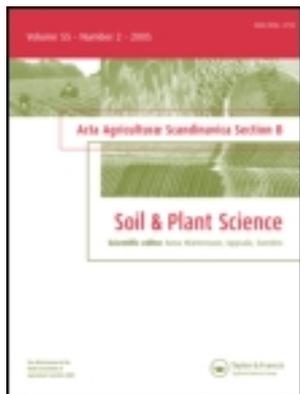


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ORIGINAL ARTICLE

Genetic properties of drought tolerance indices in sunflower

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Abstract

The objective of the present study was genetic analysis of yield-based drought tolerance indices using the diallel method. Twenty-one genotypes of sunflower (*Helianthus annuus* L.) derived from a half diallel cross between six inbred lines were evaluated in both stress and non-stress conditions using a randomized complete block design for each one. Eight drought tolerance indices comprising stress tolerance index (STI), mean productivity (MP), geometric mean productivity (GMP), harmonic mean (HM), stress susceptibility index (SSI), tolerance index (TOL), yield index (YI) and yield stability index (YSI) were calculated based on grain yield under stress and non-stress environments. Significant genotypic differences were observed in TOL, GMP, MP, STI, HM and YI. Diallel analyses revealed the importance of both additive and non-additive gene effects in GMP, STI, HM and YI. However, the Baker ratio supported the predominance of an additive effect in their expression. Our results demonstrated that SSI, YSI, TOL and MP are not reliable indices to select drought tolerant genotypes in sunflower breeding programmes because of their low heritability. Indices such as GMP, STI, HM and YI were moderately heritable and are usually able to select high-yielding genotypes in both environments and could be usefully employed in drought tolerance breeding programmes of sunflower.

Keywords: Combining ability analysis, *Helianthus annuus* L., heterosis, index, water treatment \times genotype interaction.

Introduction

Sunflower (*Helianthus annuus* L.) is one of the most important sources of vegetable oil in the world. Drought is the main environmental constraint, which occurs in many parts of the world every year, often having devastating effects on crop productivity. Hence, improved tolerance to drought has been a goal in crop improvement programmes since the dawn of agriculture (Ludlow & Muchow, 1990). Loss of yield is the main concern of plant breeders and they hence emphasize on yield performance under moisture-stress conditions. But variation in yield potential could arise from factors related to adaptation rather than to drought tolerance. Thus, drought indices providing a measure of drought based on yield loss under drought conditions compared with normal conditions are being used in screening drought-tolerant genotypes (Mitra, 2001). Fischer and Maurer

(1978) proposed a stress susceptibility index (SSI) for evaluating the susceptibility of lines in dry conditions. Rosielle and Hamblin (1981) defined stress tolerance (TOL) as the differences in yield under stressed (Y_s) and non-stressed (Y_p) environments and mean productivity (MP) as the average yield of Y_s and Y_p . Bouslama and Schapaugh (1984) suggested a yield stability index (YSI). Fernandez (1992) defined a new advanced index (STI = stress tolerance index), which can be used to identify genotypes that produce high yields under both stress and non-stress conditions. Further, Gavuzzi et al. (1997) defined yield index (YI) as the yield of a given genotype in a stressed condition on average yield of all genotypes in the same condition. Another yield-based estimate of drought tolerance is geometric mean (GM), often used by breeders interested in relative performance since drought stress can vary in severity over years (Ramirez Vallejo & Kelly, 1998). Drought tolerance indices have been

used for screening drought tolerant genotypes in some breeding programmes (Ndunguru et al., 1995; Razi & Assad, 1998; Daneshian & Jonoubi, 2008; Ghafari, 2008; Agbicodo et al., 2009). An ideal selection index must be able to distinguish genotypes that have uniform superiority in both stressed and non-stressed environments and be heritable. Drought tolerance indices have been compared by some researchers (Fernandez, 1992; Richard, 1996; Abebe et al., 1998; Sio-Se Mardeh et al., 2006; Jafari et al., 2009), but their genetic properties and heritabilities have been little investigated (Saba et al., 2001; Dashti et al., 2007). This might be one of the main reasons for the lack of significant progress in breeding for drought tolerance based on selection index methodology. Diallel cross analysis is an efficient method in the genetic analysis of characters (Hill et al., 2001). For the estimation of general and specific combining ability effects, none of the mating designs supply as much information as the diallel analyses proposed by Griffing (1956). The general combining ability (GCA) refers to the average behaviour of an inbred parent in a series of hybrid combinations, and it is associated to the additive action of the genes (Rojas & Sprague, 1952). The specific combining ability (SCA) refers to those instances in which certain hybrid combinations are either better or poorer than would be expected on the average performance of the inbred parents considered and it is associated to the effect of dominance (Rojas & Sprague, 1952). Griffing's (1956) diallel methods have been extensively used in crop plants (Evans et al., 1966; Stuthman et al., 1971; Borges, 1987; Pixley & Bjarnason, 1993; Kang et al., 1995, 1999; Zhang et al., 1996). Gardner and Eberhart (1966) proposed alternative analyses of data from diallel crosses that help to establish useful heterotic patterns. Heterosis effects and combining ability serve as a guide for choice of parents for breeding programmes. The objective of the present study was genetic analysis of yield-based drought tolerance indices using a diallel method.

Materials and methods

Five sunflower recombinant inbred lines (RILs) out of 126 together with their paternal line (RHA266) were selected on the basis of their contrasting responses to water stress and different agronomical characteristics revealed in our previous experiments (Table I) (Poormohammad Kiani et al., 2007a, 2007b, 2008, 2009). These lines are F₉ pure lines which were developed through single seed descent from F₂ plants derived from a cross between 'PAC2' and 'RHA266'. RHA266 was obtained from a cross between *Helianthus annuus* and *Peredovik* by USDA and PAC2 (developed by INRA-France) is an inbred line from a cross between *H. petiolaris* and 'HA61' (Gentzmittel et al., 1995). This public RILs population has been widely used for genetic analysis of complex traits in sunflower (Rachid Al-Chaarani et al., 2004, 2005; Abou Al Fadil et al., 2007; Darvishzadeh et al., 2007; Poormohammad Kiani et al., 2007a, 2007b, 2008, 2009). The six genotypes were grown and crossed in a diallel mating system without reciprocals to produce 15 F₁ hybrid combinations. The parental genotypes and their F₁ hybrids were grown in the greenhouse under controlled conditions. Plants were individually grown in plastic pots containing a mixture of 40% soil, 40% compost and 20% sand as described by Poormohammad Kiani et al. (2007a, 2007b). Temperature was maintained at 25/18 ± 2 °C (day/night) and relative humidity at about 65/85 ± 5%. Supplementary light was provided to obtain 16-h light period. Twenty one genotypes were evaluated in both stress and non-stress conditions using a randomized complete block design for each one. In order to simulate natural water deficit conditions (similar to field) a progressive water stress from mild stress to severe stress was imposed on 45-day-old plants at a stage near flower bud formation (R1) (Schneiter & Miller, 1981) for a period of 12 days (Poormohammad Kiani et al., 2007a, 2007b). Both well-watered and water-stressed plants were weighed and water loss

Table I. Sunflower lines and their characteristics used in experiment for studying genetic properties of drought tolerance indices.

Sunflower line	Type	Origin	Characteristics (Poormohammad Kiani et al., 2007a, 2007b, 2008, 2009)
C104	RIL	France	Good water status and osmotic adjustment as well as biomass and yield under water-stressed conditions
LR25	RIL	France	Good water status and osmotic adjustment as well as biomass under water stress conditions but it lost grain weight under water-stressed conditions
LR4	RIL	France	Average water status and osmotic adjustment as well as biomass and yield under water-stressed conditions
C100	RIL	France	Good water status and osmotic adjustment but very low in yield under both well-watered and water-stressed conditions
LR55	RIL	France	The lowest water status traits and osmotic adjustment as well as biomass and yield under water-stressed conditions
RHA266	BL	USA	Low water status traits and osmotic adjustment and average biomass and yield under water-stressed conditions

BL, breeder's line; RIL, recombinant inbred line.

replaced carefully. Well-watered plants (control) received sufficient water to maintain soil water content close to field capacity. Water-stressed plants were subjected to a progressive water stress and irrigated with a water volume of 60%, 50% and 40% of field capacity (each for 4 days) during 12 days and continued up to harvest. Plants were harvested at maturity, and then the grain yield was recorded for every plot. The drought tolerance indices were calculated for every genotype using the corresponding well-watered and water-stressed plots in each block. The resulting data were analysed as obtained from a randomized complete block design. Drought tolerance indices were calculated using the equations cited in Table II.

Statistical analysis

Analysis of variance was performed using the general linear model (GLM) procedure in the SAS software version 9.1 (SAS Institute Inc, NC, USA). Analysis II of Gardner and Eberhart (1966) was used to

estimate the genetic effects for which Singh (1978) has provided details of necessary calculations. The statistical model is as following:

$$Y_{jj'} = \mu_v + 0.5(v_j - v_{j'}) + v\bar{h} + v(h_j - h_{j'}) + vs_{jj'}$$

where $Y_{jj'}$ mean of a parent when $j=j'$ and mean of a cross when $j \neq j'$, μ_v = mean of all parents; v_j and $v_{j'}$ are effects for variety j and j' , respectively, when parents are included in the analysis; \bar{h} = average heterosis; $v=0$ when $j=j'$ and $v=1$ when $j \neq j'$; h_j and $h_{j'}$ = variety heterosis for variety j and j' , respectively; $s_{jj'}$ = specific heterosis. Variety effect (v_j) is the difference between the mean performance per se of each parent and the mean of all parents. Heterosis effect ($h_{jj'}$) arises as a consequence of differences in gene frequencies in two populations and dominance of more favourable alleles. Further, the ' $h_{jj'}$ ' effect is partitioned into three components (\bar{h} , h_j and $s_{jj'}$). Average heterosis (\bar{h}) contributed by a particular set of parents used in a set of diallel crosses is the difference between the mean of all crosses and the mean of all parents. Variety heterosis (h_j) is the

Table II. Indices used for evaluation of the responses of sunflower inbred lines and their F₁ hybrids to drought conditions.

Drought tolerance indices	Equation	Reference
Stress Susceptibility Index	$SSI = \frac{1 - \left(\frac{Y_S}{Y_P}\right)}{1 - \left(\frac{\bar{Y}_S}{\bar{Y}_P}\right)}$	Fischer & Maurer (1978)
Geometric Mean Productivity	$GMP = \sqrt{(Y_S)(Y_P)}$	Fernandez (1992) and Kristin et al. (1997)
Mean Productivity	$MP = \frac{Y_S + Y_P}{2}$	Rosielle & Hamblin (1981)
Harmonic Mean	$HM = \frac{2(Y_P \cdot Y_S)}{Y_P + Y_S}$	Jafari et al. (2009)
Tolerance index	$TOL = Y_P - Y_S$	Rosielle & Hamblin (1981)
Stress Tolerance Index	$STI = \frac{(Y_S)(Y_P)}{(\bar{Y}_P)^2}$	Fernandez (1992)
Yield Index	$YI = \frac{Y_S}{\bar{Y}_S}$	Gavuzzi et al. (1997)
Yield Stability Index	$YSI = \frac{Y_S}{Y_P}$	Bouslama & Schapaugh (1984)

Y_S and Y_P are stress and optimal (potential) yield of a given genotype, respectively. \bar{Y}_S and \bar{Y}_P are average yield of all genotypes under stress and optimal conditions, respectively.

contribution to heterosis by population 'j' in its crosses, measured as a deviation from average heterosis. Specific heterosis (s_{ij}) effect measures the deviation between the observed performance of the specific cross and its expected performance based on ' v_j ', ' \bar{h} ' and ' h_j ' effects. Data were also analysed using Griffing's method II model 1 (Griffing, 1956). Diallel analyses were conducted using the SAS programme developed by Zhang et al., (2005). Heritability of the indices was estimated as follows (Nyquist, 1991; Falconer & Mackay, 1997):

$$h^2 = \frac{\delta_g^2}{\delta_g^2 + \delta_e^2}$$

where δ_g^2 is the genotypic variance, δ_e^2 is the error variance and r is the number of replications. Correlations between traits were determined using SAS PROC CORR (SAS Institute Inc, NC, USA).

Results and discussion

Analysis of variance showed significant difference among genotypes for grain yield in each of two conditions (Table III), indicating genetic variability for grain yield in both well-watered and water-stressed conditions. In combined analysis of variance significant water treatment and genotype effect was observed for grain yield while no significant water treatment \times genotype interaction effect was observed suggesting that response to water status by a given genotype in relation to other genotypes does not vary between water treatments (Table III). In an experiment the relative influence of water irrigation in improving productivity of some barley genotypes under low rainfall condition of Saudi Arabia was investigated (Refay, 2010). The experiments included the combination of four barely genotypes and five water irrigation regimes. Results indicated that drought stress condition at a high level has significant effects on all of the studied characters.

However, interaction effects for most of the parameters remained non-significant.

There were significant genotypic differences in TOL, GMP, MP, STI, HM and YI (data not presented) indicating the heritability of drought tolerance indices, and therefore potentially their usefulness for screening drought tolerant genotypes in breeding programmes. Analysis II of Gardner and Eberhart (1966) showed that both v_j and h_{ij} variances were significant for Y_p and Y_s as well as for MP, GMP, STI, HM and YI indices indicating the importance of both additive and non-additive gene effects in their expression. In analysis II of Gardner and Eberhart (1966), the single mean square for parents (i.e. varieties) contains all variation due to additive effects and some dominance while the mean square for heterosis is all due to dominance and differences in allelic frequencies between any two populations (Gardner & Eberhart 1966; Ouendeba et al., 1996). Among the partitioned component of heterosis, specific heterosis was only found to play a major role in STI index ($P < 0.1$) (Table IV). Specific heterosis seems to be a less important source of variation in varietal diallel crosses and has shown to be non-significant in the analysis of variance in most studies (Viana, 2000; Hallauer & Miranda Filho, 1988). Genotypes LR25 had positive and significant variety effects for Y_s and GMP, HM and YI indices while the C100 genotype had negative and significant variety effects for them (Table V). A parent with a significant positive v_j value would contribute with a high level of resistance whereas a parent with a negative value would contribute with a high level of susceptibility. LR25 and C100 genotypes were also involved in crosses giving a high specific heterosis effect in drought conditions (Table VI). The only index that shows above mentioned situation is YI (Table VI). This index could be usefully employed in hybrid breeding programmes of sunflower. Considering the above results, two genotypes (LR25 and C100) represent good choices with which to initiate drought tolerance breeding programmes.

Table III. Mean squares for grain yield of sunflower genotypes under optimal and stress conditions.

Source of variation	Individual			Combined	
	df	MS _{YP}	MS _{YS}	df	MS
Water treatment				1	2.39**
Replication/Water treatment	2	0.07 ^{ns}	0.21 ^{ns}	4	0.09 ^{ns}
Genotype	20	0.99**	0.29**	20	0.12**
Genotype \times Water treatment				20	0.04 ^{ns}
Residual	25	0.30	0.09	70	0.04
CV		20.96	19.92		16.82

df, degrees of freedom; MS, mean of squares; Y_p , yield of a given genotype in optimal (potential) conditions; Y_s , yield of a given genotype in stress conditions. **, significant at 0.01 probability level; ns, not significant at 0.05 probability level.

Table IV. Estimates of variety (v_i) and variety heterosis (h_i) effect from analysis II of Gardner and Eberhart (1966) and mean squares of general and specific combining abilities based on Griffing's Method II and Model I for grain yield of sunflower genotypes under optimal and stress conditions, as well as for calculated different drought tolerance indices.

MS												
YSI	YI	HM	STI	GMP	MP	TOL	SSI	YS	YP	df	Source of variation	
Griffing's Method II and Model I												
0.01 ^{ns}	0.102*	0.33*	0.08*	0.36*	0.40 ^{ns}	0.49 ^{ns}	0.02 ^{ns}	0.24*	0.61 ^{ns}	5	GCA	
0.02 ^{ns}	0.11**	0.41**	0.11**	0.49**	0.62**	0.98*	0.02 ^{ns}	0.27**	1.05**	15	SCA	
–	0.65	0.62	0.59	0.60	0.56	0.50	–	0.64	0.54		$2S_{gca}/2S_{gca}S_{sca}$	
Analysis II of Gardner and Eberhart												
0.02 ^{ns}	0.15**	0.49**	0.09*	0.53**	0.57*	0.71 ^{ns}	0.03 ^{ns}	0.35*	0.87*	5	Variety	
0.02 ^{ns}	0.13**	0.44**	0.11**	0.52**	0.64**	0.98 ^{ns}	0.02 ^{ns}	0.31**	1.06**	15	Heterosis (h_{ij})	
0.0009 ^{ns}	0.85**	3.24**	0.86**	4.00**	4.91**	5.84**	0.004 ^{ns}	2.06**	7.80**	1	Average heterosis (h)	
0.005 ^{ns}	0.05 ^{ns}	0.12 ^{ns}	0.01	0.12	0.13 ^{ns}	0.12 ^{ns}	0.009 ^{ns}	0.11 ^{ns}	0.17 ^{ns}	5	Variety heterosis (h_i)	
0.03 ^{ns}	0.06 ^{ns}	0.19 ^{ns}	0.06*	0.22	0.29 ^{ns}	0.73 ^{ns}	0.03 ^{ns}	0.15 ^{ns}	0.57 ^{ns}	9	Specific heterosis (s_{ij})	

df, degrees of freedom; MS, mean of squares. Y_P , yield of a given genotype in optimal (potential) conditions, Y_S , yield of a given genotype in stress conditions; SSI, Stress Susceptibility Index; TOL, Tolerance index; MP, Mean Productivity; GMP, Geometric Mean Productivity; STI, Stress Tolerance Index; HM, Harmonic Mean; YI, Yield Index; YSI, Yield Stability Index. * and **, significant at 0.05 and 0.01 probability level, respectively; ns, not significant at 0.05 probability level.

Partitioning sum of square for genotype based on Griffing's diallel analysis method into general and specific combining abilities revealed that variance of general and specific combining abilities was significant for indices GMP, STI, HM and YI whereas for TOL and MP indices, only variance due to SCA was significant (Table IV). The significant effects of general and specific combining abilities again indicated the importance of both additive and non-additive genetic components in controlling traits. The relative importance of general and specific combining ability in determining progeny performance is assessed according to the ratio presented by Baker (1978). The ratio close to 1:1 for a given trait shows that additive gene effects are more important than non-additive ones. In our study the Baker's ratio was near to 1.0 for GMP, STI, HM and YI, supporting the preponderance of additive gene effects involved in the genetic control of these indices whereas for others, it demonstrated the preponderance of non-additive gene effects. The additive variance is the main determinant of the observable genetic properties of the population and selection response (Falconer & Mackay, 1997). Higher genetic advances could be realized when using characters with higher additive genetic variance for selection. The conspicuity of additive inheritance indicates the possibility of improving drought tolerance through conventional breeding programmes and by using the heritable indices such as GMP, STI, HM and YI.

Heritability of indices is presented in Table VII. It was very low for TOL and moderate for MP, GMP, HM, STI and YI. On the other hand GMP, STI, HM and YI showed high content of GCA variance in

both analysis methods. Thus, selection for drought tolerance in sunflower using GMP, STI, HM and YI might be more fruitful than selection for that based on MP and TOL.

Inheritance of several yield-based drought tolerance indices was studied by Saba et al. (2001) in winter wheat genotypes. In their study, genetic components of variance and heritabilities were estimated using Gardner and Eberhart's method III. Significant GCA was obtained for GMP, MP, STI and TOL but not for SSI. The SCA effects were also highly significant for GMP, MP and STI. However, additive variances were more important than dominance ones. Heritability estimates were very low for SSI, low for TOL, but moderate for GMP, MP and STI. In another study Dashti et al. (2007), using a segregating population of 96 wheat doubled haploid lines derived from a cross between Chinese spring (CS) and SQ1, detected three QTLs for SSI on chromosomes 7A, 4B and 6B, two QTLs on chromosomes 5A and 5B for MP and only one QTL for each of STI, GMP and TOL indices. The QTL effects of drought tolerance indices ranged from 13 to 36%. Yue et al. (2005), using a population consisting of 180 rice recombinant inbred lines developed from a cross between Zhenshan 97 and an IRAT109, reported two and five QTLs for drought resistance indices in Paddy and Sandy soil conditions respectively. The QTL effects of drought tolerance indices ranged from 4.90 to 19.05%.

The suitable index must have significant correlation with yield in both conditions (Blum 1988). A correlation coefficients matrix (Table VIII) indicated that firstly, grain yield under non-stress condition was correlated with stress condition and

Table V. Estimates of variety (v_i) and variety heterosis (h_i) effect from analysis II of Gardner and Eberhart (1966) for different drought tolerance indices estimated from a diallel cross of six sunflower lines evaluated under controlled conditions.

Drought tolerance indices																				
YSI		YI		HM		STI		GMP		MP		TOL		SSI		YS		YP		Parents
h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	h_j	v_j	
0.03	0.002	0.17	-0.21	0.29	-0.37	0.10	-0.10	0.31	-0.41	0.32	-0.45	0.21	-0.39	-0.06	0.03	0.27	-0.32	0.36	-0.53	RH
-0.01	-0.01	-0.04	0.03	-0.08	0.08	-0.04	0.00	-0.10	0.09	-0.12	0.09	-0.11	0.15	0.01	0.03	-0.07	0.05	-0.15	0.13	A266
-0.05	0.03	-0.09	0.24	-0.13	0.45	0.00	0.17	-0.09	0.45	-0.03	0.44	0.12	0.41	0.04	0.01	-0.14	0.38	0.02	0.51	LR55
0.04	-0.11	-0.05	-0.07	-0.13	-0.04	-0.05	-0.02	-0.16	0.03	-0.19	0.12	-0.30	0.40	-0.05	0.12	-0.08	-0.10	-0.27	0.24	LR4
-0.04	0.14	-0.06	0.34**	-0.07	0.51*	0.01	0.18	-0.05	0.47*	-0.03	0.43	0.12	-0.02	0.05	-0.18	-0.09	0.52**	0.01	0.38	C104
0.02	-0.05	0.07	-0.34**	0.11	-0.63**	-0.02	-0.22*	0.09	-0.64**	0.05	-0.63*	-0.03	-0.55	0.01	-0.01	0.11	-0.53**	0.03	-0.73*	LR25
0.00		0.32**		0.62**		0.32**		0.69**		0.77**		0.84**		0.02		0.50**		0.97**		C100
																				AVG H

Y_B , yield of a given genotype in optimal (potential) conditions; Y_S , yield of a given genotype in stress conditions; SSI, Stress Susceptibility Index; TOL, Tolerance index; MP, Mean Productivity; GMP, Geometric Mean Productivity; STI, Stress Tolerance Index; HM, Harmonic Mean; YI, Yield Index; YSI, Yield Stability Index. * and **, significant at 0.05 and 0.01 probability level, respectively.

Table VI. S_{ij} effects of sunflower lines for different drought tolerance indices in single-cross hybrids.

YSI	YI	HM	STI	GMP	MP	TOL	SSI	YS	YP	Parents
-0.09	0.04	0.14	0.14	0.22	0.32	0.57	0.09	0.05	0.49	RHA266* LR55
-0.07	-0.03	-0.02	0.00	0.01	0.04	0.17	0.08	-0.04	0.09	RHA266*LR4
0.07	0.03	0.00	-0.04	-0.03	-0.04	-0.25	-0.09	0.05	-0.12	RHA266*C104
0.02	-0.26*	-0.49**	-0.28**	-0.53**	-0.57*	-0.60	-0.05	-0.40*	-0.70*	RHA266*LR25
0.06	0.22*	0.37*	0.18	0.32	0.26	0.11	-0.02	0.34*	0.25	RHA266* C100
0.10	0.03	-0.04	-0.09	-0.13	-0.22	-0.55	-0.11	0.04	-0.40	LR55*LR4
0.00	0.14	0.27	0.14	0.29	0.31	0.33	0.01	0.21	0.38	LR55*C104
-0.03	-0.08	-0.14	-0.08	-0.14	-0.13	-0.09	0.03	-0.12	-0.14	LR55*LR25
0.02	-0.13	-0.22	-0.12	-0.25	-0.28	-0.27	-0.02	-0.19	-0.34	LR55*C100
0.14	0.03	-0.04	-0.06	-0.17	-0.31	-0.66	-0.12	0.04	-0.52	LR4*C104
-0.08	0.03	0.12	0.12	0.19	0.27	0.50	0.08	0.04	0.42	LR4*LR25
-0.09	-0.05	-0.02	0.03	0.09	0.23	0.54	0.07	-0.08	0.41	LR4*C100
0.07	-0.08	-0.21	-0.14	-0.27	-0.35	-0.57	-0.09	-0.12	-0.50	C104*LR25
-0.13	-0.27	-0.43	-0.18	-0.37	-0.30	0.01	0.11	-0.42	-0.24	C104*C100
0.15	0.23*	0.30	0.10	0.20	0.09	-0.39	-0.15	0.36*	-0.08	LR25*C100

Y_p , yield of a given genotype in optimal (potential) conditions; Y_s , yield of a given genotype in stress conditions; SSI, Stress Susceptibility Index; TOL, Tolerance index; MP, Mean Productivity; GMP, Geometric Mean Productivity; STI, Stress Tolerance Index; HM, Harmonic Mean; YI, Yield Index; YSI, Yield Stability Index. * and **, significant at 0.05 and 0.01 probability level, respectively.

Table VII. Estimates of genetic variance (V_g), environmental variance (V_E) and heritability (h^2) for grain yield of sunflower in stressed and non-stressed environments as well as calculated different drought tolerance indices.

Genetic parameters	Y_p	Y_s	SSI	TOL	MP	GMP	STI	HM	YI	YSI
V_g	0.231	0.068	0.000	0.168	0.147	0.122	0.024	0.103	0.029	0.000
V_E	0.301	0.087	0.033	0.403	0.161	0.131	0.030	0.115	0.036	0.022
h^2	0.43	0.44	0.00	0.29	0.48	0.48	0.45	0.47	0.44	0.00

Table VIII. Phenotypic correlation between different drought tolerance indices and mean yield of sunflower inbred lines and their F_1 hybrids under optimal and stress conditions.

	Y_p	Y_s	SSI	TOL	MP	GMP	STI	HM	YI
Y_s	.673**								
SSI	.421**	-.253							
TOL	.958**	.433**	.612**						
MP	.982**	.802**	.275	.886**					
GMP	.921**	.905**	.120	.772**	.978**				
STI	.886**	.867**	.124	.744**	.939**	.963**			
HM	.823**	.969**	-.039	.628**	.915**	.979**	.945**		
YI	.674**	1.000**	-.253	.434**	.802**	.906**	.867**	.969**	
YSI	-.423**	.249	-1.000**	-.612**	-.278	-.123	-.127	.036	.249

Y_p , yield of a given genotype in optimal (potential) conditions; Y_s , yield of a given genotype in stress conditions; SSI, Stress Susceptibility Index; TOL, Tolerance index; MP, Mean Productivity; GMP, Geometric Mean Productivity; STI, Stress Tolerance Index; HM, Harmonic Mean; YI, Yield Index; YSI, Yield Stability Index. **, significant at 0.01 probability level.

secondly, MP, STI, HM and YI have high correlation with yield in non-stress (Y_p) and stress conditions (Y_s), demonstrating that these indices could be effectively used for screening drought resistant genotypes in sunflower breeding programmes. Positive correlations between Y_p and Y_s have been observed with other crop species, such as wheat, rice and sugar beet (Sadiq et al., 1994; Pantuwang et al., 2002; Ober et al., 2004) but the results are not

in agreement with those of Sio-Se Mardeh et al. (2006) who found that cultivars of wheat with low yield potential were more productive under stress conditions. Water-use efficiency (the slope of the relationship between biomass accumulation and water use) is constant across a range of water availability (Tanner & Sinclair, 1983). This may explain the positive relationship that we observed between yield in non-stress and stress conditions.

Low-yielding genotypes would use less water in general, and therefore should have more soil water available under drought. Alternatively, it could have been that genotypes with high yield potential were more aggressive in water extraction than genotypes with less vigour. Direct measurements of water use may indicate the prospects for exploiting any genotypic differences in water use efficiency. In other crops, there are examples of selection for increased water-use efficiency to improve yields in water-limited conditions (Boyer, 1992; Richards et al. 2002).

In conclusion, our results showed that SSI, YSI, TOL and MP are not useful indices to select for drought tolerant genotypes in sunflower breeding programmes because of negligible heritability of SSI and YSI. TOL was less heritable than other indices and usually not able to identify genotypes with both high yield and drought tolerance characteristics. Indices GMP, STI, HM and YI were moderately heritable and are usually able to select high-yielding genotypes in stress and non-stress environments. Complementary studies using molecular markers technology are being undertaken in our department that will help us to investigate the genetic properties of drought tolerance indices in more detail.

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