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Relationship between drought and excess moisture tolerance in tropical maize *(Zea mays L.)*

[1*]P.H. Zaidi, Mamata Yadav, D.K. Singh and R.P. Singh

[1]International Maize and Wheat Improvement Center (CIMMYT), C/O ICRISAT, Patancheru 502 324 (A.P.), India
[2]Maize Research, Pusa Campus, New Delhi-110 012, India

[1]Corresponding author: phzaidi@cgiar.org*

Abstract

Maize crops grown during summer-rainy season in Asian tropics are prone to face both drought and excess moisture stress due uneven distribution patterns of monsoon rains in the region. We attempted to identify the relationship between drought and excess moisture tolerance through evaluation of a set of elite maize inbred lines, including lines with known performance under drought, excess moisture and normal inbred lines with unknown performance under either of the stresses. Under normal moisture, performance of normal lines was slightly better than drought and excess moisture lines. However, under stress condition performance of normal lines was very poor with average yield 9.1% under drought and 18.7% under excess moisture stress in comparison to normal moisture. On the other hand, drought lines yielded up to 61.8% under drought and 52.1% under excess moisture in comparison to their yields under normal moisture. Performance of excess moisture lines was also good across stress environments with average yield 68.2% under excess moisture and 35.6% under drought. Relationship between yields under drought and excess moisture stress was strong and significant with drought lines ($R^2 = 0.587^{**}$), but it was relatively weak with excess moisture lines ($R^2 = 0.288^{*}$), while the relationship highly weak with normal lines ($R^2 = 0.043^{ns}$). Our results suggest that improved performance of drought tolerant lines across environments might be related to constitutive changes in stress-adaptive secondary traits such as - anthesis-silking interval <5.0 days, reduced barrenness, delayed senescence and minimum loss of leaf chlorophyll under stress conditions. These constitutive changes with selection and improvement for flowering stage drought tolerance might resulted in improved performance of genotypes under both drought and excess moisture stress, without any yield penalty under normal moisture.

Keywords: Drought, secondary traits, excess moisture, *Zea mays*

Introduction

Drought and excess moisture stress are the two major abiotic stresses limiting maize production in large part of South and South-East Asia, and many other parts of the world. These two stresses accounted for approximately 28% loss of maize production in lowland tropics (Edmeades et al., 2006). Losses due to drought in lowland tropics averaged 17% (Edmeades et al., 1992), and it reached up to 60% in severely drought-affected regions/seasons (Rosen and Scott, 1992). Excess moisture or temporary excess moisture, caused by high water table and/or poor drainage, is second most important production constraints for maize crop in South and South-East Asia, where it causes an estimated loss up to 15% (Rathore et al., 1996). In India, approximately 2.4 m ha (~ 32.4%) of total maize growing areas is prone to face drought or excess moisture stress (AICRP, 2006). Occasional exposure to both the stresses in during same crop cycle, i.e. excess moisture at vegetative stage and drought during flowering and grain filling stage, is common.

In general, most of our modern high yielding varieties are developed under favorable environments and optimal input conditions. Therefore, it is not surprising that they face high yield penalties under marginal and less favorable environments. Blum (1997) suggested that advantage of germplasm improvement for high yield under optimal conditions is realized under mild stress conditions as well. However, expression of stress-adaptive genes under adverse condition protects heavy yield losses. Selection and improvement under optimal conditions may not be suitable for the target areas prone to abiotic constraints (Simmonds, 1991). Therefore, in order to achieve improved and stable yields in stress prone environments it is desirable to improve tolerance to major abiotic constraints prevalent in target environment. In past, development of tolerant genotypes for individual stresses, like drought (CIMMYT, 1999) and excess moisture (Rathore et al., 1998; Zaidi et al., 2003 and 2007) have been successfully attempted. However, major challenge is to put together multiple abiotic stress tolerance and develop productive genotypes tolerant to both drought and excess moisture stresses. Previous studies showed that there was significant spillover between stresses, such as - drought and low-nitrogen stress in tropical maize (Bänziger et al., 1999, 2002; Zaidi et al., 2004). We attempted to assess the relationship between drought and excess moisture stress tolerance, and to establish the extent and direction of spillover between these two stresses in tropical maize.

Materials and Methods

Germplasm

A total 72 advance generation elite maize inbred lines (S_6-S_n) were included in this study. This includes 21 drought lines derived from drought tolerant populations (DTP-white and DTP-yellow) of CIMMYT (International Maize and Wheat Improvement Center, Mexico), 26 excess moisture lines from stress physiology program, Directorate of Maize Research and 25 normal high yielding inbred lines from All India Coordinated Maize Research Project were used in this study. DTPs were constituted at CIMMYT during mid 1980s using 25 putative drought tolerant sources, including Tuxpeno Sequia C_8, Latente, Michoacan 21, Suwan 1, crosses of CIMMYT populations 22, 32, 62, 64, 66, Corn Belt hybrids and germplasm from Thailand, Brazil and South Africa. Details of selection and improvement procedure are described elsewhere (Edmeades and Deutsch, 1994). S_1 progenies derived from C_9 of DTP-white and yellow populations were first screened for common lowland tropical diseases, including Maydis and Turcicum leaf blight, and common rusts prevalent at CIMMYT lowland tropical research station at Poza Rica, Veracruz, Mexico (21^{o}N, 60 masl). Selected disease free progenies were evaluated under three water regimes, including intermediate (IS) or grain filling drought, severe (SS) or full season drought and normal moisture (NM) conditions, at CIMMYT sub-tropical research station at Tlaltizapan, Mexico (18^{o}N, 940 masl) during rain–free winter season of 2000. Promising lines across three environments were selected and advanced to S_3. A total 214 S_3 lines, including 121 DTP-white and 93 DTP-yellow lines were imported from CIMMYT and planted at maize research farm, Indian Agricultural Research Institute, New Delhi, India (28.4^{0}N, 77.1^{0}E, 228.2 masl) during *Kharif* (summer-rainy season) of 2003 and evaluated for their *per se* performance and adaptation in Indian tropics. Selected best lines were evaluated under two moisture regimes, i.e. severe or full season drought stress and normal moisture (NM) conditions at off-season maize nursery at Hyderabad, India (17^{0}N, 78^{0}E, 530 masl) during *Rabi* (rain-free winter season) of 2003 and 2004. Lines with established and consistent response in two years under severe drought stress, including nine tolerant (DT), seven moderately tolerant (MDT), and five highly susceptible (DS), were selected for present study. Similarly, 26 elite inbred lines with consistent performance under excess moisture stress, including 12 tolerant (WT), 9 moderately tolerant (MWT) and 5 highly susceptible (WS), were selected from line evaluation trials conducted on tropical/subtropical lines during 1998-2003 to identify tolerant sources of germplasm for excess moisture stress. Details of germplasm screened and selection and improvement procedure for excess moisture stress is described elsewhere (Zaidi et al., 2007). Normal inbred lines (25) included advance generation productive lines of All India Coordinated Maize Research Project, selected and improved under optimal input conditions for various agronomic traits, important diseases, and

Table 1. Mean of different stress-adaptive traits observed on various group of inbred lines grown under normal and excess moisture or drought stress conditions.

	No. of nodes with brace roots		**Root porosity (%)**		**Change (%) in chlorophyll during one week of WL**		**Senescence (1-10)**		**Leaf rolling (1-5)**	
*Genotypes	NM	WL	NM	WL	NM	WL	NM	DR	NM	DR
Normal lines	1.21	1.66	2.51	11.46	15.84	-26.48	1.1	5.1	1.0	2.9
DT-lines	1.22	1.42	2.82	16.16	16.25	1.05	1.3	2.0	1.1	1.4
MDT-lines	1.14	1.26	2.12	13.30	16.07	0.65	1.2	3.7	1.0	2.7
DS-lines	1.20	1.43	1.95	13.38	17.60	-3.45	1.1	4.2	1.1	2.9
WT-lines	1.45	2.73	2.66	33.50	16.56	9.40	1.1	3.5	1.0	1.9
MWT-lines	1.15	2.19	2.54	26.71	15.73	4.87	1.3	2.8	1.0	1.8
WS-lines	1.06	1.11	2.30	10.67	19.62	-33.60	1.1	4.0	1.0	3.3
Mean	1.20	1.69	2.42	17.88	16.81	-6.79	1.19	3.61	1.04	2.42
LSD	G=NS	E=0.23**	G=2.72*	E=2.72**	G=2.50*	E=1.01**	G=NS	E=0.56**	G=NS	E=0.33**
	G x E=0.29*		G x E=3.84*		G x E=3.53*		G x E=0.69**		G x E=0.40**	
CV (%)	17.02		21.99		29.56		21.45		18.95	

* DT = drought tolerant, MDT = moderately drought tolerant lines, DS = drought susceptible lines, WT = excess moisture tolerant lines, MWT = moderately excess moisture tolerant lines, WS = excess moisture susceptible lines.

insect-pests, combining ability and yield potential.

Experimental site, cultural practices and stress treatment

Experiments were conducted during *Kharif* (summer-rainy season) of 2005 and 2006 at maize research farm, Indian Agricultural Research Institute, New Delhi, India (28.4^0N, 77.1^0E, 228.2 masl). Soil of the experiment farm is characterized as sandy loam with a pH of 7.8. Three sets of all genotypes, first under rain-out shelter for exposing to drought stress at flowering, second in excess moisture block, and third as unstressed control, were planted in field using an alpha (0, 1) lattice design (Patterson and Williams, 1976) with two replications. All entries were over sown and thinned to one plant per hill at V_{2-3} growth stage to give a population density of 55000 plants ha^{-1}. Each entry was planted in two rows, each 3.0 m long, with 0.25 m spacing within and 0.75 m between rows. Before planting 60 kg nitrogen (N) ha^{-1} in form of urea, 60 kg phosphorous ha^{-1} as single super phosphate, 40 kg potassium ha^{-1} as muriate of potash and 10 kg zinc as zinc sulfate was applied as basal dose. Second and third dose of N (each 30 kg N ha^{-1}) was side-dressed at knee-high and tasseling stages. Experiments were kept free from insect-pests, weeds and diseases using recommended package of practices.

Drought experiment was grown in motorized moveable rain-out shelter and exposed to severe drought stress by switching on rain-sensor (Schneider, 2003) at about three weeks before 50% male flowering. The depleting moisture content within root zone at different soil profile (0-100cm) was monitored at regular intervals (Fig. 1), using

Table 2. Mean of different traits and grain yield observed on various group of inbred lines grown under normal, excess moisture and drought stress conditions

	Chlorophyll (SPAD unit)			Anthesis-silking interval (d)			Ears per plant			Grain yield (t/ha)		
Genotypes*	NM	WL	DR	NM	WL	DR	NM	WL	DR	NM	WL	DR
Normal lines	40.4	28.4	32.1	1.63	8.10	12.05	1.11	0.55	0.40	2.41	0.45	0.22
DT-lines	42.8	31.7	39.9	1.61	3.92	2.86	1.13	0.93	0.91	2.38	1.24	1.47
MDT-lines	43.0	26.6	38.5	1.43	4.15	5.41	1.11	0.84	0.74	2.39	0.57	0.92
DS-lines	41.6	27.7	33.6	1.56	4.60	11.90	1.11	0.69	0.32	2.32	0.48	0.12
WT-lines	42.5	32.5	36.3	1.71	2.43	4.74	1.12	0.98	0.72	2.39	1.63	0.85
MWT-lines	43.6	27.2	34.6	1.70	3.52	8.60	1.06	0.89	0.42	2.31	0.93	0.74
WS-lines	39.6	21.3	29.6	1.68	13.68	9.68	1.06	0.38	0.31	2.33	0.21	0.08
Mean	41.8	28.0	34.9	3.54	5.77	7.89	1.10	0.75	0.55	2.36	0.79	0.63
LSD	G=3.59	E=4.74	GxE=6.21	G=0.36	E=0.14	GxE=0.63	G=0.11	E=0.16	GxE=0.18	G=0.16	E=0.26	GxE=0.28
F-sig (%)	NS	1.00	5.00	5.00	1.00	5.00	NS	5.00	5.00	5.00	1.00	5.00
CV (%)		6.74			14.38			10.23			8.96	

** DT = drought tolerant, MDT = moderately drought tolerant lines, DS = drought susceptible lines, WT = excess moisture tolerant lines, MWT = moderately excess moisture tolerant lines, WS = excess moisture susceptible lines.*

Delta-T profile probe PR-1. Rain-sensor was switched off when moisture content reached to permanent wilting point at 20 cm profile depth and population mean for anthesis-silking interval reached to >8.0 days (Bänziger et al., 2000). In excess moisture experiment, flooding treatment was applied continuously for seven days at knee-high stage (V_{7-8} growth stage). Excess moisture experiments was planted in a field specially designed for this purpose, where standing water depth in field could be managed precisely (Zaidi et al., 2007). After completion of stress treatment field was completely drained out. Experiment under normal condition was managed as per agronomic recommendations under optimal supply of moisture.

Observations

Leaf senescence was scored at one week after 50% male flowering using 1-10 scale (1 = 10% and 10 = 100% dead leaf area). Leaf rolling was score using 1-5 scale (1 = no rolling and 5 = fully rolled) at the time 50% anthesis. *In vivo* chlorophyll content was measured in ear leaf at the time of 50% anthesis using a Minolta SPAD-502 chlorophyll meter. In excess moisture trial, chlorophyll in top most fully expanded leaf was measured just before imposing excess moisture treatment and immediately after draining out the field, and percent change in chlorophyll during stress treatment was computed. Number of nodes with brace root was recorded at 50% anthesis on 10 plants by counting number of aboveground nodes bearing brace roots and averaged. Root porosity was measured using pycnometer method (Noordwijk and Brouwer, 1988), which is based on comparison of density of intact root tissues including air-filled pores, and that of root homogenate without air spaces. Days to anthesis and silking was recorded when 50% plants extruded anther or produced visible silk. Anthesis-silking interval (ASI) was calculated as difference between number of days to 50% silking and 50% anthesis. In stress trials, both under drought and excess moisture, few highly susceptible entries failed to reach to 50% silking, resulting in barren plants. In such cases maximum days to 50% silking of the trial was considered as days to 50% silking for those entries for calculation of ASI. However, complete barrenness in those genotypes was considered as such, and ears per plant and final grain yield were recorded as zero. At maturity, ears were harvested, excluding two plants close to alley at both ends of rows. Ears were oven dried to a constant moisture level and grain yield was recorded on a shelled grain basis and adjusted to 15% grain moisture.

Statistical analysis

Analysis of variance (ANOVA) for each trial was calculated using ALPHA-program (CIMMYT, 1999), considering entries as fixed and replicates, plots and incomplete blocks within replicates as random factors. Lattice-adjusted means were computed for each trial. Combined analysis of two years data was conducted using GenStat v. 8, which indicated that year and year x genotype effects were non-significant. Data for both years was pooled after further testing homogeneity of error variance using Hartley's F_{max} test (Ott, 1988). Top ranking best entries in individual and across environment were selected using a multi-trait selection index (CIMMYT, 1999). Test of significance of differences between selected best genotypes and population means was computed using Student's t-test. Analysis of variance of pooled data for different environments was conducted using MSTATc program (MSTATc, 1990), and used to examine partitioning of total sum of squares to genotypes, environment and genotype x environment interaction, and to assess the contribution of each component in performance of genotypes. Site (i.e. environment) regression model (SREG), which consists multiplicative terms of main effect of genotypes and genotype x environment interaction (GGE), was used to assess both general and specific adaptation of genotypes (Crossa and Cornelius, 1997). SREG analysis was conducted using yield data of all genotypes from all the environments as described by Zobel et al. (1988). Correlation coefficient and linear regression between morpho-physiological traits and grain yield, and between yields in different environment was computed using MSTATc.

Results

Performance of genotypes across environments

Inbred lines were severely stressed under both drought and excess moisture condition, however, inhibitory effects were comparatively stronger under drought stress (Table-1 and 2). Excess moisture environment significantly enhanced brace root development and root porosity (Table-1). However,

Table 3. Analysis of variance of important parameters under normal, drought or excess moisture stress and across three environments.

Across two environments, i.e. normal and drought or excess moisture

		Brace root		Root porosity		Change in chlorophyll content under WL		Senescence		Leaf rolling	
Source	DF	MS	% of total SS	MS	% of total SS	MS	% of total SS	MS	% of total SS	MS	% of total SS
Environment	1	33.34**	26.70	28528.2**	65.89	8115.27**	54.01	551.54**	54.60	139.9**	43.62
Error	2	0.56	0.45	80.10	0.19	393.55	2.62	3.46	0.34	1.15	0.36
Genotype	71	0.68	0.55	102.9*	0.24	40.37*	0.27	2.91	0.29	1.15	0.36
G x E	71	0.57*	0.45	98.37**	0.23	29.97*	0.20	3.31**	0.33	1.31**	0.41
Error	142	0.01	0.01	2.23	0.01	7.94	0.05	0.07	0.01	0.02	0.01

Across three environments, i.e. normal, excess moisture and drought

		Chlorophyll		ASI		Ears per plant		Grain yield	
Environment	2	5763.77**	23.62	1857.76**	14.48	9.47**	19.74	137.3**	33.99
Error	3	13.76	0.06	0.21	0.00	0.28	0.58	0.73	0.18
Genotype	71	92.26	0.38	60.28*	0.47	0.19	0.40	1.08*	0.27
G x E	142	40.95*	0.17	33.89*	0.26	0.10**	0.20	0.34*	0.08
Error	213	5.82	0.02	0.06	0.00	0.01	0.01	0.01	0.00

Asterisk (*and **) indicate statistical significance at P <0.01 and 0.05, respectively

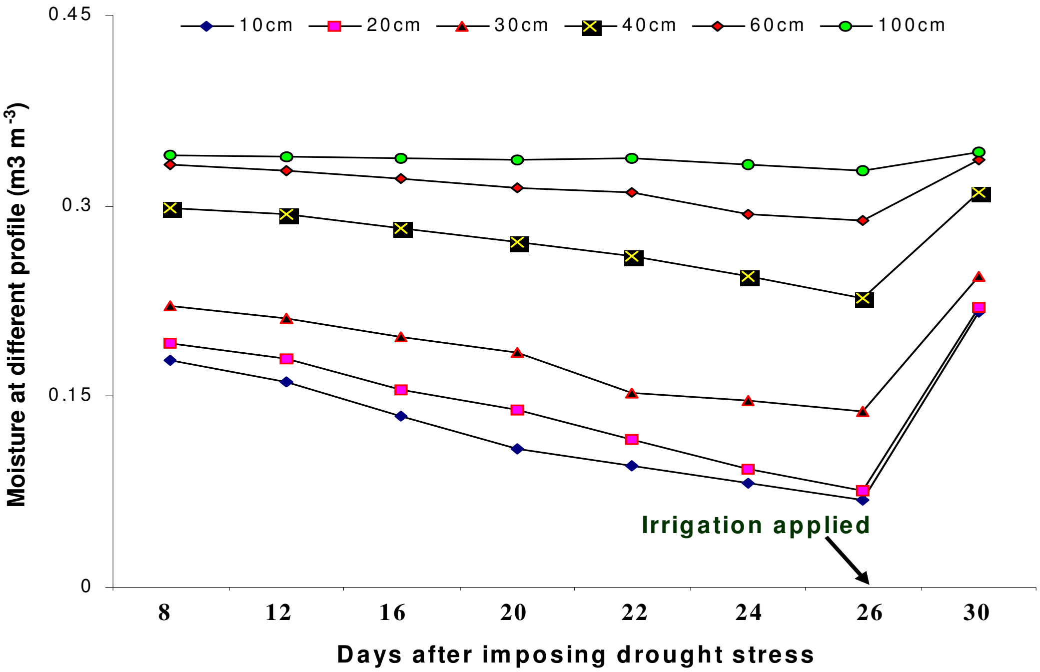

Fig1. Change in moisture content in soil profiles after imposing drought stress.

impact was more pronounced on WT and MWT-lines. Brace root development increased by 79.2 and 90.4% in MWT and WT-lines, respectively. Many fold increase in root porosity was observed in all the group of entries, which ranged from 3.6 times in WS-lines to 11.6 times WT-lines. Loss of chlorophyll content (Table-2) was comparatively higher under excess moisture (28.2%) than drought (11.6%). Among various group of genotypes, maximum average chlorophyll loss was observed in DS-lines (26.3%) followed by normal lines (24.1%). Minimum loss of chlorophyll was in excess moisture lines (15.3±0.3) followed by DT-lines (17.5%). In most of the lines, there was significant decrease in chlorophyll content during excess moisture period, except in WT and DT-lines (Table-1). Waterlogging lines showed even increase (11.4%) in chlorophyll during period of excess moisture, while normal lines showed loss of chlorophyll to the extent of 46.5%. At reproductive stage, inhibitory effect of stresses was comparatively smaller on days to 50% anthesis, but days to 50% silking was significantly delayed (data not shown). This resulted in large anthesis-silking interval (ASI) under both stresses (Table-2). Across stress environment, normal and WS-lines were most affected group of genotypes for ASI, while DT-lines were able to maintain ASI <5.0 days under both stress conditions. In general, genotypic variability for ears per plant (EPP) was non-significant under normal moisture. However, stressed environment resulted in severe cob barrenness, which resulted in reduced number of ears per plant under excess moisture (36.5%) and drought stress (46.4%). Next to selected susceptible entries, loss in EPP was highest in normal lines, both under excess moisture (50.5%) and drought stress (64.0%). Inhibitory effects of stresses on important secondary traits eventually resulted in severe yield losses under both stresses.

Table 4. Selected best and worst entries across environment and their ranking and performance under normal, excess moisture and drought conditions

			Rank				Chlorophyll (SPAD unit)		Anthesis-silking interval (d)		Ears per plant		Grain yield (t/ha)	
Entry	Pedigree	Reaction	Overall	NM	WL	DR	WL	DR	WL	DR	WL	DR	WL	DR
BEST														
40	DTPWC9-F115-1-4-1	DT	1	4	9	1	29.4	40.4	3.4	2.1	0.91	0.87	1.94	1.81
13	,5406-119P28TSR-(S2)-3-1-2-2-B-B-B	DT	2	19	15	3	27.8	40.7	4.6	1.3	1.18	0.97	1.43	1.70
17	DTPYC9-F134-2-3-2	DT	3	12	13	5	29.2	32.4	4.4	3.2	0.96	0.91	1.54	1.54
42	DL-18-12-1-2	WT	4	19	3	14	32.0	41.9	2.4	4.4	0.99	0.97	2.09	1.12
46	WL18-*-*-4-1-2-1-B	WT	5	5	1	13	34.6	36.5	2.2	2.3	0.96	0.99	2.13	1.15
18	DTPYC9-F103-5-4-1	DT	6	9	19	6	34.0	32.5	2.5	3.9	1.07	1.01	1.10	1.45
37	WL7-*-*1-6-2-2-1-B	WT	7	23	12	11	33.4	45.8	2.8	2.3	1.04	1.04	1.58	1.20
38	WL29-*-*-3-7-2-3-B	WT	8	15	5	17	37.3	50.0	2.7	3.4	0.95	0.89	1.83	1.37
20	DTPWC9-F18-1-2-2	DT	9	36	27	7	22.0	39.7	1.5	2.0	0.94	1.01	1.24	1.47
21	DTPWC9-F55-1-2-1	DT	10	22	26	9	30.3	39.2	4.0	4.6	0.99	0.97	1.01	1.25
						Mean	31.2	40.2	2.9	3.3	0.97	0.96	1.59	1.41
		Deviation from population mean					*1.2*	*3.3**	*-3.9***	*-4.3***	*0.27***	*0.37***	*0.85***	*0.76***
WORST														
62	V-341	NM	68	29	34	53	24.7	29.0	6.2	7.0	0.68	0.42	0.77	0.01
69	KDM-347	NM	69	27	68	57	21.8	21.9	12.6	21.7	0.48	0.09	0.03	0.00
60	CM105	NM	70	16	67	47	30.7	37.6	9.1	1.3	0.52	0.41	0.05	0.04
8	DTPYC9-F46-3-4-1	DS	71	11	63	63	28.6	20.4	9.2	11.5	0.38	0.36	0.10	0.00
32	WL36-*-*-4-7-2-1-B	WS	72	24	64	49	26.8	31.6	20.0	6.4	0.41	0.26	0.09	0.03
						Mean	26.5	28.09	11.43	9.56	0.49	0.31	0.21	0.02
		Deviation from population mean					*-3.5**	*-8.9***	*4. 6***	*2.04**	*-0.18*	*-0.40***	*-0.53**	*-0.63**

Asterisk (* and **) indicate statistical significance of Student's t-test at P<0.05, 0.01.

Loss of yield ranged from 38.2 (DT-lines) to 96.6 % (WS-lines) under drought and 31.8 (WT-lines) to 91.0% (WS-lines).

Analyses of variance of key secondary traits and grain yield indicate that genotypic variability was more pronounced under stress condition (Table-3). Impact of environment was comparatively much stronger than genotype and genotype x environment (G x E), which accounted for maximum proportion of total sums of squares for all the traits. Across two environments, analysis (normal vs. drought or excess moisture) showed that impact of excess moisture environment was relatively much stronger on root porosity followed by percent change in chlorophyll content under stress, while plant senescence was most affected secondary trait under drought. Next to environment contribution of G in total variance was higher than G x E under excess moisture, while under drought stress G x E contributed more than G. Analyses of variance across three environments i.e. normal, drought and excess moisture showed that impact of environment was highest on final grain yield followed by chlorophyll content. Next to environment contribution of G in total variance was higher than G x E for all the traits, including grain yield. Contribution of G was highest in variance for ASI followed by ears per plant and least in case of grain yield.

Performance of selected genotypes under individual and across environments

Comparison of performance of top ranking 10 best entries in one environment and their performance in other two environments showed remarkable variations in performance (Fig. 2). None of the entry out of best 10 entries under normal moisture was able to perform under stress conditions, except DTPWC9-F115-1-4, which belongs to group of drought tolerant lines and ranked number one under drought and number nine under excess moisture. Other two entries, i.e. WL18-⊗-⊗-4-1 and HKI-1105, did well under excess moisture stress but their performance was poor under drought. All selected best entries under excess moisture performed fairly well under normal moisture (grain yield >2.0 t/ha). However, under drought stress only three entries, i.e. DTPWC9-F115-1-4, WL29-⊗-⊗-3-7 and DL-18-12 were able to yield >1.0t/ha. Performance of top ranking best 10 entries under drought stress was comparatively much better in other two environments as well. All these entries performed well under normal moisture conditions, and except entry 2, 8 and 10, all performed well under excess moisture stress as well (Fig. 2). Among total 21 drought lines, 3 ranked among top 10 entries under excess moisture and 2 out of best 10 entries under normal moisture condition.

Among top ranking best 10 entries across three environments, 7 entries ranked among top 10 genotypes under drought, 4 entries among top 10 under excess moisture and 3 under normal environment (Table-4). Comparison of performance across three environments to individual environment indicates that high and consistent performance of entries across environment was closely related to performance under drought environment followed by excess moisture. All the best 10 entries across environments ranked among top 20 entries under drought; while under excess moisture 8 out of 10 entries were among top 20 genotypes. However, ranking of those selected entries was inconsistent under normal moisture condition. Worst five entries across environments were poor performing entries under both drought and excess moisture stress. However, their ranking under normal moisture conditions was much higher. Top ranking genotypes across environments revealed remarkable improvements in stress-adaptive traits under drought and excess moisture conditions (Table-4). Traits observed across three environments showed that improved and stable performance was related to significant gains in chlorophyll content, EPP and ability to maintain ASI <5.0 days. On the other hand, poor performing entries suffered with significant loss in chlorophyll, EPP along with poor synchrony between male and female flowering. Gains were comparatively much higher with stress-specific traits, such as high brace root and root porosity under excess moisture and low senescence and leaf rolling under drought (data not shown). Improvements in stress-adaptive secondary traits eventually resulted in significant gains in grain yield under both the stresses, along with good yields under normal moisture.

SREG analysis for GGE highlights behavior of environments in discriminating genotypes (Fig. 2). Drought stress was the best environment in discriminating genotypic response, followed by excess moisture conditions. Genotypes with negative PC1 and PC2 scores indicate negative G x E interaction with optimal conditions, whereas, entries with negative PC1 and positive PC2 value indicate

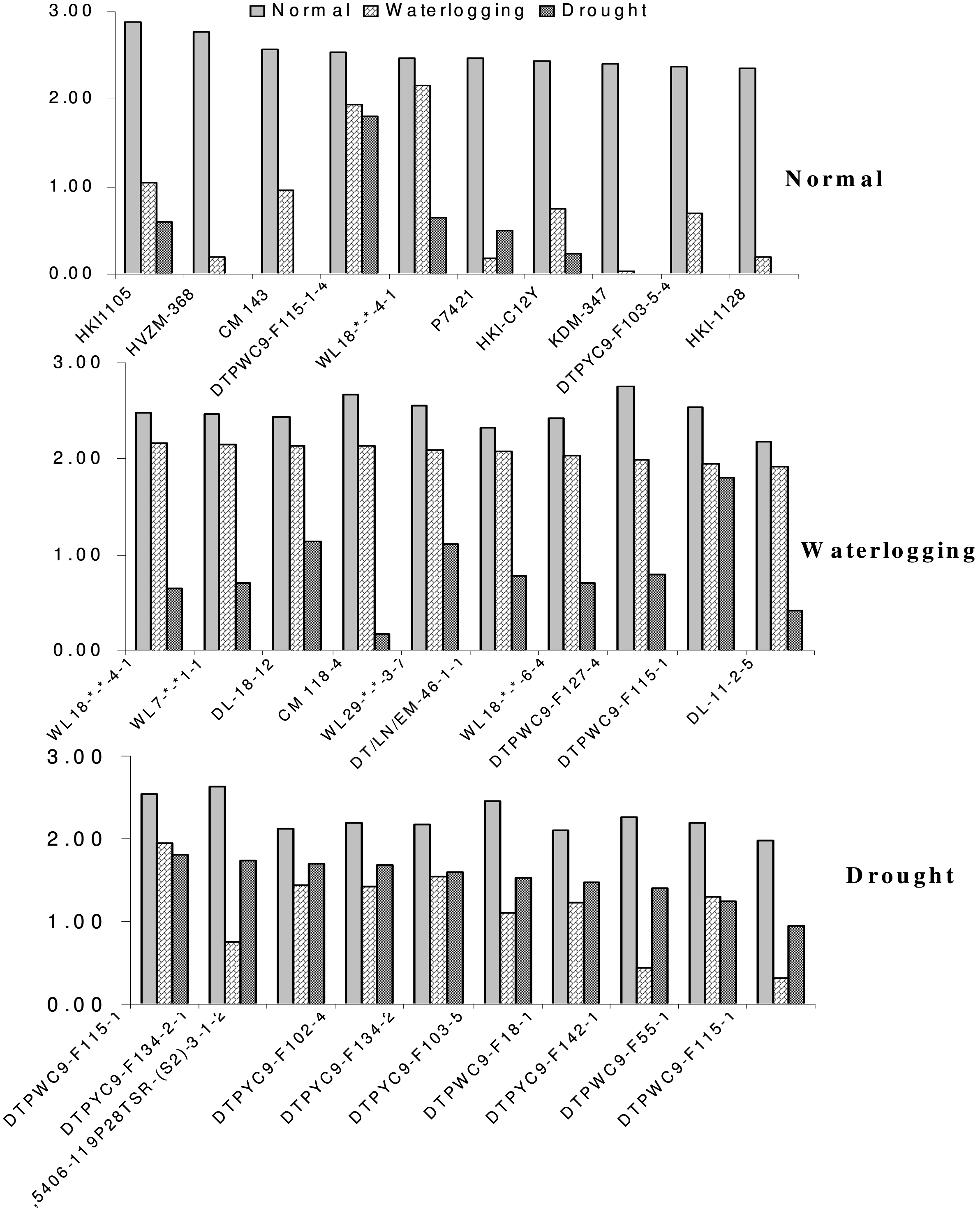

Fig. 2: Top ranking best 10 entries under normal, excess moisture and drought stress and their performance in other two environments.

Table 5. Phenotypic correlation coefficients between grain yield and different morpho-physiological traits observed under normal, excess moisture and drought stress.

Environment	Brace root	Root porosity	Chlorophyll content	Change in CHL during WL	Senescence score	Leaf rolling score	Anthesis-silking interval	Ears per plant
				Across all the lines				
Normal	ns	ns	0.34*	ns	ns	ns	ns	ns
Excess moisture	0.67**	0.73**	0.44**	0.56**	-	-	-0.65**	0.68**
Drought	**-**[a]	-	0.47*	-	-0.52*	-0.42*	-0.53**	0.59**
				Drought lines				
Normal	ns	ns	0.38*	ns	ns	ns	ns	ns
Excess moisture	0.45*	0.56**	0.51*	0.62**	-	-	-0.68**	0.71**
Drought	-	-	0.60**	-	-0.57**	-0.64**	-0.64**	0.73**
				Excess moisture lines				
Normal	ns	ns	0.42*	ns	ns	ns	ns	ns
Excess moisture	0.65**	0.72**	0.56**	0.69**	-	-	-0.64**	0.70**
Drought	-	-	0.62**	-	-0.45*	-0.52*	-0.58**	0.62**
				Normal lines				
Normal	ns	ns	0.32*	ns	ns	ns	ns	ns
Excess moisture	0.44*	0.45*	0.45*	0.43*	-	-	-0.38*	0.39*
Drought	-	-	0.41*	-	-0.42*	ns	-0.42*	0.41*

Asterisk (* and **) indicate statistical significance at P <0.01 and 0.05, respectively; ns indicate non-significant correlation, [a] *not measured*

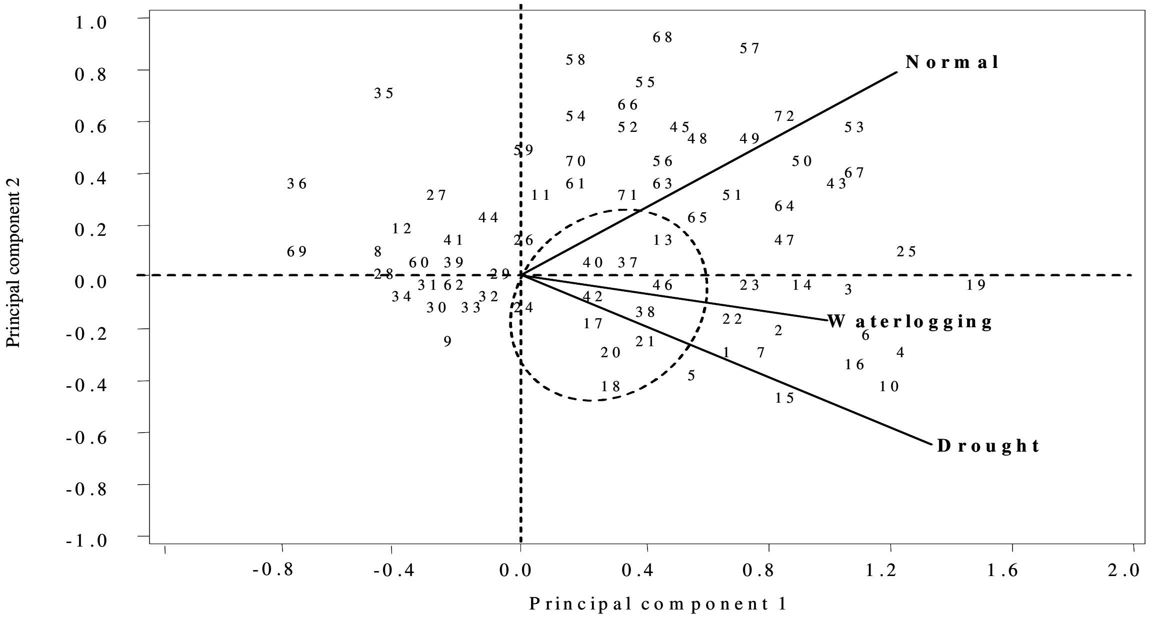

Fig. 3: GGE-biplot of the 1st and 2nd principal components for grain yield. Line encircles genotypes indicate the best genotypes across the three environments. Lines drawn to environments indicate direction of increasing performance in that environment.

strong negative interaction with drought stress and also with excess moisture stress. In general, a large proportion of genotypes were clustered in opposite direction of drought and excess moisture stress. Genotypes with positive PC1 and either positive or negative but small PC2 scores were identified best entries with relatively high mean yield and high stability across environments.

Relationship between secondary traits and yield and between yields under different environments

Phenotypic correlation analysis showed that relation of various traits with grain yield varied significantly in different environment (Table-5). Across germplasm as well as different type germplasm, all secondary traits, except chlorophyll content, showed weak and non-significant relationship with grain yield under normal moisture. However, all secondary traits were strongly related to grain yield under stress environment. In case of normal lines, relationship of various secondary traits with yield under stress was weak in comparison to both drought and excess moisture lines. Selection and improvement for drought tolerance resulted in improved relationship between grain yield and various secondary traits under both drought and excess moisture stress. Lines selected and improved for excess moisture stress also showed similar improvement in magnitude of relationship between secondary traits and stress yield. Relationship between yields of drought lines with secondary traits was strong and significant under drought stress. In addition, there was significant correlation between traits observed under excess moisture stress and yields under excess moisture. Excess moisture yield showed strong correlation with root porosity followed by loss of chlorophyll content during stress, while drought yield showed high dependence on ears per plant and ASI.

Relationship between grain yields in one environment with secondary traits observed in other two environments was analyzed to assess whether performance of some traits can be used to predict the performance in other environments (Table-6). Yield under normal moisture had least dependence on the secondary traits observed under stress environments, except chlorophyll. However, a significant relation was observed among yields of three environments,

Table 6. Grain yield under normal, excess moisture and drought stress as a function of the traits observed in other environments.

Grain yield	**Traits/ conditions**	**Senescence**	**Leaf rolling**	**Brace root**	**Root porosity**	**Change (%) in chlorophyll under WL**	**Chlorophyll**	**Anthesis-silking interval**	**Ears per plant**	**Grain yield**
Normal (NM)	WL	-	-	ns	ns	ns	0.24*	ns	ns	0.42*
	DR	ns	ns	-	-	-	ns	ns	ns	0.43*
Excess moisture (WL)	NM	ns	ns	0.22*	ns	ns	0.31*	ns	ns	ns
	DR	-0.36*	-0.32*	-	-	-	0.38*	-0.52**	0.55**	0.48**
Drought (DR)	NM	ns	ns	ns	ns	ns	0.26*	ns	ns	0.23*
	WL	-	-	ns	ns	0.35*	0.29*	-0.42**	0.45**	0.48**

probably because during selection and improvement for stress tolerant genotypes yield under normal moisture was also taken into consideration. All the traits observed under drought stress showed significant relationship with excess moisture yield. Similarly, drought yield showed significant relationship with most of the traits observed under excess moisture stress; however, key excess moisture traits, i.e. - brace root and root porosity had no relation with drought yields. Brace root development ability under normal moisture showed significant relationship with excess moisture yield. Chlorophyll content under normal moisture showed positive and significant relationship with yield under both drought and excess moisture conditions.

Regression analysis using yield data of all types of germplasm under different environment showed that yield under normal moisture had no relations with both drought and excess moisture yields (Fig. 4a). However, yields under drought and excess moisture showed positive and significant relationship (Fig. 4b). Analysis of relationship between yield under drought and excess moisture in individual group of genotypes (Fig. 5) showed that there was no relation in case of normal lines ($R^2 = 0.0427^{ns}$), while relationship improved when it is computed on excess moisture lines ($R^2 = 0.288^*$), and it was relatively strong in case of drought lines ($R^2 = 0.587^{**}$). Mean square for regression between yields under different environment was statistically significant in case of only drought and excess moisture yields (Table-7). In case of individual group of genotypes mean square of regression was non-significant with normal lines, while it was statistically significant at P = 0.05 with excess moisture lines and at P = 0.01 with drought lines.

Discussion

Genetic enhancement for improving water stress tolerance, including flowering stage drought and knee-high stage excess moisture, resulted in significant spillover effect across moisture regimes (Table-1 and 2). However, gains across environment were comparatively large with selection for drought tolerance than under excess moisture stress. It might be due to fact that, in general, maize is comparatively more stressed under drought than under excess moisture. Similar gains under low-nitrogen stress with recurrent selection for mid-season drought tolerance have been reported by Bänziger et al. (1999, 2002) and Zaidi et al. (2004). Selection for tolerance to mid-season drought stress consistently improved stress-adaptive secondary traits, which are in both the stresses such as – chlorophyll content, ASI and ears per plant (Table-2). These constitutive changes might facilitate in sustaining photosynthetically effective green leaf area, synchronization of male and female flowering and decreased ears and kernel abortion under stress conditions. Edmeades et al. (1993).

Table 7. Analysis of variance for regression between yield under drought and water logging stress in different group of genotypes and across all the genotypes.

Source	Drought lines			Drought Vs Excess moisture Excess moisture lines			Normal lines		
	df	SS	MS	df	SS	MS	df	SS	MS
Regression	1	6.013	6.013**	1	4.443	4.443*	1	0.165	0.165^{ns}
Residual	18	4.225	0.235	25	10.985	0.439	23	3.696	0.161
Total	19	10.238		26	15.428		24	3.861	

Across all the lines

		Normal Vs Drought		Normal Vs Excess moisture		Drought Vs Excess moisture	
	df	SS	MS	SS	MS	SS	MS
Regression	1	0.142	0.142^{ns}	1.226	1.226^{ns}	1.043	1.043^{ns}
Residual	70	24.712	0.353	31.072	0.444	18.911	0.270
Total	71	24.854		33.298		24.855	

Asterisk (*and **) indicate statistical significance at P <0.01 and 0.05; ns indicate non-significant regression

reported that tropical maize populations improved for mid-season drought tolerance showed reduced ASI and barrenness under drought and high-density stress. Short ASI under stress conditions was found to be associated with increased partitioning of photo-assimilates to developing ears at reproductive phase (Edmeades et al., 1993). Selection for tolerance to drought tolerance likely improves sink capacity of reproductive parts, particularly developing ears, through constitutive changes that contribute to increased tolerance to drought and other abiotic stresses (Westgate and Boyer, 1986). Lafitte and Edmeades (1995) reported that selection for drought resulted in a higher number of kernels achieving minimum biomass needed to prevent kernel abortion at onset of linear growth phase (tolerance to lag phase drought). It is the stage when developing kernels achieve the ability to access pre-anthesis photosynthates (Heisey and Edmeades, 1999), resulting in greater sink strength in developing kernel under both stressed and unstressed environments.

Under drought or excess moisture conditions, apart from primary stresses in respective environments, maize plants also face nutrient stress due to slow nutrient mineralization and remobilization of nutrients in dry and compact soils under drought (Shepherd, 1984; Patterson et al., 1993) and leaching and poor uptake of nutrients under waterlogged conditions (Rathore et al., 1998; Steffens et al., 2005). Pre-mature senescence and severe leaf chlorosis are common symptoms under drought and excess moisture (Table-1 and 2), in spite of well-fertilized conditions, which indicate low nitrogen availability to plants. Improvement of germplasm with a focus on mid-season drought tolerance might have improved nutrient uptake/use efficiency (Banziger et al., 2002). These characteristics in stress tolerant might be major factors responsible for reduced kernel abortion by

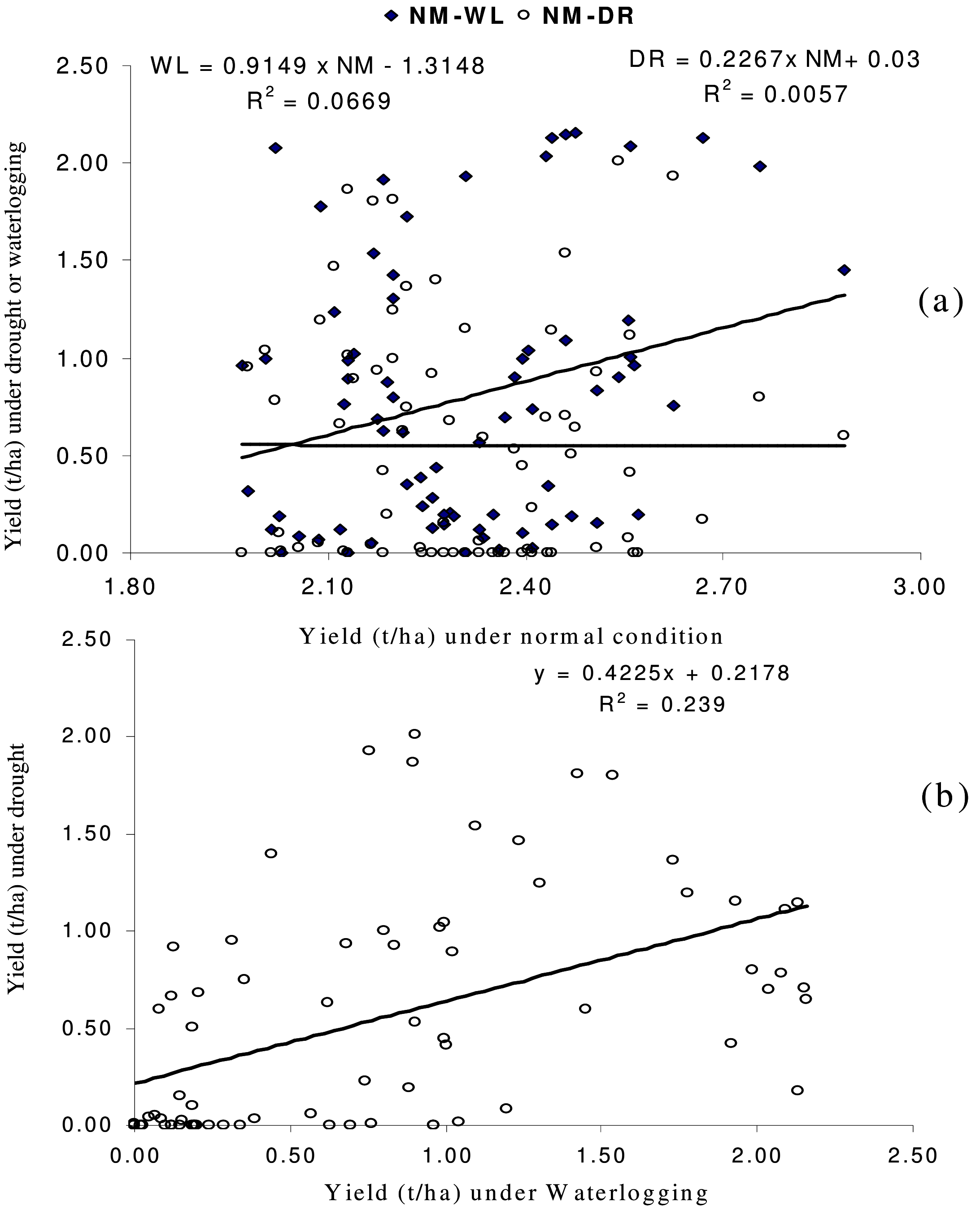

Fig.4: Relationship between (a) grain yield under normal and drought/excess moisture stress and (b) excess moisture and drought stress.

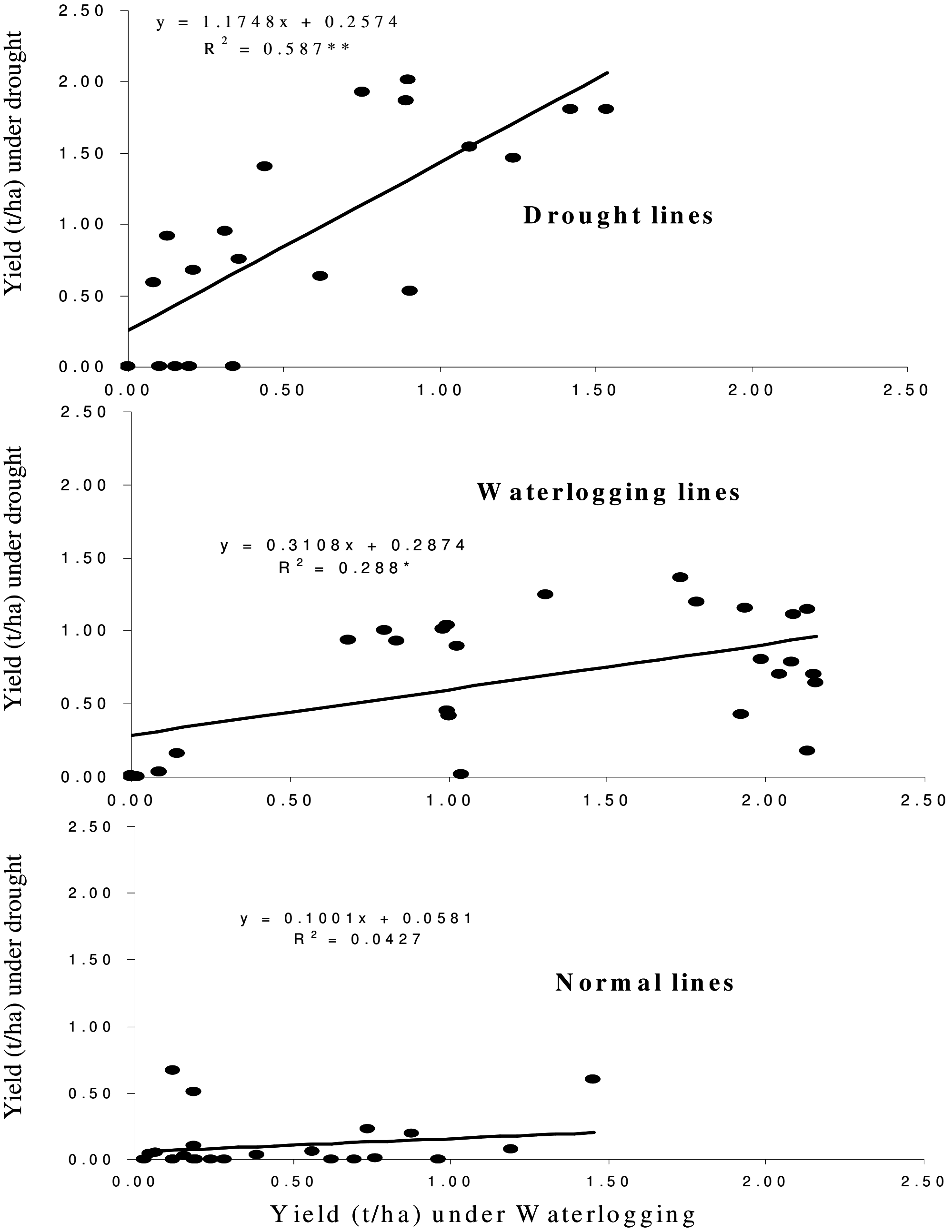

Fig 5. Relationship between grain yield under excess moisture and drought stress in drought, excess moisture and normal lines.

improved nutrient and assimilate supply during lag phase of grain filling (Westgate and Boyer, 1986). Delayed leaf senescence and stay-green characters might facilitate kernel growth and assimilate accumulation during later grain filling stage (linear phase), resulting in more number of fully developed kernels per ears and higher kernel weight, and therefore, improved yields in drought tolerant lines across moisture regimes (Table-2, Fig. 2). Similar observations under drought and low-nitrogen stresses in tropical maize germplasm were also reported by Lafitte and Edmeades (1995) and Zaidi et al. (2004). Delayed senescence and maintenance of leaf chlorophyll content under drought or excess moisture stress might have increased production of carbohydrate by allowing greater intercept of radiation with time and absorbing a large fraction of incident light (Muchow and Sinclair, 1994). Our results showed that selection for drought tolerance (and excess moisture) has improved the magnitude of correlation between different important secondary traits and yield, both under drought and excess moisture conditions (Table-5). However, with normal lines, key traits such as ASI, ears per plant, senescence and leaf chlorophyll showed relatively weak correlations with grain yield under stress conditions. In general, there was least genotypic variability for stress related traits under unstressed conditions, and non-significant correlations with final grain yield (Table-5). However, genotypic variability for these traits become large under both drought and excess moisture stresses, and therefore, can be selected and further improved along with grain yield. Out of total ten best inbred lines across three moisture regimes, six lines were best drought tolerant and four best excess moisture tolerant lines (Table-4). These genotypes had short ASI, relatively high chlorophyll content and number of ears per plant under both the stresses. They suffer minimum with leaf rolling during flowering and leaf senescence at late grain filling stage under drought stress, and possess high root porosity and brace root, and minimum loss of chlorophyll during excess moisture stress. These superior characteristics might eventually result in high and stable yields across moisture regimes. GGE-biplot analysis showed that drought environment was discriminated far from normal conditions and excess moisture environment was in between normal and drought environment, but relatively closer to drought (Fig. 3). Entries with positive and small PC1 and PC2 values (except entries 13, 37 and 40 with small negative PC2) were identified the best entries in terms of improved stable performance across moisture regimes. Zaidi et al. (2004) also reported similar trend in tropical maize hybrids grown under drought, low nitrogen and normal conditions.

Phenotypic correlation analysis between secondary traits and grain yield showed that, in general, relationship was relatively week and statistically non-significant under normal moisture, while under stress environment grain yield showed strong dependence on stress-adaptive traits (Table-5). In addition, relationship between secondary traits and yield under stress was comparatively much stronger in case of drought lines, followed by excess moisture lines. Regression analysis between yields under different environment showed that performance of genotypes under drought or excess moisture could be least predicted through performance normal condition (Fig. 4a). This suggests that selection and improvement for yield under optimal conditions may be a suitable approach for favorable environments, but not for marginal areas where abiotic constraints such as drought and excess moisture are prevalent. Castleberry et al. (1984) examined Corn Belt hybrids developed under optimal input conditions from a period of more than 50 years and found very low selection gains under low soil fertility. Similarly, Martinez-Barajas et al. (1992) reported that progress from selection for high yield under well-watered conditions was greatly reduced under water deficit conditions.

In general, relationship between performance under drought and excess moisture stress was weak and statistically non-significant (Fig. 5). However, analysis of individual group lines showed that it was weakest in case of normal lines ($R^2 = 0.0427$), it improved with excess moisture lines ($R^2 = 0.288^*$) and relationship was strong and significant with drought lines ($R^2 = 0.587^{**}$). These findings suggest that spillover from drought towards excess moisture is relatively much stronger than vice-versa. Duvick (1995) proposed that major goal of tropical maize improvement program should be to improve and stabilize yield, and broaden adaptation through increased tolerance to various stresses. It is possible to have stable but low yield under drought and low fertility prone areas by selecting for earliness (Edmeades et al., 1995). However, selection of germplasm for mid-season drought tolerance, followed by evaluation of selected entries under excess moisture stress, may prove to be a better approach to develop genotypes with improved and stable yields across different regimes of water availability in tropics.

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