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Effective Selection Criteria for Assessing Plant Stress Tolerance

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ABSTRACT

Selection criteria for identifying genotypes with high stress tolerance and high yield potential were compared using a moderate stress (Stress Intensity, SI [1-(mean stress yield ($Y_{\bar{s}}$) / mean potential yield ($Y_{\bar{p}}$)], 0.23) and a severe stress (SI, 0.76) AVRDC mungbean yield data sets. Selection based on Tolerance (TOL), difference between potential yield (Y_p) and the yield in stress environment (Y_s) favored genotypes with low yield potential. Selection based on the Mean Productivity (MP), [MP = $(Y_p + Y_s) / 2$] favored the genotypes with high yield potential. The Stress Susceptibility Index (SSI), SSI = $[1 - (Y_s / Y_p)] / SI$, also favored stress-tolerant genotypes with low yield potential. These selection criteria failed to identify genotypes with both high yield and stress tolerance potentials. Thus a selection criterion, Stress Tolerance Index (STI), is proposed here which identifies genotypes with high yield and stress tolerance potentials. The STI considers the potential yield under nonstress environments, yield under stress environments, and the stress intensity. The STI is estimated as: $(Y_p \times Y_s)/(Y_{\bar{p}})^2$. The larger the value of STI for a genotype in a stress environment, the higher was its stress tolerance and yield potential. The interrelationships among these stress tolerance criteria are illustrated by the multivariate biplot display.

INTRODUCTION

Yield trials to evaluate elite breeding lines in a wide range of environments are important in plant breeding. The extent of genotype by environment interactions (GEI) and their limitations to progress in selection is recognized, and has been extensively documented (Allard and Bradshaw 1964; Hill 1975; Fernandez et al. 1989; Fernandez 1991a). Significant GEI results from a change in the magnitude of yield differences among genotypes in diverse environments or change in the relative ranking of genotypes (Fernandez 1991a). Several yield stability analyses have been reported for identifying environmentally sensitive and insensitive genotypes when they are evaluated over a series of diverse environments (Finlay and Wilkinson 1963; Eberhart and Russell 1966; Tai 1971; Shukla 1972; Fernandez et al. 1989).

Yield trials are also conducted in two contrasting environments; nonstress and stress. Plants are commonly considered under stress when they experience a relatively severe shortage of an essential constituent, or an excess of potentially toxic or damaging substances. The field stress environment is characterized primarily by low inputs, suboptimal levels of irrigation, nutrients, temperature, and plant protection measures (Blum 1988). Selection of genotypes that are adapted to both stress and nonstress environments was the main objective of these yield trials. This approach is more appropriate when the genotypes are usually grown under optimal growing conditions, but periodic biotic and abiotic stress conditions may occur.

Several selection criteria are proposed to select genotypes based on their performance in stress and nonstress environments (Fischer and Maurer 1978; Rosielle and Hamblin 1981). Rosielle and Hamblin (1981) defined stress tolerance (TOL) as the difference in yield between the stress (Y_s) and nonstress environment (Y_p), and mean productivity (MP) as the average yield of Y_s and Y_p. Fischer and Maurer (1978) proposed a stress susceptibility index (SSI), expressed by the following relationship: $SSI = [1 - (Y_s/Y_p)] / SI$. SI is the stress intensity and is estimated as $[1 - (\bar{Y}_s/\bar{Y}_p)]$, where $\bar{Y}_s$ and $\bar{Y}_p$ are the mean yields over all genotypes evaluated under stress and nonstress conditions.

Rosielle and Hamblin (1981) showed that the genetic correlation between Y_s and Y_p and the ratio of genetic variances between $\sigma^2_{Y_s}$ and $\sigma^2_{Y_p}$ determines the outcomes of genotypic selection based on MP and TOL. Under most yield trial conditions, the correlation between Y_s and Y_p is between 0 and 0.5 and the genetic variance ratio is < 1. Thus genotypic selection for yield under a nonstress environment would increase the average nonstress yield, and selecting genotypes under stress conditions would increase the mean stress yield. Selection based on stress tolerance was efficient in improving yield under stress conditions, whereas the selected genotypes performed poorly under nonstress environments.

Frey (1964) selected oat genotypes under stress and nonstress environments. The heritability estimates for yield were higher in the nonstress environment than in the stress environment. Selection based on the nonstress environment outperformed the selection from the stress environment, whereas genotypes selected based on their performance in the stress environment performed well only in the stress environment. Generally, the evaluation in the nonstress environment allowed a better expression of genotypic potential, with higher heritability estimate yield and its yield components than genotypes evaluated under the stress environments.

Selection for yield potential is more effective under nonstress environments because of greater genetic variance and heritability under these conditions (Roy and Murty 1970; Daday et al. 1973). Genotypic and GEI variances are usually higher when growing conditions are favorable since the nonstress environmental conditions allow the genotypes to express their genetic maximum potential. Heritabilities for yield were higher in an optimal environment and the rate of genetic advance through selection was usually greater (Blum 1988).

Genotypes can be categorized into four groups based on their performance in stress and nonstress environments: genotypes express uniform superiority in both stress and nonstress environments (Group A); genotypes perform favorably only in nonstress environments (Group B); genotypes yield relatively higher only in stress environments (Group C); and genotypes perform poorly in both stress and nonstress environments (Group D). The optimal selection criterion should distinguish Group A from the other three groups. However, the stress tolerance indicators, TOL, MP, and SSI, failed to distinguish Group A genotypes from the other three groups.

In this paper I define a new stress tolerance index, STI, which can be used to identify genotypes that produce high yields under both nonstress and stress environments. The interrelationships between STI and other reported stress tolerance attributes (MP, TOL, and SSI), and the differential yield responses of genotypes under two contrasting environments, are illustrated by the multivariate exploratory data analysis, biplot display.

THEORY

Definition of Stress Tolerance Attributes

Let Y_p = the potential yield of a given genotype in a nonstress environment; Y_s = the yield of a given genotype in a stress environment; $Y_{\bar{p}}$ = mean yield in nonstress environment; and $Y_{\bar{s}}$ = mean yield in stress environment. The following stress tolerance attributes are defined from these four yield measurements:

$$\text{Stress intensity (SI)} = 1 - \left(\frac{Y_{\bar{s}}}{Y_{\bar{p}}}\right) \qquad (1)$$

It ranges between 0 and 1 and the larger the value of SI, the more severe is the stress intensity.

$$\text{Mean productivity (MP)} = \frac{(Y_s + Y_p)}{2} \qquad (2)$$

This index favors higher yield potential and lower stress tolerance. Rosielle and Hamblin (1981) showed that under most yield trials, the correlations between MP and Y_p, and MP and Y_s would be positive. Thus, selections based on MP generally increase the average performance in both stress and nonstress environments. However, MP fails to distinguish the Group A and the Group B genotypes.

$$\text{Tolerance (TOL)} = (Y_p - Y_s) \qquad (3)$$

A larger value of TOL represents relatively more sensitivity to stress, thus a smaller value of TOL is favored. Selection based on TOL favors genotypes with low yield potential under nonstress conditions and high yield under stress conditions. Under most yield trials, the correlations between TOL and Y_p would be negative and correlation between TOL and Y_s would be positive. Thus, TOL fails to distinguish between Group C and Group A.

$$\text{Stress susceptibility index (SSI)} = \frac{1 - \left(\frac{Y_s}{Y_p}\right)}{\text{SI}} \qquad (4)$$

The smaller the value of SSI, the greater is the stress tolerance. Under most yield trials TOL and SSI are positively correlated. Selection based on SSI favors genotypes with low yield potential and high yield under stress conditions. Thus, SSI also fails to distinguish Group A from Group C.

$$\text{Geometric mean productivity (GMP)} = \sqrt{(Y_s \times Y_p)} \qquad (5)$$

MP is based on the arithmetic means and therefore it has an upward bias due to a relatively larger difference between Y_p and Y_s, whereas the geometric mean is less sensitive to large extreme values. Thus GMP is a better indicator than MP in separating Group A from other groups.

$$\text{Stress tolerance index (STI)} = \left(\frac{Y_p}{Y_{\bar{p}}}\right)\left(\frac{Y_s}{Y_{\bar{s}}}\right)\left(\frac{Y_{\bar{s}}}{Y_{\bar{p}}}\right) = \frac{(Y_p)(Y_s)}{(Y_{\bar{p}})^2} \qquad (6)$$

STI is estimated based on GMP and thus the rank correlation between STI and GMP is equal to 1. The higher the value of STI for a genotype, the higher its stress tolerance and yield potential. The stress intensity value is also incorporated in the estimation of STI. Thus STI is expected to distinguish Group A from Group B and Group C.

Biplot Display of a Two Way Table

Biplots (Gabriel 1971) are useful for description and summary of a multivariate data matrix in exploratory data analysis. The biplot is a graphical display of points representing the *n* rows (genotype) and *m* columns (attributes) of a two-way data matrix. A two-dimensional approximation to a two-way table (rows × column) can be obtained from the first two-principal components. The biplot will display most of the variation of the two-way data matrix. The relative angles between the vector lines will represent the correlations among the stress-tolerant attributes. The biplot permits the detection of clusters (groups of similar genotypes), outliers (unusual genotypes), and strongly correlated and poorly correlated variables (Fernandez 1991b). Thus, biplots are appealing because they provide an opportunity to detect the pattern from the noise in a complex data structure. The feasibility of using biplot techniques to analyze genotype × environment interactions are discussed elsewhere (Kempton 1984; Fernandez 1991b).

MATERIALS AND METHODS

Two data sets from the yield trials of advanced mungbean (*Vigna radiata* (L.) Wilczek) breeding lines conducted at the Asian Vegetable Research and Development Center (AVRDC), Shanhua, Taiwan, during the summer and fall seasons in 1984 were used in this study. At AVRDC, advanced breeding lines (F_7 and later generations) are evaluated in separate yield trials for at least 5 consecutive years in three diverse seasons (spring, summer, and fall) per year. Photoperiod, temperature, and distribution of mungbean pests and diseases varied during these seasons (Fernandez and Shanmugasundaram 1988; Fernandez and Chen 1989). The summer season provides the ideal environment and the fall season is unfavorable for mungbean production at AVRDC. Two elite yield trials with 21 mungbean genotypes with optimum (nonstress) and minimum (stress) input-management conditions (AVRDC 1987) were conducted in the summer and fall of 1984. A split plot arrangement in a random complete block design with three replications was used. The average yields of mungbean lines evaluated in two seasons under stress and nonstress conditions are presented in Tables 1 and 2. The SI in the summer and the fall seasons were 0.23 and 0.76, respectively. The data were analyzed and the stress-tolerant estimates were computed using PC-SAS (SAS 1988a).

The biplot display of principal component analysis (Gabriel 1971) was used to identify stress-tolerant and high-yielding genotypes and to study the interrelationship between the stress-tolerant attributes. The PC-SAS procedures, GLM, PRINCOMP, GPLOT (SAS 1988a) and PRINQUAL (SAS 1988b) were used in developing the SAS codes to display the biplots.

RESULTS AND DISCUSSION

The stress tolerance attributes for the mungbean genotypes estimated from Y_s and Y_p under the moderate stress and the severe stress are given in Tables 1 and 2, respectively. The correlation coefficients between Y_s and Y_p ($\gamma_{Ys,Yp}$) were 0.46 for the moderate stress and 0.22 for severe stress conditions. Thus, the degree of linear association between Y_s and Y_p decreases with the increase in SI. The ratio of genetic variances between the σ^2_{Ys} and σ^2_{Yp} (K) was 0.45 for the moderate stress and 0.68 for the severe stress conditions. The increase in the genetic variance ratio under severe stress was due to a decrease in σ^2_{Yp} from 40401 (summer season) (Table 1) to 8281 (fall season) (Table 2). Under both stress conditions, the mean GMP was smaller than the mean MP.

Table 1. Estimates of stress tolerance attributes from the potential yield and the stress yield data for mungbean genotypes evaluated under moderate stress (SI = 0.23) in the summer season.

Line	Y_p	Y_s	MP	GMP	TOL	SSI	STI
VC1647B	1269	1157	1213	1212	112	0.38	0.55
VC1560D	1371	985	1178	1162	386	1.22	0.51
VC2719A	1414	1179	1296	1291	235	0.72	0.63
VC2802A	1426	1301	1363	1362	125	0.38	0.69
V3726	1437	1043	1240	1224	394	1.19	0.57
VC2763A	1442	1314	1378	1377	128	0.38	0.71
VC2720A	1519	1111	1315	1299	408	1.16	0.64
VC2771A	1534	1431	1482	1482	103	0.29	0.83
VC2572A	1550	1239	1394	1386	311	0.87	0.72
VC3061A	1614	1314	1464	1456	300	0.80	0.79
VC1973A	1619	1182	1400	1383	437	1.16	0.72
VC2755A	1620	1292	1456	1447	328	0.88	0.79
VC2764C	1659	1199	1429	1410	460	1.19	0.75
VC1482E	1744	1360	1552	1540	384	0.95	0.89
VC3012A	1751	1387	1569	1558	364	0.89	0.92
VC2764B	1785	1320	1552	1535	465	1.13	0.89
VC2754A	1838	1435	1636	1624	403	0.95	0.99
VC2762A	1850	1063	1456	1402	787	1.84	0.74
V3476	1854	1487	1670	1660	367	0.85	1.04
VC2768A	1875	1185	1530	1491	690	1.60	0.84
VC2307A	2034	1304	1669	1629	730	1.55	0.99
Mean	1629	1252	1440	1425	377	0.97	0.77
S	201	135	143	139	189	0.41	0.15

Y_p = Potential yield; Y_s = Yield under stress; MP= Mean Productivity; GMP =Geometric Mean Productivity; TOL= Tolerance; SSI = Stress Susceptibility Index; STI = Stress Tolerance Index.

Table 2. Estimates of stress tolerance attributes from potential yield and stress yield data for mungbean genotypes evaluated under severe stress (SI = 0.76) in the fall season.

Line	Y_p	Y_s	MP	GMP	TOL	SSI	STI
VC2307A	1226	401	813	701	825	0.88	0.26
VC1560D	1270	274	772	590	996	1.02	0.18
V3726	1287	293	790	614	994	1.00	0.19
VC2755A	1287	184	735	486	1103	1.12	0.13
VC2572A	1288	180	734	481	1108	1.12	0.12
VC2763A	1299	292	795	615	1007	1.01	0.20
VC3061A	1307	422	864	743	885	0.88	0.29
VC2754A	1351	391	871	727	960	0.93	0.28
VC2762A	1351	284	817	619	1067	1.03	0.20
VC1973A	1364	361	862	702	1003	0.96	0.26
VC2720A	1366	361	863	702	1005	0.96	0.26
VC2764B	1373	208	790	534	1165	1.11	0.15
VC2802A	1386	416	901	759	970	0.91	0.30
VC2719A	1388	433	910	775	955	0.89	0.32
VC1647B	1403	325	864	675	1078	1.00	0.24
VC2764C	1406	258	832	602	1148	1.06	0.19
VC2771A	1469	344	906	711	1125	1.00	0.27
VC2768A	1485	317	901	686	1168	1.03	0.25
VC1482E	1490	323	906	694	1167	1.02	0.25
VC3012A	1529	304	916	682	1225	1.05	0.25
V3476	1571	397	984	790	1174	0.98	0.33
Mean	1376	322	849	661	1054	1.00	0.23
S	91	75	65	88	105	0.07	0.05

Y_p = Potential yield; Y_s = Yield under stress; MP= Mean Productivity; GMP =Geometric Mean Productivity; TOL= Tolerance; SSI = Stress Susceptibility Index; STI = Stress Tolerance Index.

The correlations between Y_p and (MP, TOL, SSI, and STI) and the correlations between Y_s and (MP, TOL, SSI, and STI) under both stress conditions are illustrated by scatter plots in Fig. 1-4. The scatter plots indicated that MP and STI were better predictors of mean Y_p and mean Y_s than TOL and SSI under moderate stress (Fig. 1-2). Under the severe stress, MP and TOL were better predictors of the mean Y_p than SSI and ST; whereas SSI and STI were better predictors of mean Y_s than MP and TOL (Fig. 3-4). Overall, STI was a better predictor of mean Y_s and mean Y_p under both stress conditions. The observed correlation coefficients between $\gamma_{Yp.MP}$, $\gamma_{Yp.TOL}$, $\gamma_{Ys.MP}$, and $\gamma_{Ys.TOL}$ were in close agreement with the theoretical correlation coefficients reported by Rosielle and Hamblin (1981).

The correlation coefficients and the scatter plots are useful in finding out the degree of overall linear association between any two attributes. For example, selecting genotypes based on SSI will increase the overall mean yield of the stressed environment. However, the effectiveness of genetic gain based on the observed correlation may not reflect the genetic gain of individual genotypes. Effective selection based on individual genotypes is considered more important in pureline selection of self-pollinated crops. Thus, a better approach than a correlation analysis is needed to identify the Group A genotypes.

Three-D plots among Y_s (x-axis), Y_p (y-axis) and STI (z-axis) are presented (Fig. 5) to show the interrelationships among these three variables, to separate the Group A genotypes from the other groups (Groups B,C,D), and to illustrate the advantage of STI as a selection criterion for identifying high-yielding and stress-tolerant genotypes. The X-Y plane is divided into four segments by drawing intersecting lines through Y_s and Y_p and the four groups are marked as Group A to Group D (Fig. 5). In moderate stress, most of the Group A genotypes showed high STI (V3476, VC2754A, VC2307A, VC3012A, VC1482E, VC2764B) (Fig. 5a). Two other genotypes (VC2771A, VC2768A) also expressed moderate STI values (0.68-0.88). However, VC2771A was more suitable for stress conditions (Group C) and VC2768A was more suitable for nonstressed environments (Group B) (Fig. 5a). Conversely, selection based on SSI favored VC2771A, VC2763A, VC2802A, and VC1647B belonging to the other groups (Groups A, B, D). Furthermore, SSI failed to identify the high-yielding and stress-tolerant genotypes, such as V3476, VC2754A, and VC3012A, in the moderate stress trial.

In severe stress conditions, most of the Group A genotypes (V3476, VC2719A, VC2802A, VC2771A, and VC1482E) also had high STI values. However, Group C genotypes (VC3061A, VC2307A, and VC2754A) also showed high STI values. Although STI was favoring genotypes with high yield potential and stress tolerance under severe conditions, more weight was given to stress tolerance. Under severe stress, SSI also identified most of the Group A genotypes. This was confirmed by a large absolute correlation (-0.84) between SSI and STI under severe stress conditions.

Thus, the 3-D plot (Y_s-Y_p-STI) separated the Group A genotypes from the other groups more effectively and was useful in studying the relationship between STI and Y_s and Y_p. In a 3-D plot, only the relationships between any three variables can be studied at once. To investigate the relationships between more than three variables, a multivariate display such as a biplot can be used.

Biplot Display of 21 Genotypes × 6 Stress Tolerance Attributes

For a two-way table consisting of genotypes and the stress-tolerant attributes, the relationship between the genotypes (row points) and stress tolerance attributes (vector coordinates) can be plotted in the same graph (the biplot). The biplot provides a useful tool for data analysis and allows the visual appraisal of the structure of a large two-way data matrix. In the moderate stress, the first dimension explained about 69% of the variation in the data matrix (21 × 6) and had a high correlation among Y_p, MP, and STI. Thus, the first dimension can be named as the yield potential component which separated the high yielders from the low yielders. The angles and the directions between the attribute vectors illustrate the strength and the direction of correlation between any two attributes. Significant positive correlations between $\gamma_{STI.MP}$, $\gamma_{Yp.STI}$, and $\gamma_{Ys.STI}$ were revealed in the biplot (Fig. 6a). The second dimension

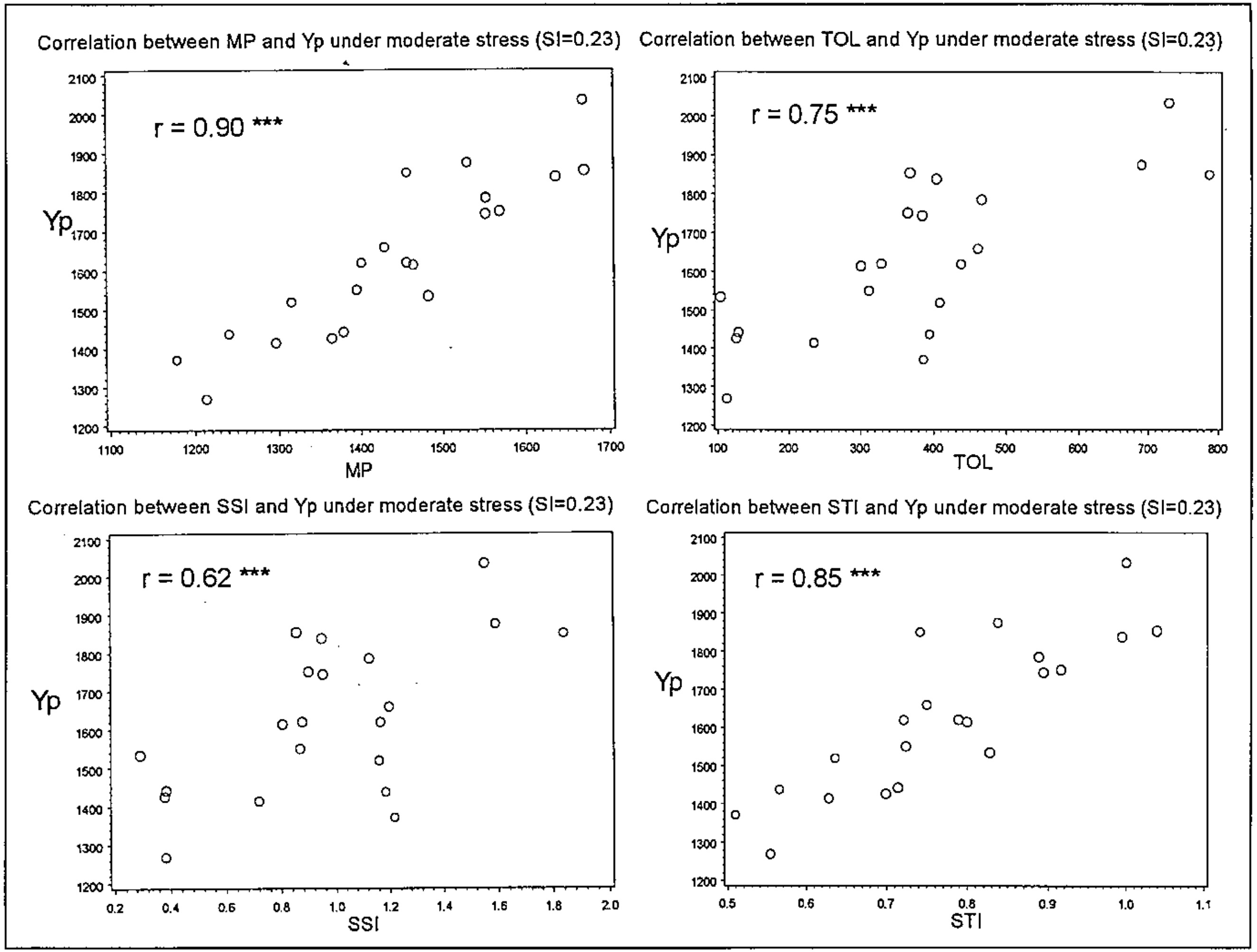


Fig. 1. **Correlation between potential yield (Y_p) and other stress tolerance attributes under moderate stress (SI=0.23).**

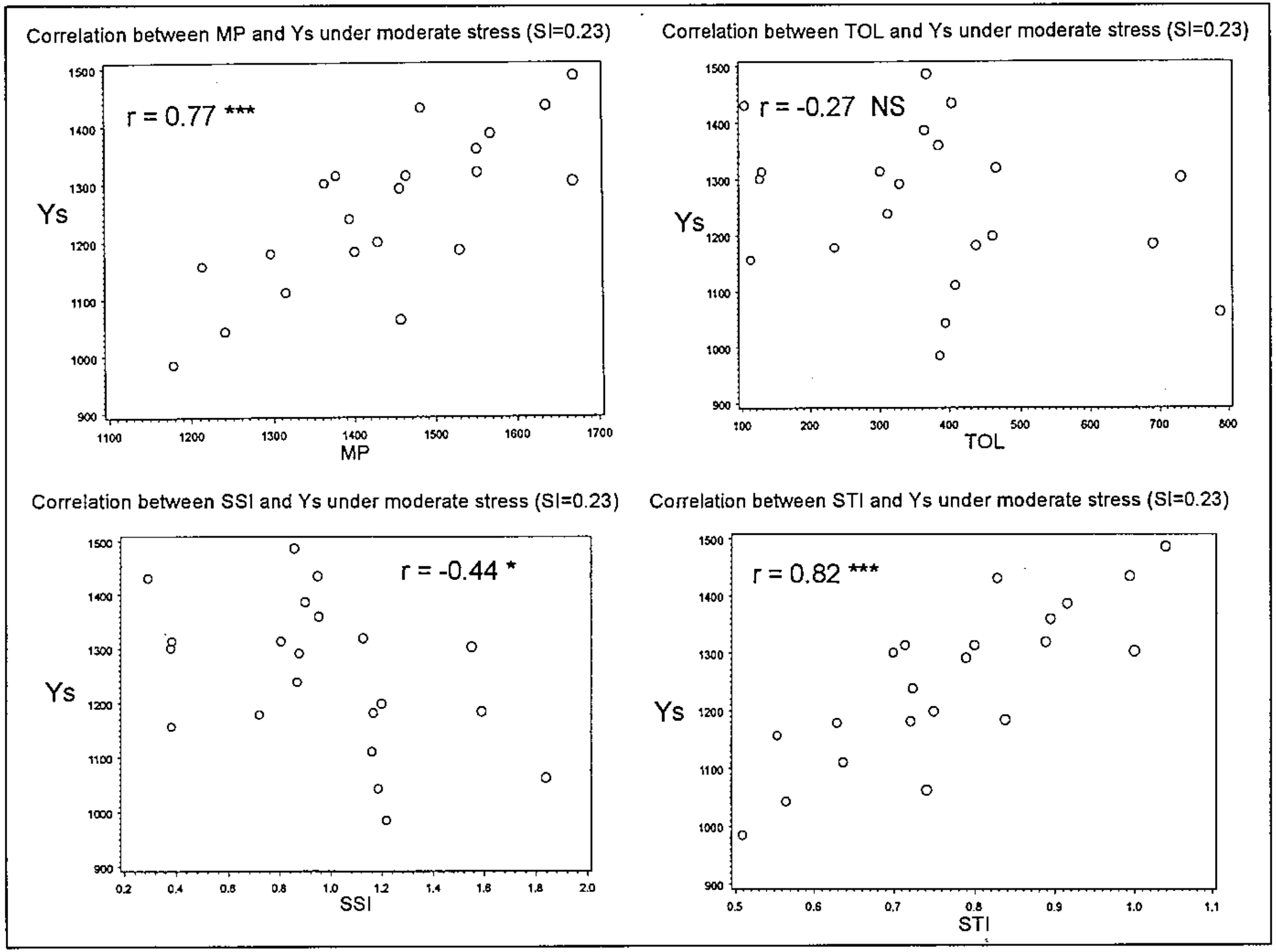


Fig. 2. Correlation between stress yield (Y_s) and other stress tolerance attributes under moderate stress (SI=0.23).

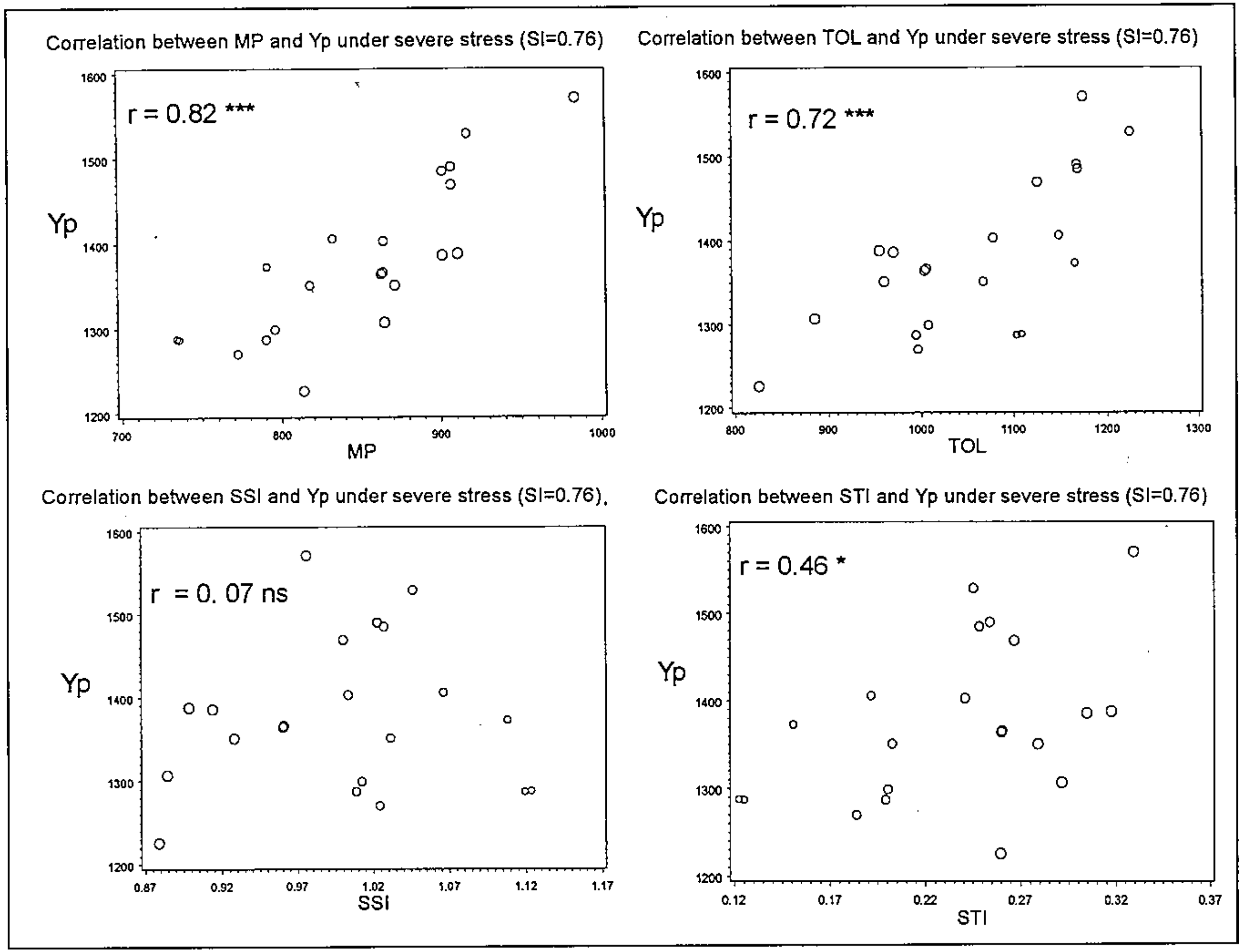


Fig. 3. Correlation between potential yield (Y_p) and other stress tolerance attributes under severe stress (SI=0.76).

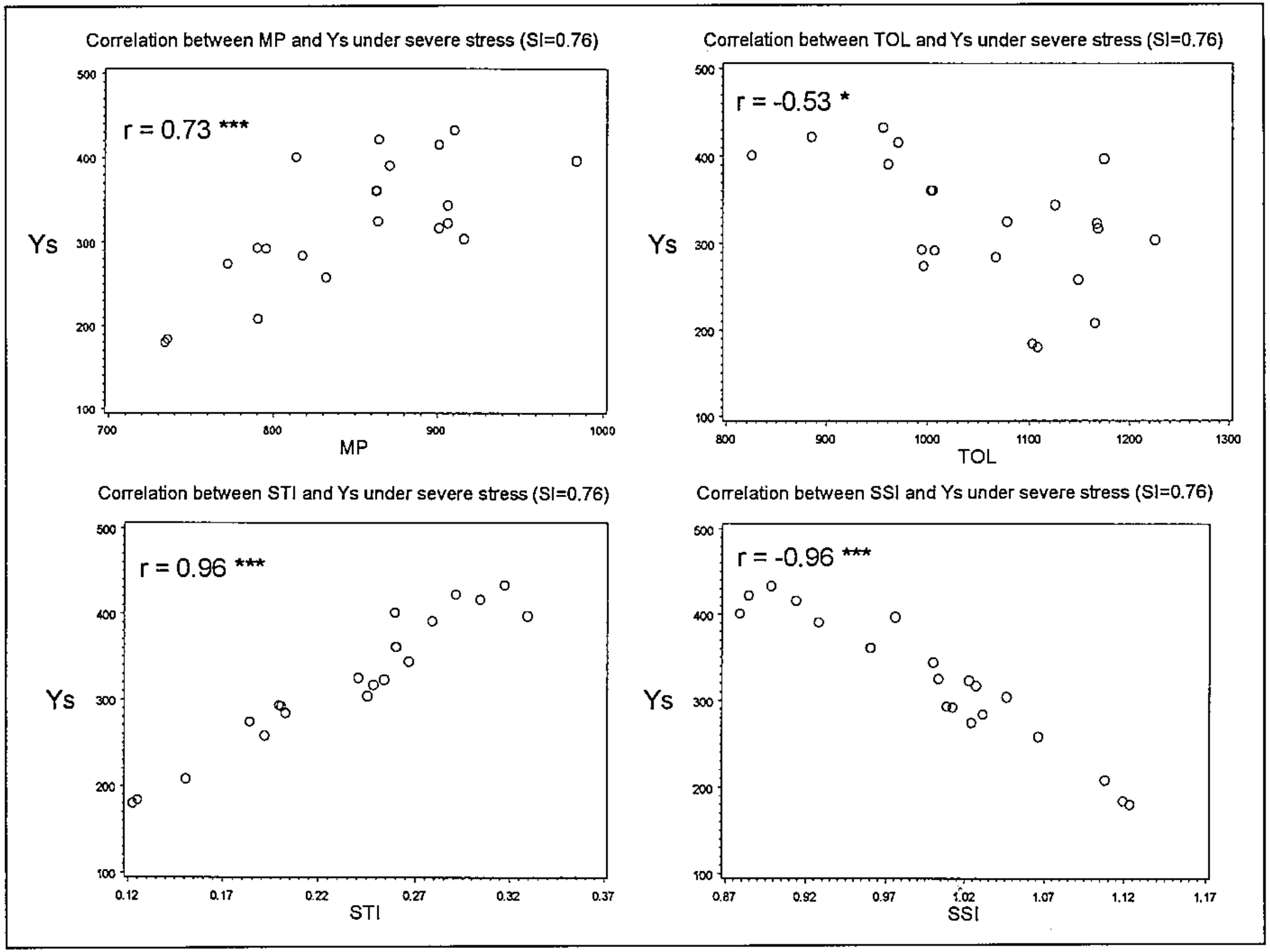


Fig. 4. Correlation between stress yield (Y_s) and other stress tolerance attributes under severe stress (SI=0.76).

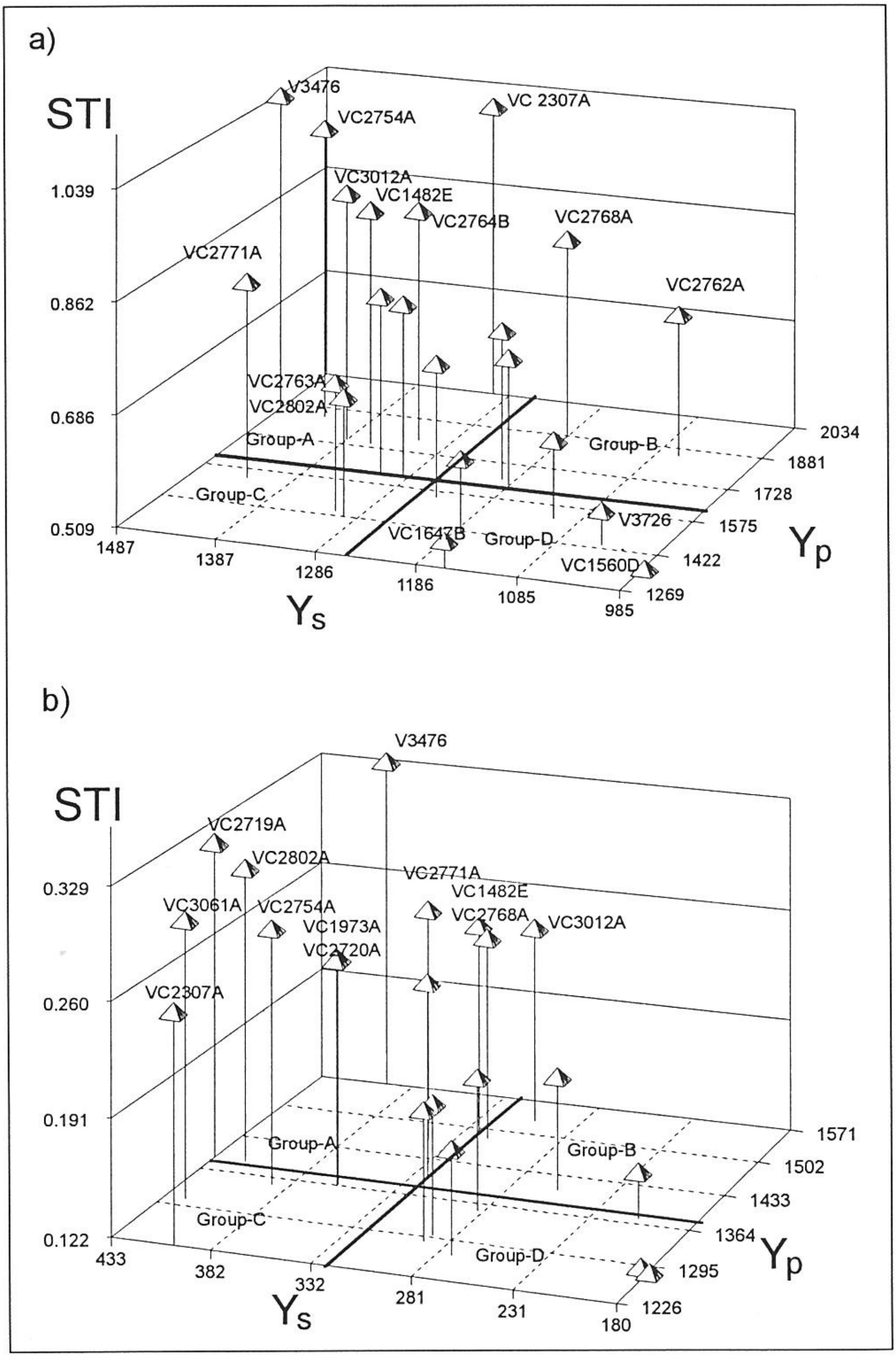
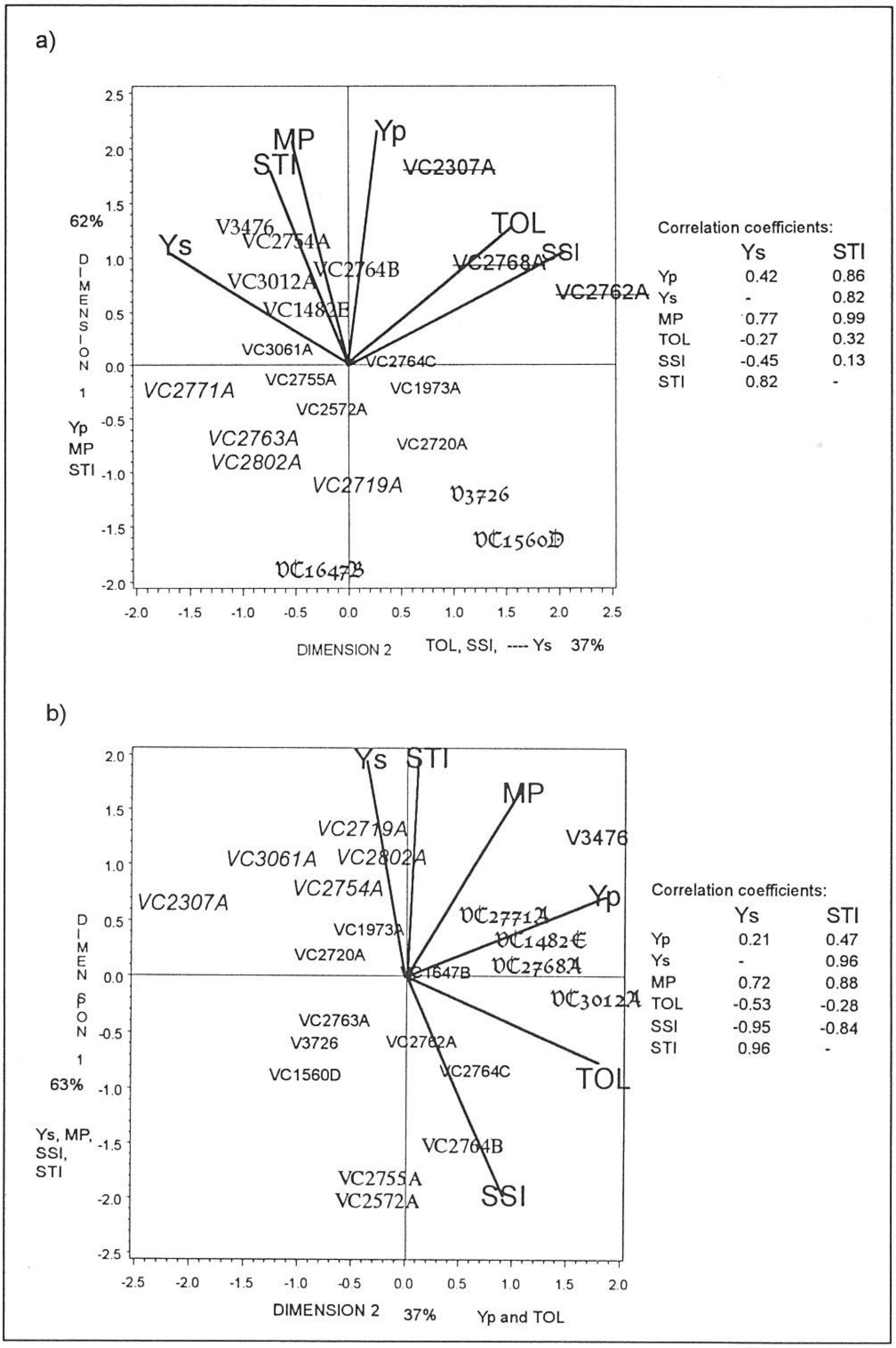


Fig. 5. The 3-D plots among STI, Y_p, and Y_s under moderate (a, SI=0.23) and severe stress (b, SI=0.76) conditions.



a) Correlation coefficients:

	Ys	STI
Yp	0.42	0.86
Ys	-	0.82
MP	0.77	0.99
TOL	-0.27	0.32
SSI	-0.45	0.13
STI	0.82	-

b) Correlation coefficients:

	Ys	STI
Yp	0.21	0.47
Ys	-	0.96
MP	0.72	0.88
TOL	-0.53	-0.28
SSI	-0.95	-0.84
STI	0.96	-

Fig. 6. The biplot display of stress-tolerant attributes and mungbean genotype yield levels under moderate (a, SI=0.23) and severe stress (b, SI=0.76) conditions.

explained about 30% of the total variability and had positive correlations with TOL and SSI and negative correlation with Y_s. Thus, the second component can be named a stress-tolerant dimension and it separates the stress-tolerant genotypes from stress-susceptible genotypes. In relation to these two components, the genotypes fall into distinct clusters that correspond to their yield potentials and stress tolerance. Stress-tolerant attributes Y_s, STI, MP, and Y_p favored genotypes V3476, VC2754A, VC2764B, VC3012A, and VC1482E. VC2771A, VC2763A, VC2802A, and VC2719A were favored by SSI and TOL.

In severe stress, the first dimension explained about 63% of the variation in the data matrix (21 × 6) and had a high correlation among Y_s, MP, SSI, and STI. Thus, the first dimension can be named as a mean productivity – stress tolerance component which separated the high average yielders and stress-tolerant genotypes from the low average yielders and stress-susceptible genotypes. Significant positive correlations between $\gamma_{STI.MP}$, and $\gamma_{Y_s.STI}$ and significant negative correlations between $\gamma_{Y_s.SS}$ were observed (Fig. 6b). The second dimension explained about 36% of the total variability and had positive correlations with TOL and Y_p. Thus, the second component can be named a yield potential dimension and it separates the high-yielding genotypes in the nonstress environment from low-yielding genotypes. In relation to the two components, the genotypes fall into distinct clusters which correspond to their average yield potentials and stress tolerance. The stress-tolerant attributes Y_s, STI, SSI and MP favored genotypes, VC2719A, VC2754A, VC2802A, VC3061A, and VC2307A. VC2771A, VC1482E, VC3012A and VC2768A were favored by Y_p and susceptible to stress.

Thus the biplot technique provides a graphical representation of interaction patterns that allows the response of each genotype in each stress-tolerant attribute predicted by the principal component model to be directly identified. Because of its geometrical properties, the expected response of a genotype and its stress-tolerant attributes may be derived from visual inspection of its relative position on the biplot.

It can be concluded that STI is an overall index of yield potential and stress tolerance. The 3-D plot between Y_s-Y_p-STI can be used effectively to distinguish the high-yielding genotypes both in the nonstressed and stressed environments. The multivariate biplot aids the plant breeder in investigating interrelationships between many correlated attributes and to select desirable genotypes.

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