental environments

The study was conducted under optimal, low N and drought conditions. The experimental environments are described below:

Environment 1: Optimal conditions

A basal dressing fertiliser of 20 kg N ha^{-1}, 44 kg P ha^{-1} and 30 kg K ha^{-1} was applied at planting, and a top dressing fertiliser of 92 kg N ha^{-1} was applied 30d later. Trials and nurseries depended on summer rainfall for water (Table 1). The trials were conducted at Chilanga during 2004/05 to 2006/07 seasons and at Golden Valley during 2006/07 season. The nurseries were conducted at Chilanga during 2004/05 and Nanga during 2005/06 seasons.

Long term annual rainfall at Chilanga, Golden Valley, Nanga and Kabwe is estimated as 800 - 1000mm (Bunyolo et al., 1997); while at Lusitu and Luangwa, the estimate is 600 - 800mm. Initial soil fertility at each trial (Table 2), during the evaluation of testcrosses (2006/07 season), was determined by Zambia Agriculture Research Institute (ZARI) based on Woode (1988).

Environment 2: Low N conditions

The trial was located at Golden Valley during 2004/05, 2005/06 and 2006/07 seasons and at Kabwe during 2006/07. The respective blocks had been depleted of N by continuously growing maize at high density (extract crop) for several previous seasons and removing the biomass after each crop. Nitrogen was not applied to the trials. However, the recommended 44 and 30kg K ha^{-1} were applied at planting. The trial depended on summer rainfall for water (Table 1). Initial soil fertility at each trial was determined prior to planting (Table 2).

Environment 3: Drought conditions

The trial was located at Nanga during 2004/05 and 2005/06 seasons and was conducted at Lusitu and Luangwa during 2006/07. Full fertilisation was applied as basal dressing at the rate 20, 44 and 30kg K ha^{-1} at planting. Top dressing fertiliser of 92 kg N ha^{-1} was applied 30 days after planting. The experiment was conducted during the dry season (May - October) to control water supply. It depended on irrigation water and an estimated 640 mm of water was applied per season. Irrigation was withdrawn for 35 days about 60 days after planting (about a week before anthesis of the earliest entry) and when soil moisture content was below 50% of the field capacity. Time to withdraw irrigation depended on the amount of heat units the genotypes required to flower during the earlier optimal trial in summer. Soil moisture level (volume of water per volume of soil) at the trial sites was monitored by measurements every 10 days (at 300 mm, 600 mm and 900 mm depth) by the Soil Physics Laboratory at Zari. Soil moisture content was measured using the oven method. Two irrigations were applied after the moisture withdrawal period. Water was applied to trials using the sprinkler irrigation during the first and second seasons while furrow

Table 2. Results of soil analysis at trial sites.

Trial site	Soil depth (mm)	Trial	Hand text	pH ($CaCl_2$)	Org (C %)	N (%)	P (ppm)	K (me %)
	200	Optimal	SCL	5.7	2.13	0.15	8	0.97
	400	Optimal	SCL	5.1	1.94	0.14	5	0.94
Chilanga	200	Optimal	SCL	6.9	2.13	0.15	18	0.77
	400	Optimal	SCL	6.4	0.33	0.02	3	0.61
G. Valley	200	Low N	SCL	5.7	1.20	0.09	36	3.40
	400	Low N	SCL	5.6	0.42	0.03	6	3.38
Kabwe	200	Low N	SL	5.3	1.19	0.09	38	0.33
	400	Low N	SL	5.1	1.17	0.08	28	0.31
Lusitu	200	Drought	SL	7.6	0.64	0.04	86	1.00
	400	Drought	SL	7.5	0.11	0.01	69	0.51
Luangwa	200	Drought	SCL	7.6	0.44	0.03	96	0.97
	400	Drought	SCL	7.7	0.37	0.02	84	0.77

Key for soil texture: S = Sand, LS=loamy sand, SL= sandy loam, SC= sandy clay, SCL= sandy clay loam. Key for soil pH_2: < 4.0 = extremely acid, 5.0-4.0 = strongly acid, 5.0 - 7.0 medium acid, 7.0=neutral, >7.0 alkaline.

irrigation was used during the third season.

Experimental design and management

The performance of the 96 LRs and four check varieties was conducted as a 10 x 10 simple lattice design with two replications under optimal, low N and drought conditions at Chilanga, Golden Valley and Nanga, respectively during the 2004/05 season. The plot size was one row, 5 m long, 0.75 m between rows, and two plants per hill spaced 0.5 m within the row (22 plants per row; total 22 plants per entry). There were two border rows at either end of a trial. The established plant density was 53,333 plant per ha. The trials were maintained clean of weeds by hand weeding. Planting and harvesting were done by hand. Two border rows and plants at two hills at either end of the plot were excluded from the harvest (whole plot).

Anthesis day (AD) and silking day (SD) were obtained as number of days after planting until 50% of plants were shedding pollen and silking, respectively. The ASI was calculated as SD - AD. Leaf rolling (Lroll) was measured by scoring on a scale from zero (unrolled, turgid leaves; desirable) to one (severely rolled leaves; undesirable) while Lsene was measured during grain filling by estimating the fraction of area which had turned brown (dead leaf). Tassel size (Tsize) was determined as the number of primary branches of the tassel per plant. At harvest, the number of ears with at least one fully developed grain expressed as a fraction of number of plants at harvest was used to determine EPP. Grain yield was measured as weight of shelled grains (t ha^{-1}) adjusted to 12.5% grain moisture. Grain texture was measured on a scale 0 to 1, where; kernel of deep depression (fully dent) = 0, medium depression = 0.25, mild depression = 0.5, roughly smooth = 0.75, smooth (fully flint) = 1.0. Data were analyzed within each environment using GenStat (Payne et al., 2007) and genotypic means were computed. Under each trial a selection index (SI) was calculated for respective traits in order to combine information on secondary traits with that of GY. Calculation of the selection index was as described by Banziger et al. (2000). Information on GY, EPP, ASI and Lsene was used in calculating selection indices and trait weights used were 5, 2, -1 and -2. The preferred trend was increasing GY and EPP and that of reducing ASI and Lsene.

The best four LRs (4% selection intensity) under optimal, low N, drought and across the three environments were identified using the index. Fourteen S_1 lines from each of the 16 identified LR were randomly selected (a total of 224 S_1 lines). The performance of the S_1 lines per se was evaluated and at the same time, these were crossed to the tester and testcrosses evaluated for performance in the 2005/06 season.

Evaluation of S_1 lines for performance per se

All the 224 S_1 lines and one check (ZM521) were planted in performance trials under optimal, low N and drought conditions at Chilanga, Golden Valley and Nanga, respectively, during the 2005/06 season. Each trial was laid out as a 15 x 15 lattice design with two replications under each environment. The plot size was one row, 5 m long, 0.75 m between rows, and two plants per hill spaced 0.5 m within the row. The established plant density was 53,333 plant per ha. The trials were maintained clean of weeds by hand weeding. Recording of main characteristics and analysis of S_1 lines data was the same as in performance trial described earlier. Planting and harvesting were done by hand. Plants from two border rows and those at two hills at either end of the plot were excluded from the harvested whole plot.

Evaluation of testcrosses

The best 22 S_1 lines under optimal, low N, drought and across the environments (88 in total, 10% selection intensity) were identified and their respective TCs selected for evaluation during the 2006/07 season. The 88 TCs and 12 checks were evaluated for their performance under low N and optimal conditions at Golden Valley (GV) and Kabwe. Above normal rainfall was received at GV and plants were sometimes under waterlogged conditions (Table 1). In order to obtain adequate seed for evaluation, all the bulked seeds of each of the selected TC were mixed and a sample drawn at random. The trials were laid out as a 10 x 10 lattice design with two replications. The checks included seven popular OPVs, four popular hybrids and a LR. The plot size was one row, 5 m long, 0.75 m between rows, and two plants per hill spaced 0.5 m within the row (). The established plant density was 53,333 plant per ha. The trials were maintained clean of weeds by hand weeding. Recording of main characteristics was as in the performance trial described earlier. Planting and harvesting was carried out by hand.

Analysis of testcross data

Data was analyzed using GenStat (Payne et al., 2007). A selection index (SI) for each entry per trial was determined as above. Phenotypic correlations among various traits were also calculated. Relative grain yield of a genotype was calculated by expressing its GY as percentage of the mean grain yield of the trial. Grain yield greater than GY of the tester, expressed heterosis of a genotype. Low N tolerance index (LNTI) was defined as GY reduction due to low N stress in comparison to that under optimal conditions at the same site, and was calculated as:

$(1 - (GY_{LN}/GY_{OP}) \times 100\%$

Where: GY_{LN} = grain yield under low N environment and GY_{OP} = grain yield under optimal environment.

Analysis of variance for GY was performed for each trial and main effects of the factors and their interaction effects, were analyzed in terms of their importance in influencing GY. Varieties with significant GE interaction effects were assessed for crossover type of interaction effects using ranks of genotypes at Golden Valley (GV) and Kabwe. A genotype that changed its ranking reflected a crossover type of GE interaction effect. Estimates of genotypic variance (V_G) and error variances (V_E) were calculated from the expected mean squares of the analysis of variance (Falconer and Mackay, 1996). Broad sense heritabilities (H^2) for traits were calculated as: $H^2 = V_G / (V_G + V_E/r)$ where r = number of replicates. Genetic correlations (r_G) were calculated as follows: $r_G = Cov_G / sqrt[V_G(High N)*V_G(Low N)]$, where Cov_G = genetic covariance, sqrt = square root of, as in Bolanos and Edmeades (1996). General combining ability (GCA) effects for each trait and genotype were calculated as a deviation from the grand mean (Hallauer and Miranda, 1988).

RESULTS

Performance of landraces under low N and optimal conditions

Analysis of variance showed that differences in the performance of LRs were significant ($p \leq 0.05$) for GY under low N. Grain yield ranged from 1.36 (LR67) to 6.57t ha^{-1} (LR35) under optimal conditions and ranged from 0 (LR34) to 2.67t ha^{-1} (LR79) under low N conditions. The best check under both conditions was ZM421 which ranked 2nd under optimal (6.48t ha^{-1}) and 8th under low N conditions (1.56t ha^{-1}). Under low N, GY of the best check was significantly different ($p \leq 0.05$) from that of the best genotype (LR79). The four highest yielding LRs under low N conditions were LR49, LR4, LR79 and LR93 in that order. The 10 lowest yielding genotypes under low N conditions were all LRs with LR34 collected from Masaiti failing to achieve any GY. Each genotype under optimal conditions at GV achieved GY above the trial mean of the low N trial also at GV. Of the top 10 genotypes, based on selection index, only one was a check (ZM421) and it ranked 8th. Landraces LR49, LR4, LR79 and LR93 were ranked 1st, 2nd, 3rd and 4th respectively, in tolerance to low N, maintaining their ranking in GY. Among the top 10 most tolerant genotypes, LR49, LR79, LR93 and LR11 were selected as they had many S_1 lines and adequate amount of seed per S_1. All the 10 least yielding genotypes were LRs with the lowest being LR11 (Sesheke) that failed to achieve any yield.

Performance *per se* of S_1 Lines under low N and optimal conditions

It was found that S_1 lines were significantly different ($p \leq 0.05$) for GY under low N. Grain yield ranged from 0.16 (S_1 line 59, progeny of LR21) to 11.14t ha^{-1} (S_1 line 14, progeny of LR38) under optimal conditions, while it ranged from 0 (S_1 line 167, progeny of LR5) to 2.46t ha^{-1} (check, ZM521) under low N conditions (Table 3). The 10 highest yielding S_1 lines were progenies of LR40 (S_1 line 193), LR38 (S_1 line 11), LR26 (S_1 line 28), LR21 (S_1 line 68), LR38 (S_1 line 13), LR93 (S_1 line 109), LR84 (S_1 line 127), LR26 (S_1 line 25), LR84 (S_1 line 135), and LR86 (S_1 line 35) in that order. Based on the selection index, S_1 line 80 (progeny of LR11) was the most tolerant to low N. This was followed by S_1 line 11 (progeny of LR38), ZM521 and S_1 line 13 (progeny of LR38) in that order.

Despite LR49 being found the most tolerant genotype to low N in the first season (2004/05), none of its S_1 lines were among the top 25 (11%) under low N conditions. In fact, the highest yielding S_1 line of the LR ranked 51st out of the 225 genotypes evaluated. However, LR11 (ranked 10th in tolerance to low N) had its S_1 lines ranked first and 11th in tolerance to low N. The other two selected LRs in season 1 only contributed one S_1 line each ranked 12th and 16th for LR93 and LR79, respectively. Other LRs which were not found superior under low N conditions (but found best under drought, optimal or across the three environments) contributed S_1 lines among the top 25 genotypes tolerant to low N. Therefore, of the 56 S_1 lines (4 landraces × 14 S_1 lines) whose parents were superior under low N

Table 3. Top and bottom S_1 lines under low N (based on SI) and optimal conditions (based on GY alone).

Performance under low N					Performance under optimal		
S_1 line	LR	GY (t ha^{-1})	Rank GY	Rank SI	S_1 line	LR	GY (t ha^{-1})
Top 10							
80	LR11	1.95	12	1	14	LR38	11.14
11	LR38	2.29	3	2	32	LR86	8.13
ZM521-c	ZM521	2.46	1	3	183	LR40	8.12
13	LR38	2.24	6	4	53	LR76	8.08
68	LR21	2.26	5	5	29	LR86	7.87
38	LR86	1.87	14	6	193	LR40	7.86
193	LR40	2.39	2	7	136	LR84	7.80
25	LR26	2.09	9	8	5	LR38	7.36
28	LR26	2.28	4	9	174	LR35	7.24
165	LR5	1.62	27	10	45	LR76	6.82
Mean		2.14					8.04
Bottom 10							
196	LR40	0.14	208	216	117	LR74	1.08
214	LR49	0.51	167	217	84	LR11	1.03
223	LR49	0.24	201	218	203	LR79	1.01
116	LR74	0.23	204	219	213	LR49	0.91
224	LR49	0.02	219	220	97	LR12	0.79
97	LR12	0.10	212	221	138	LR84	0.68
91	LR12	0.07	217	222	214	LR49	0.68
180	LR35	0.10	211	223	25	LR26	0.52
222	LR49	0.00	221	224	43	LR76	0.19
87	LR12	0.11	210	225	59	LR21	0.16
Mean		0.15					0.70
Trial statistics							
Max		2.46					11.14
Min		0.00					0.16
Mean		0.90					3.69
SE		± 0.47					± 1.86
LSD		0.93					3.67
P value		0.00					0.001

conditions only about 7% were tolerant to low N.

Performance of TCs under low N and optimal environments

Grain yield of testcrosses

The best 22 S_1 lines (10%) were selected and their respective TCs evaluated for tolerance to low N stress. In order to determine homogeneity of variances between the trial at Golden Valley and that at Kabwe, respective mean square error (MSE) at the sites was used. The ratio of MSE_{large} to MSE_{small} between the two sites was 13 hence the results for each trial site are reported separately (Table 4). According to Mead et al. (2003) when the ratio of MSE_{large} to MSE_{small} was above 4 (or 6 if number of sites is large), combined analysis was not effective because of non-homogeneity of variances. Genotypes were found significantly different under low N (GV and Kabwe) and optimal (GV) conditions.

These results show that genotypes achieved higher GY under low N at Golden Valley than at Kabwe. Grain yields at Golden Valley ranged from 0.22 to 2.24 t ha^{-1}, while at Kabwe GY ranged from 0.09 to 0.98 t ha^{-1}. However, the best yielder at Golden Valley (TC56 progeny of LR84 with 2.24t ha^{-1}) only produced 0.48t ha^{-1} at Kabwe. The highest yielding line at Kabwe did not make it into the top

Table 4. Top and bottom testcrosses (TCs) and checks under low N based on average rank of grain yield when grown at Golden Valley and Kabwe, under optimal and low N conditions.

TC	LR	GY - Low N			GY – optimal (GV)	Rel. GY reduction (%)	% grain yield above	
		GV	Kabwe	Average Rank			Best check	Tester
Top 10								
TC77	LR40	2.01	0.73	6.00	1.85	-9.00	16.00	112.00
TC72	LR35	2.22	0.61	10.00	1.89	-18.00	19.00	119.00
TC28	LR76	1.75	0.84	11.50	2.20	21.00	9.00	100.00
TC53	LR84	1.78	0.65	14.50	1.88	5.00	18.00	116.00
TC49	LR84	1.58	0.92	15.50	2.22	29.00	11.00	103.00
TC35	LR12	1.56	0.73	18.00	2.13	27.00	2.00	87.00
TC32	LR11	1.97	0.55	19.50	1.96	-1.00	12.00	105.00
TC54	LR84	1.88	0.58	20.00	1.28	-48.00	6.00	95.00
TC70	LR35	1.68	0.61	20.00	1.69	1.00	1.00	85.00
TC27	LR76	1.42	0.81	22.50	1.67	15.00	1.00	85.00
Mean		1.78	0.70		1.88			
Bottom 10								
82 (c)	MMV600	1.09	0.27	80.50	1.60	32.00	-30.00	28.00
TC2	LR38	0.52	0.45	81.00	2.12	76.00	-50.00	-20.00
TC65	LR85	0.96	0.35	82.50	1.84	48.00	-30.00	26.00
TC51	LR84	1.14	0.09	83.50	2.09	45.00	-50.00	-1.00
TC21	LR86	0.54	0.41	83.50	1.67	68.00	-50.00	-10.00
TC12	LR86	1.13	0.11	84.00	2.10	46.00	-30.00	35.00
TC86	LR79	0.88	0.34	86.00	2.39	63.00	-40.00	15.00
TC64	LR85	0.61	0.37	86.50	1.74	65.00	-50.00	-10.00
TC26	LR76	0.73	0.32	88.50	1.26	43.00	-50.00	-10.00
100(c)	MMV400	0.57	0.26	93.50	1.40	59.00	-60.00	-20.00
Mean		0.82	0.30		1.82			
Statistics								
Max		2.24	0.98	93.50	2.69	88.00	20.00	120.00
Min		0.22	0.09	6.00	0.53	-254.00	-60.00	-25.00
Mean		1.34	0.48	50.50	1.91	26.00	-20.00	51.00
SE		±0.55	±0.14		±0.39			
LSD		1.10	0.28		0.78			
P value		0.00	0.00		0.03			

10 either. Across sites performance of the genotypes was based on the average rank of GY between the sites (calculated as arithmetic mean of ranks of a genotype in GY under low N at GV and Kabwe). Testcross TC77 (progeny of LR40) with 2.01t ha^{-1} at GV and 0.73t ha^{-1} at Kabwe was the highest yielding genotype over locations.

The lowest yielding genotype was a check MMV400 that achieved 0.57 and 0.26t ha^{-1} at GV and Kabwe, respectively. All the top 10 genotypes for GY were TCs and the best check was a LR which ranked 20th. The 10 highest yielding genotypes were also superior to both the best check and the tester which ranked 82nd.

In comparing GY of genotypes under the low N and optimal trials both at Golden Valley, it was found that the mean trial yield (environmental index) was higher under optimal conditions (1.91t ha^{-1}) than under low N conditions (1.34t ha^{-1}). However, some genotypes yielded more under low N than under the optimal environment. Testcrosses TC56 and TC72 yielded more under low N than optimal environment, by 18.3% and 17.7%, respectively. The Low N tolerant index (LNTI), also called relative yield reduction ranged from -254 to 88% with an average of 26%. Testcross TC56 and TC72 were ranked 5th and 6th respectively, in LNTI (Table 5). The best genotype in LNTI was TC16 (progeny of LR86) which yielded 254% more under low N (1.87t ha^{-1}) than under optimal conditions (0.53t ha^{-1}). Among the top 10 genotypes in GY (based on average ranks), four had negative

Table 5. Ranking of testcrosses under low N based on average rank.

TC	Grain yield -low N			LNTI	Selection index		Rank of average GY rank
	Landrace	GV	Kabwe		GV	Kabwe	
Top 10							
TC77	LR40	6	6	8	28	5	1
TC72	LR35	2	18	6	4	21	2
TC28	LR76	20	3	41	9	3	3
TC53	LR84	17	12	20	10	25	4
TC49	LR84	29	2	50	14	2	5
TC35	LR12	31	5	49	42	12	6
TC32	LR11	8	31	14	2	33	7
TC54	LR84	14	26	2	15	46	8
TC70	LR35	23	17	17	40	26	9
TC27	LR76	41	4	31	27	4	10
Bottom 10							
82 (c)	MMV600	72	89	54	72	99	91
TC2	LR38	98	64	98	96	65	92
TC65	LR85	83	82	76	82	74	93
TC21	LR86	97	70	95	88	71	94
TC51	LR84	67	100	69	48	97	95
TC12	LR86	69	99	70	66	98	96
TC86	LR79	89	83	93	91	83	97
TC64	LR85	94	79	94	94	75	98
TC26	LR76	92	85	65	93	77	99
100 (c)	MMV400	96	91	91	98	94	100

LNTI while the bottom 10 had yield reductions of between 32 and 76% (Table 4).

Genotypes were ranked in decreasing order in GY under low N (at GV and Kabwe) and under optimal conditions (GV). The best genotype ranked 1 while the worst was ranked 100. Similarly, the genotypes were ranked in decreasing order in LNTI between the low N trial at GV and the optimal trial at the same site. The rank were then correlated (r). Rank of GY under low N conditions was significantly correlated (r = 0.904*) with LNTI rank, but was negatively correlated (r = -0.441*) with rank under optimal conditions. Similarly, significant rank correlation was also found between average rank and rank in GY at Golden Valley (r = 0.732*) and Kabwe (r = 0.735*).

Tolerance of testcrosses to low N

Based on selection indices, TC56 (progeny of LR84) was the most tolerant to low N stress at GV and TC19 (progeny of LR86) at Kabwe (Table 6). The five most tolerant genotypes under low N conditions at GV were progenies of LR84, LR11, LR93, LR35 and LR38 while at Kabwe they were LR86, LR84, LR76 (contributed two TCs) and LR40. The checks generally yielded low at both GV and Kabwe. The highest ranking of GY for the checks was MM603 (ranked 7th) at GV, while at Kabwe, none of the checks was among the top 10 in tolerance to low soil N. Among the 10 least tolerant genotypes for Low N stress based on the SI were two checks (Pop25 and MMV400) at GV and three checks (MMV400, MMV400 and Pool16) at Kabwe.

When genotypes were ranked based on average GY under low N between GV and Kabwe; it was found that the best five testcrosses were progenies of LR40, LR35, LR76 and LR84 (contributed two TCs). These LRs were among the 10 LRs that contributed TCs which were most tolerant to low N stress based on selection indices at both GV and Kabwe. None of the checks was among the top 10 genotypes based on average GY but two of them (MMV600 and MMV400) were among the 10 least tolerant genotypes based on the average rank of GY. The most tolerant genotypes to low N stress based on LNTI were progenies of LR86 (two TCs) and LR84 (two Tcs). The best check (Pool16) ranked 4th and was the only check among the top 10 in LNTI. However MMV400 and Pop25 were among the poorest for LNTI. The highest yielding genotype under low N conditions based on average rank was TC77 (progeny of LR40), which ranked 5th at Kabwe and 28th at GV in tolerance to low N stress based on SI and 8th in LNTI. The most low N tolerant genotype at GV based on SI was TC 56 (progeny of

Table 6. Top and bottom 10 genotypes in selection index, average GY and LNTI under low N conditions.

Based on selection index				Based on grain yield			
Golden valley		Kabwe		Average GY rank		LNTI	
TC	LR	TC	LR	TC	LR	TC	LR
Top 10							
TC56	LR84	TC19	LR 86	TC77	LR40	TC16	LR86
TC32	LR11	TC49	LR 84	TC72	LR35	TC54	LR84
TC39	LR93	TC28	LR 76	TC28	LR76	TC10	LR86
TC72	LR35	TC27	LR 76	TC53	LR84	Pool16	Pool16
TC7	LR38	TC77	LR 40	TC49	LR84	TC56	LR84
TC85	LR79	TC17	LR 86	TC35	LR12	TC72	LR35
MM603	MM603	TC80	LR 40	TC32	LR11	TC25	LR76
TC37	LR12	TC31	LR 21	TC54	LR84	TC77	LR40
TC28	LR76	TC55	LR 84	TC70	LR35	TC83	LR40
TC53	LR84	TC52	LR 84	TC27	LR76	TC85	LR79
Bottom 10							
TC86	LR79	TC23	LR 76	MMV600	MMV600	MMV400	MMV400
Pop25	Pop25	TC62	LR 85	TC2	LR38	TC22	LR76
TC26	LR76	TC16	LR 86	TC65	LR85	TC86	LR79
TC64	LR85	MMV400	MMV400	TC21	LR86	TC64	LR85
TC15	LR21	TC57	LR 84	TC51	LR84	TC21	LR86
TC2	LR38	TC29	LR 21	TC12	LR86	TC15	LR21
TC40	LR93	TC51	LR 84	TC86	LR79	Pop25	Pop25
MMV400	MMV400	TC12	LR 86	TC64	LR85	TC2	LR38
TC92	LR49	MMV600	MMV600	TC26	LR76	TC24	LR76
TC24	LR76	Pool16	Pool16	MMV400	MMV400	TC92	LR49

LR84) which ranked 15th in average rank of GY and 5th in LNTI. The most low N tolerant genotype at Kabwe based on SI was TC19 (progeny of LR86) which ranked 25th in average rank of GY and 74th in LNTI. TC16 (progeny of 86) which was the best genotype in LNTI was 56th in average GY and 20th in SI at GV but 93rd in SI at Kabwe.

The results also show that only LR11 and LR79 which were among the top 10 genotypes in tolerance to low N during 2004/05 season contributed testcrosses (TC32 and TC85, respectively) which were among the top 10 genotypes under low N conditions based on SI. Other TCs among the top 10 were derived from S_1 lines of the best LRs under drought, optimal and across the three environments. However, all the top 10 TCs under low N conditions at Kabwe were progenies of LRs which were among the top 10 genotypes (based on SI) under drought conditions during 2004/05 season. Five of the top 10 genotypes under low N at GV were progenies of LRs which were among the top 10 genotypes under drought conditions during the 2004/05 season. LR35, LR76 and LR86 which were among the top 10 genotypes based on GY under optimal conditions (2004/05 seson) contributed TCs which were among the top 10 genotypes under low N based on SI. They included TC72 (progeny of LR35) and TC28 (progeny of LR76) at Golden Valley. Others were TC27 and TC28 (both progenies of LR76), and TC17 and TC19 (both progenies of LR86). The best check in tolerance to low N stress was MM603 which ranked 7th while ZM421 (21st) was the second best check at GV. ZM421 was best check under low N at Kabwe but ranked 29th based on SI. Based on rank of selection indices, the top 10 genotypes in tolerance to low N stress were selected equally from Golden valley and Kabwe (Table 6). The best genotype under optimal conditions across sites was the tester which achieved 2.46t ha^{-1} at GV and 5.44t ha^{-1} at Chilanga. None of the top 10 TCs were derived from LRs that were among the top 10 under low N conditions in the first season (2004/05). However, they included three TCs of LR86 that was among the best 10 in GY under optimal conditions during the 2004/05 season.The best 10 genotypes under optimal conditions were selected based on average rank of GY at Chilanga and at Golden Valley.

General combining ability (GCA) estimates of S_1 lines

In estimating the GCA effects, deviations from the grand

Table 7. Correlations and heritability of GY with some secondary traits of TCs under low N and optimal conditions.

	Correlation (r) with GY under		Heritability of traits under	
Trait	**Low N conditions**	**Optimal conditions**	**Low N conditions**	**Optimal conditions**
ASI	-0.092	0.046	0.56 ± 0.78	-0.37 ± 1.10
EPP	0.551*	-0.037	0.30 ± 0.91	0.17 ± 0.95
Gtext	-0.233*	-0.221*	0.33 ± 0.89	0.46 ± 0.84
Lroll	0.083		0.23 ± 0.93	-
Lsene	0.199*	-0.223*	0.02 ± 0.87	0.31 ± 0.91
Tsize	0.210*	0.035	0.56 ± 0.78	0.62 ± 0.74
GY			0.38 ± 0.87	0.32 ± 0.90

* Significant at $p \leq 0.05$.

mean were divided by the standard deviation among the means, so that everything is expressed in terms of number of standard deviations centred on a mean of zero. The checks were left out of the calculations of the mean, since they were not crossed to the common tester. Values greater than two (t-test) were significant ($p \leq 0.05$). The results showed that all the 10 highest yielding genotypes under low N and optimal conditions at GV had significant ($p \leq 0.05$) positive GCA effects for GY. The majority of these genotypes had significant GCA effects for Lsene, EPP and Gtext under low N than optimal conditions. Half of the genotypes had significant ($p \leq 0.05$) GCA effects for Lroll under low N conditions. However, the GCA effects for ASI and Tsize were not significant ($p \leq 0.05$) under both low N and optimal conditions.

Phenotypic correlation of GY with secondary traits under low N and optimal conditions

Phenotypic correlations (r) of GY with secondary traits under low N and optimal environments from GV were compared. The results showed that GY correlated significantly ($p \leq 0.05$) with EPP (r= 0.551*), Gtext (r= -0.233*), Lsene (r= 0.199*) and Tsize (r= 0.210*) under low N conditions (Table 7). Grain yield was non-significantly correlated with ASI (r= -0.092) and Lroll (r= 0.083). GY correlated significantly ($p \leq 0.05$) with only Lsene (r= -0.223*) and Gtext (r= -0.221*) under optimal conditions.

Heritability estimates of secondary traits and grain yield

Broad sense heritability (H^2) for GY was 0.38 under low N conditions at GV and was lower than that of ASI and Tsize (Table 7). Under optimal conditions also at GV, H^2 was 0.32 and was lower than that for Tsize and Gtext. Golden Valley received above normal rainfall during the 2006/07 season and the optimal trial was waterlogged twice at about anthesis (January - February, 2007) when 68% of the season's rain was received at the site. Genetic correlation of GY between the optimal and low N conditions at GV was 0.458.

DISCUSSION

Genotype × environment interaction effects (GE) under low N

The results showed that genotypes evaluated during the three seasons (2004/05, 2005/06 and 2006/07) were significantly different. This meant that the genotypes could be discriminated from each other during each season of evaluation and superior performers selected for further improvement. The two sites used in evaluating TCs in season 3 (GV and Kabwe) were also significantly different implying that, although both sites had been depleted of N, they were different. According to soil analysis (Table 2), the two trial sites differed in soil type and amount of rainfall received which probably affected varietal performance at the two sites. While soils at GV were sandy clay loamy, those at Kabwe were sandy loam. The two probably differed in retention of nutrients and water in the soil. According to Hongbotn (1974) the soils at Kabwe were drained of nutrients. Golden Valley received about 100 mm more rainfall than at Kabwe and the heavier soils at the site probably retained more water and nutrients for the growing plants than at Kabwe.

The best four genotypes in GY under low N conditions were TC77, TC72, TC28 and TC53 progenies of LR40, LR35, LR76 and LR84, respectively, (Table 5) revealing the genetic potential of the LRs for GY under the N stress. None of the checks was among the top 10 highest yielding genotypes at the two sites. Superiority in tolerance of a genotype under low N conditions was also estimated based on average rank of selection indices at the two sites. It was found that TC28, TC49, TC72 and TC56 progenies of LR76, LR84, LR35, and LR84 were the most tolerant to low N at the two sites. Further, all the four highest yielding genotypes at the two sites were also among the 10 most tolerant genotypes to Low N. Therefore, the most tolerant genotypes to low N conditions were appropriate for cultivation in both areas and their respective S_1 lines as well as landraces (LR76, LR84, LR35, LR40 and LR11) should be used as base germplasm in breeding for the abiotic stress tolerance (Table 6). A released hybrid, MM603, was the best check and among the top 10 genotypes under low N conditions. This finding means that the hybrid should be a preferred variety for cultivation by resource poor farmers in agro-ecological Region II where both trials were located. However, MMV400, Pool16 and MMV600 were among the 10 genotypes with lowest tolerance to low N and their production could require adequate N fertilisation.

Performance of landraces

The results showed that some LRs achieved higher GY than checks under low N conditions. LR49 had the highest yield of 2.67t ha^{-1} which was greater than the best check (ZM421). LR49, LR4, LR79 and LR93 were found to be the highest yielding genotypes under low N conditions and were considered as low N tolerant. However, GY has low H^2 under low N conditions (Banziger and Lafitte, 1997) which limited its sole use in selecting superior genotypes under the stress, and thus selection index (SI) was preferred because it summarizes the worth of a genotype using information from other relevant traits (Banziger et al., 2000). In this study, heritability of GY at GV was slightly higher under low N than under optimal conditions. This was due to water logging in the optimal trial which was on heavier soil than the low N trials. Some LRs tolerated low N stress more than the checks, and of the top 10 genotypes in tolerance to low N, only one was a check (ZM421) and it ranked 8^{th}. Landraces LR49, LR4, LR79 and LR93 (in that order) were the four most tolerant genotypes to low N stress. These should be used in developing low N tolerant varieties in regions with low soil N.

Performance of S_1 lines

Crossing of S_1 lines to a tester identified the S_1 lines that combined well with it. The tester had alleles that complemented superior S_1 lines under low N by combining well with them. Such materials (LR or S_1 lines) are important germplasm for use in developing improved varieties targeting the low soil N environment. Evaluation of the S_1 lines under low N conditions did not only aid in identifying those that were superior under low N conditions, but also in selecting against materials with unwanted traits (such as low yielding, low prolificacy, high leaf senescence and wide ASI). The most tolerant genotypes to low N stress were S_1 lines 80 (progeny of LR11) and 11 (progeny of LR38). The check (ZM521) was third but was highest in GY. The superiority of the two S_1 lines derived from the landrace meant the S_1 and by inference their respective LRs, had inherent ability to tolerate low soil N. Of the top 10 S_1 lines, only one was derived from the top 10 LRs in tolerance to low N. Low tolerance to low N stress by the majority of S_1 lines derived from LRs which were among the best 10 under the abiotic stress could have been as a result of selfing that was carried out in the nursery. Selfing affects every locus and reduces both fertility and fitness (Falconer and Mackay, 1996). This probably affected the S_1 lines, hence their general lower performance than the check. Selfing reduced heterozygosity by one half and increased the frequency of dominance and recessive homozygotes at each selfing generation. However, allele frequency in the population does not change but assemblage of genes into genotypes changes (Falconer and Mackay, 1996). Therefore, progenies of selfing were not likely to perform the same as their respective parents. Another benefit of selfing to breeding is the exposure of deleterious alleles that are exposed in heterozygous individuals and selected against, thereby improving the breeding materials. Further selfing in unselected germplasm can cause severe inbreeding depression as homozygosity of rare recessive alleles increase (Falconer, 1981). However, crossing of such inbred materials restores hybrid vigour (heterosis) where the progeny performs better than its parents. Superiority of some S_1 lines under low N conditions (Table 3) shows that inherent ability for tolerating the abiotic stress existed in them and can be used in crop improvement targeting low N environments.

Performance of testcrosses under low N conditions

Grain yield under low N conditions

The results showed that some TCs yielded higher under low N conditions than the checks. The top 10 genotypes in GY at GV and Kabwe were all TCs. The four highest yielding genotypes under low N conditions across the sites were TC77, TC72, TC28 and TC53 which were progenies of LR40, LR35, LR76 and LR84, respectively. The findings meant that the TCs and by inference their respective S_1 lines and LRs had superior GY potential over the checks under low N conditions. Good performance of TCs may also be the result of positive heterosis and thus developing hybrids for low N envronment could be effective.

The results also show that TCs were not only superior to checks in GY under low N but under optimal conditions as well. Evaluation of TCs under low N and optimal conditions at GV revealed that all the 26 highest yielding genotypes at GV were TCs, while under optimal conditions the best check was ranked 4^{th} and all other genotypes among the top 21 were TCs. Further, among the top 10 genotypes under optimal conditions were two testcrosses, TC51 and TC52, which were progenies of LR84 that contributed four TCs among the top 10 genotypes under low N conditions. This implies that LR84 had inherent ability for performance under both low N and optimal conditions. For the reason that farmers cultivate maize under varying soil fertility levels, high yield under low N and optimal conditions is desirable and LR84 is an appropriate germplasm in developing such a variety as it posses genes for general adaptability.

Tolerance to low N by testcrossses

Low N tolerant index (LNTI) was calculated as GY reduction under low N conditions in comparison to that under optimal conditions. It ranged from -254 to 88% among the genotypes. Rosielle and Hamblin (1981) observed that selection for stress tolerance was equivalent to selection for low yield reduction between the stress and non - stress environments. Later, Banziger and Lafitte (1997) found that where yield reductions were greater than 40%, direct selection under low N conditions was effective. Genotypes that reduced GY under low N conditions were considered as those affected by the stress and those that either maintained or increased GY under low N conditions as tolerant to the stress. It was found that 16 genotypes were tolerant to low N and among them was one check (Pool16) that ranked 4th in LNTI. Therefore, TC16, TC54, TC10 and TC56 were found to be the four best tescrosses in LNTI. Testcrosses TC16 and TC10 were derived from LR86, while TC54 and TC56 were from LR84. Earlier, it was reported that LR84 was also found to be superior in GY under low N and optimal conditions. These results mean that LR84 and LR86 exhibited tolerance to low N by yielding high under the stress. When the best genotypes in tolerance to low N based on LNTI were evaluated for GY, it was found that seven of the 10 highest yielding genotypes were also found among the 10 most superior genotypes in tolerance to low N using the selection index. The four highest yielding genotypes based on average rank; TC77, TC72, TC28 and TC53 progenies of LR40, LR35, LR76 and LR84, respectively, were all among the top eight genotypes in tolerance to low N. Based on information included in calculating a selection index, the best yielding genotypes should be identified and these results generally showed that this was the case. However, differences in the ranking of genotypes using GY and SI is a matter of concern as high yielding genotypes can still be selected against. For example, a selection intensity of 5% could have failed to select TC77 and TC53 as they ranked 7th and 8th (of 100 genotypes) in tolerance to the stress. Similarly, at the same selection intensity, all the highest yielding TCs were not selected based on LNTI. All the highest yielding TCs can only be selected at 41% selection intensity when selection is based on LNTI. These results meant that selection of superior genotypes under low N conditions needs improvement. Probably the weights of traits used in the selection index should not be fixed but be calculated based on phe-notypic correlation to grain yield. However, differences in the ranking of the genotypes in GY and in tolerance to low N also indicated that there was genetic variation in the genotypes that could be exploited to develop high yielding varieties. The poor correlation between LNTI and the SI probably also reflects problems of water-logging in the optimum trial rather than that of selection for low N tolerance. Errors for differences between means are always larger than for individual means, which also contributes to the variability in LNTI estimates. The study found that the mean of the selected TCs were above trial mean for GY, EPP, Tsize, days to mid-anthesis and plant height at both GV and Kabwe. Similarly, the selected TCs had below trial mean values for ASI, Lsene and Gtext at the two sites. The selected genotypes had above trial mean value for Lroll at GV and below trial mean value achieved at Kabwe. These results generally show that the genotypes selected were high yielding and were superior in tolerance to low N stress.

The study found that all the top 10 genotypes under low N at Kabwe and five of the top 10 genotypes under low N conditions at GV were progenies of LRs that were among the top 10 in drought tolerance during the 2004/05 season. This meant that selecting for drought tolerance also improved tolerance to low N. This was in agreement with Lafitte and Banziger (1997) who achieved a 3.4% GY increase per year under low N conditions following selection under drought conditions. Achieving tolerance of both stresses in a variety was appropriate for most small-scale farmers in Regions I and II where both stresses limited maize production.

General combining ability effects of S_1 lines

General combining ability effects estimated how S_1 lines combine with the tester. Since only one tester was used, genotypes that combined well with the tester also yielded higher than those that did not. Therefore, genotypes obtained similar ranking in GCA effects and in GY. All the 10 highest yielding TCs under low N conditions had significant GCA effects for GY. The findings meant that the respective S_1 lines combined well with the tester and were superior under low N stress. Significant GCA effects meant that use of the genotypes in population improvement under low N was effective. Therefore, testcrosses TC56, TC72, TC7 and TC37 and by inferences, respective S_1 lines and LRs were selected as the most tolerant genotypes to low N stress based on GCA effects. All the 10 highest yielding TCs under low N had positive GCA effects in GY, implying that additive gene action conditioned them under the stress. The findings were in agreement with Omoigui et al. (2007) who reviewed inheritance studies of maize under low N conditions. However, Betran et al. (2003) had earlier found that non-additive gene action was important among inbred lines and hybrids under low N conditions.

Heritability and genetic correlation of secondary traits with GY

To measure the extent to which the traits were determined by genotypes, broad sense heritability (H^2) was calculated. It was found that H^2 for GY was 0.38 under low N conditions, and was higher than that for Lsene, Lroll, EPP and Gtext, but was lower than that for ASI (0.56) and Tsize (0.56). The results meant that much of the GY was not determined by genotypic effects suggesting that selection based on GY alone under low N conditions was not effective. Sibale and Smith (1997) in studying the relationship between traits and GY of maize under low N conditions in Malawi also found similar H^2 estimate (0.41). Banziger and Lafitte (1997) reported that H^2 for ASI was 0.52 and were in agreement with these results. However, although high H^2 of Tsize was found, its correlation with GY was low (r = 0.210*) and may not be effective in identifying high yielding genotypes that tolerated the low N stress. It was also found that much of the GY, Lsene, Lroll, EPP and Gtext were environmental which weakened their efficiency in selecting genotypes under low N conditions. However, Lsene, EPP, Tsize and Gtext had significant correlation with GY. Therefore, selecting large Tsize could be effective in identifying superior genotypes under low N conditions when its correlation with GY was high. This implies that its use should not be generalized but restricted to germplasm whose Tsize and GY correlated highly. The recommendation was at variance with earlier findings (Banziger et al., 2000) who did not list Tsize as one of the secondary traits in identifying superior genotypes under low N conditions. Probably, these findings are particularly relevant to unimproved germplasm which was used in the study.

Indirect selection under optimal environment was considered to select genotypes that could yield well under Low N conditions. Importance of indirectly selecting for GY under optimal conditions, for the low N environment, depended on the genetic correlation of GY under optimal to that under low N conditions. Genetic correlation (r_G) expresses the extent to which two measurements reflect the character that is genetically the same (Falconer, 1981). Grain yield genetic correlation between the low N and optimal environments was found to be 0.458. The moderate correlation meant that genotypes selected for GY in one environment may not express their superiority under the other environment. Banziger et al. (1997) also found positive genetic correlations of GY between low and optimal conditions which decreased with increasing LNTI under low N conditions, indicating importance of specific adaptability of genotypes.

Selection of genotypes tolerant to low N

Banziger et al. (2000) reported that information on GY, EPP, ASI and Lsene should be used in selecting genotypes that tolerate low N. In this study, GY, ASI, EPP Tsize, Lsene, Lroll, and Gtext were evaluated for their relevance in identifying maize genotypes tolerant under low N conditions. Since small-scale farmers selected their seeds also based on superiority in grain flintiness, its evaluation assessed effectiveness of farmer selection in the study areas.

Significant correlations of GY with EPP (moderate, r = 0.551*), Gtext (weak, r = -0.233*), Lsene (weak, r = 0.199*) and Tsize (weak, r = 0.21*) were found implying that respective traits weakly explained GY. Comparatively, Banziger and Lafitte 1997) found strong correlations of GY with EPP (r = 0.78, high) and r = 0.42 (moderate) for Lsene. The results showed that Lsene should be weighed less than EPP in calculating selection indices. Negative correlation of GY with ASI (weak, r = -0.092) and Gtext (r= -0.233*) under low N conditions were found implying that they had little role in selections in this trial. Their values reduced as GY increased and were in agreement with Banziger and Lafitte (1997) for ASI. A negative correlation of GY and Gtext meant that when farmers selected their seed based on increased grain texture (flint), they also selected for low GY. It implied that farmer selection that emphasized selecting for flintiness did not help increase GY of the LRs. The number of ears per plant, Tsize and Lsene had positive correlation with GY meaning that an increase in the respective trait also indicated increased GY.

The magnitude of the correlation explained the trait's association with yield. It was found that EPP had stronger positive correlation than Tsize whose correlation was stronger than that of Lsene. Grain texture also had stronger negative correlation with GY than ASI. A trait that had stronger significant correlation with GY provided more information in estimating GY. Therefore, based on these results, the traits were listed in order of their strength in correlating with GY, as follows; EPP, Gtext, Tsize, Lsene, ASI and Lroll. Considering that Tsize had higher H^2 than EPP and Gtext, its use in selecting genotypes under low N conditions could be effective. However, the recommendation to select for increasing Tsize is at variance with other studies that have found that large tassels reduced GY, either physiologically by competition for photosynthates or physically by a shading effect (Grogan, 1956; Hunter et al., 1969; Mock and Schuetz, 1974). Magorokosho and Pixley (1997) mea-sured Tsize on a scale 1 (small) to 5 (large) while Banziger et al. (2000) reported that Tsize may be mea-sured based on the number of tassel branches or on small to large visual scale. In this study, tassel branch numbers were used to estimate its size. However, a tassel with more branches is not necessarily big in size or a larger producer of pollen than one with few branches, although branch number is positively correlated with tassel dry weight.

Conclusions

The study determined a) tolerance to low N, b) genotype

Table 8. Superior testcrosses under low N.

Testcross	S_1 line	Landrace	Region landrace was sampled from in Zambia
TC56	136	LR84	III
TC32	72	LR11	I
TC39	104	LR93	II
TC72	171	LR35	II
TC7	14	LR38	II
TC19	38	LR 86	II
TC49	127	LR 84	III
TC28	54	LR 76	II
TC27	53	LR 76	II
TC77	184	LR 40	II

x environment interaction effects; c) heritability of traits and; d) correlations of traits of maize genotypes under low N conditions. It has been found that some maize LRs tolerated the stress caused by low N more than improved maize varieties. The 10 most tolerant LRs under low N conditions were: LR49, LR,4, LR79, LR93, LR69, LR19, LR1, LR28, LR11 and LR10 (in that order). It was also found that the best 10 S_1 lines under low N conditions were: 193, 11, 28, 68, 13, 109, 127, 25, 135 and 35. Superior testcrosses under low N were as shown in Table 8.

Most of the testcrosses tolerant to low N stress were sampled from Region II implying that the area was a good source for germplasm targeting low N conditions in Zambia. Landraces LR84 and LR76 contributed two testcrosses each among the 10 best TCs under low N conditions revealing their genetic potential for tolerance to the stress. Eight of the most tolerant TCs to low N stress were progenies of the same parents that contributed eight TCs that were among the top 10 TCs under drought conditions. These include LR11, LR35, LR38, LR76, LR84 and L86. These genotypes should be used to develop varieties for tolerance to both the low N and drought stress. These results support the notion that the underlying mechanisms for low N and drought tolerance are similar. A variety that tolerates drought and low N is appropriate, especially for small-scale farmers in Regions I and II where both stresses limit maize production.

The genetic correlation of GY between the low N and optimal environments was moderate (0.458) and meant that indirect selection for low N tolerance under optimal conditions would not be very effective. Heritability of GY was low (0.38) meaning that basing selection on GY alone under Low N conditions was not effective as environment played a large part in its expression. Therefore, discrimination of genotypes based on GY alone was not effective. This meant that secondary traits should be used to supplement GY to identify superior genotypes under low N conditions. Grain yield, Tsize and EPP should be used in calculating selection indices to identify genotypes that tolerate low N.

It has therefore been found that there was adequate genotypic variation for low N tolerance among maize LRs which can be improved by selection. Landraces, S_1 lines and TCs derived from landraces superior in tolerance to low N were identified. These should be used as germplasm in developing high yielding varieties targeting low N and dry environments.

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