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Combining ability and heterosis for aluminium stress tolerance of soybean roots and shoots grown in acid sand culture

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A six parent F_2 diallel of soybeans was evaluated in potted acid sand culture with the objective of estimating combining ability and heterosis for aluminium stress tolerance. Highly significant differences were observed among the genotypes, crosses (F_2/R), Parents, F_2, Reciprocals (R) and Parents Vs (F_2/R) for the root dry weight, shoot dry weight and relative root surface area. Both general combining ability (GCA) and specific combining ability (SCA) mean squares were highly significant for the three traits, except the root dry weight, where the SCA was not significant. The result also showed the presence of both additive and dominance gene action and the preponderance of the former compared to the later, indicating the possibility of selection of pure lines from the genotypes studied. Selection from TGX 1896-3F and TGX 1844-18E and crosses involving these two genotypes on acid soil would enhance a rapid progress in the breeding of aluminium tolerant genotypes of soybeans.

Key words: *Glycine max,* diallel analysis, general combining ability, specific combining ability, additive effect, dominance effect.

INTRODUCTION

Soybean (*Glycine max* L. Merr.) is a very important oil seed crop in both human and livestock nutrition and in the industry. It therefore serves as a cheap viable alternative to animal sources of nutrients for man and livestock in developing countries of the world such as Nigeria. Nigeria's total production output of soybean had been estimated to be 50% of the country's domestic demand (FDA, 1991), despite its reputation as the largest soybean-producing country on the African continent (FAO, 2006). According to FAO (2005), the average World production of soybean for 1999 to 2003 was 177million tons/year, of which Nigeria accounted for 439,000 tons/year representing only 0.25% of the World output. This level of output of soybean grains in Nigeria can be attributed to the limited land area cultivated to the crop by soybean farmers in the country. There is therefore the need to extend the commercial production of soybean beyond its traditional areas of production in the Guinea Savanna ecology of Nigeria to the more humid rain forest and the drier Sudan Savanna ecologies of the country.

The IITA has a long history of working with soybean germplasm as part of the institute's global mandate to improve the productivity of soybean in Africa (Dashiell et al., 1991; Tefera et al., 2009) and has released many early, medium and late maturing tropically adapted varieties of the crop. While the early maturing varieties could be adapted to the Sudan Savanna, the production of soybean in the Rain Forest is limited due to the predominance of acid soils in the South – East and South – South regions of the ecology with its attendant consequence of low grain yield of <1.0 t/ha. Recent

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research efforts have led to the identification of acid/aluminium tolerant genotypes of soybean (Ojo, 2010) which could be further explored in genetic studies.

Genetic studies in generations derived from crosses between tolerant and sensitive varieties using both conventional (Bianchi-Hall et al., 1998; Spehar, 1999) and molecular techniques (Bianch-Hall et al., 2000) indicate that aluminium stress tolerance is a heritable trait and that selections could be made from crosses. The diallel analytical technique has been very useful in the estimation of hybrid vigour and gene action, and hence the identification of appropriate heterotic combinations in hybrids (Kim, 1986). The diallel supplies important information on general and specific combining abilities, genetic variances, heritability, and maternal effects among others (Vacaro et al., 2002). Such information serves as a useful guide in the determination of the overall plant breeding objective (Ojo et al., 2007). The dearth of information on diallel analysis and in particular, combining ability for aluminium stress tolerance in tropically adapted genotypes of soybean necessitated this research work. The objective of this research work was to estimate combining ability and heterosis for aluminium stress tolerance of soybean roots and shoots grown in acid sand culture.

MATERIALS AND METHODS

This experiment was carried out at the College of Agronomy Field Experiment Station of the University of Agriculture, Makurdi, Nigeria (Lat. 7º44'N, Long. 8º35'E). On the basis of the results obtained from screening experiments carried out in hydroponics, sand culture and on an acid soil between 2002 and 2004 (Ojo, 2010), six parents (TGX 1873-16E, TGX 1878-7E, TGX 1890-7F, TGX 1891-3F, TGX 1896-3F and TGX 1844-18E) were selected and crossed in all possible combinations to obtain 15 F_1s and their 15 reciprocals. The TGX 1896-3F and TGX 1844-18E genotypes were selected because they were rated as aluminium tolerant in hydroponics and sand culture, and had grain yield of >1.8 t/ha; TGX 1873-16E and TGX 1878-7E (moderately tolerant genotypes) were selected because they were outstanding in only the hydroponics and sand culture; TGX 1890-7F was selected because it had an average performance in only one culture media (the field). It was, however, rated sensitive in both hydroponics and sand culture because of its poor growth and dry matter accumulation in both media; TGX 1891-3F was selected because its performance was below average in all the three culture media. It was rated sensitive to aluminium stress tolerance in both hydroponics and sand culture and had grain yield of less 1.0 t/ha from the field.

The planting, crossing and harvesting for 2005 evaluation took place between January and May 2004. The F_1s and reciprocals were planted in the 3rd week of July 2004 and straight F_2 and reciprocal F_2 seeds were harvested and dried within the second and third weeks of November 2004. Seeds were threshed, winnowed, cleaned, packed into envelopes and labeled in the first and second weeks of December 2004 for the first year of evaluation (2005). This sequence was similarly repeated in 2005, in preparation of seeds for the 2006 evaluation. A total of 36 genotypes comprising of six parents, 15 straight F_2s and 15 reciprocal F_2s were evaluated in potted acid sand culture in 2005 and 2006. The experimental design was a randomized complete block design with 36 treatments (36 genotypes) and three blocks, giving a total of 108 pots in each year.

The experimental procedure was according to Villagarcia et al. (2001), with some modification on the time of imposition of aluminium treatment and duration of the experiment. Polyethylene pots measuring 20 cm in diameter were each filled with 10 kg builders' grade sharp sand and flushed with deionized water adjusted to pH 4.05 ± 0.05 with sulphuric acid. The sand was flushed again with deionized water adjusted to pH 7.0 to remove the acidity and allowed to drain for 24 h. Thereafter, the sand was heavily watered with deionized water and six seeds were planted in each pot and lightly covered with the sharp sand. The pots were then watered daily with deionized water (pH 7.0) until five days after planting (5 DAP) when emerged seedlings were thinned to three/pot. The watering with deionized water (pH 7.0) continued till 7 DAP. Thereafter, nutrient solution (adjusted to pH 4.05 ± 0.05) containing 450 µM Al^{3+} activity was used to water each of the pots for the next eighteen days, with each pot receiving one litre of solution per day. To avoid a build-up of nutrients, each pot was flushed daily with deionised water (adjusted to pH 4.05 ± 0.05) and a time lag of two hours was allowed for the pots to drain prior to watering with the nutrient solution containing 450 µM Al^{3+} aluminium activity. Nutrient stock solution concentration was developed following the procedures of Howell and Bernard (1961) and Villagarcia et al. (2001). The Experiment was conducted during the dry season of January to March, 2005 and repeated within the same period in 2006. Plants were harvested at 25 DAP and data were taken on root dry weight (RDW), shoot dry weight (SDW) and relative root surface area (RRSA). Plants were separated into root and shoot and data on RRSA was taken according to Carley and Watson (1966) prior to oven drying. Thereafter, root and shoot were separately dried to a constant weight at 70°C and their weights taken as RDW and SDW respectively.

The data was subjected to analysis of variance by the General Linear Model (GLM) and the Analysis of variance (ANOVA) procedures of SAS (1990). The form of the combining ability analysis of variance employed was Model 2, Method 1 of Griffing (1956) as presented by Singh (1973):

$$X_{ijkl} = \mu + g_i + g_j + s_{ij} + s_{ji} + l_k + (gl)_{ik} + (gl)_{jk} + (sl)_{ijk} + 1/bc\varepsilon\varepsilon e_{ijkmr}$$

where: X_{ijkl} = Mean of ixj genotype from kth block in l years; g_i = General combining ability (GCA) effect of the ith parent; g_j = General combining ability (GCA) effect of jth parent; s_{ij} = Specific combining ability (SCA) effect of i × jth cross; l_k = Years effect ,$(gl)_{ik}$ = Interaction of GCA effect of ith parent with; kth year ,$(gl)_{jk}$ = Interaction of GCA effect of jth parent with kth year s_{ji} = Reciprocal effect of j × ith cross; $(sl)_{ijk}$ = SCA effect of i × jth cross with kth year; $1/bc\varepsilon\varepsilon e_{ijkmr}$ = Mean error effect.

GCA and SCA effects across years were estimated, respectively (Singh, 1973), as follows:

$$\hat{g}_i = (nx_{i}.. - 2X...)/n\,(n-2)\ell$$

$$\hat{S}_{ij} = (X_{ij}./\ell) - [(X_{i}.. + X_{j}..)/(n-2)\ell] + 2X/(n-1)(n-2)\ell$$

where: n = Number of parents; $X_{i}..$, $X_{j}..$ = Array totals; ℓ = Number of years.

High parent heterosis (%) was estimated as follows:

$$h = \frac{F_2 - HP}{HP} \times 100$$

Where: h = % High parent heterosis; F_2 = F_2 generation; HP = High Parent.

The components of variance (Griffing, 1956) were estimated as follows:

Table 1. Mean squares for root and shoot characteristics analysis of variance of a six parent F_2 diallel of soybeans evaluated in an acid sand culture (450 µM Al^{3+}).

Source of variation	Df	Root dry weight (g)	Shoot dry weight (g)	Relative root surface area (g)
Years	1	0.0102	0.0038	0.0697
Reps / Years	4	0.0398	0.0063	0.2908
Genotypes(G)	35	0.1843**	0.5894**	15.1239**
Parents (P)	5	0.1421**	0.4018**	9.7292**
Crosses(F_2/Reciprocals)	29	0.1728**	0.5806**	14.4037**
F_2	14	0.1790**	0.6014**	14.9169**
Reciprocals (R)	14	0.1789**	0.6012**	14.9193**
F_2 Vs R	1	0.0038	0.0002	0.0015
P Vs (F_2/R)	1	0.7309**	1.7840**	62.9838**
G x Years(Y)	35	0.0527	0.0737	1.0803
P × Y	5	0.0406	0.0457	0.5896
(F_2/R) x Y	29	0.0551	0.0806	1.2003
F_2 × Y	14	0.0570	0.0833	1.2431
R x Y	14	0.0568	0.0833	1.2433
(F_2 Vs R) × Y	1	0.0038	0.0063	0.0001
P Vs (F_2/R) x Y	1	0.0434	0.0120	0.0526
Pooled Error	140	0.0405	0.0651	1.1218

*, **: Significant at P<0.05 and P<0.01, respectively.

$\delta^2_A = 2\delta^2_g$; $\delta^2_D = \delta^2_s$

Where: δ^2_A = Additive genetic variance, δ^2_D = Non-additive (dominance) genetic variance, δ^2_g = GCA variance, δ^2_s = SCA variance

RESULTS

Analysis of variance for root and shoot characteristics

No significant differences were observed in Years and Rep/years for root dry weight, shoot dry weight and relative root surface area (Table 1). Highly significant differences were, however, observed among the Genotypes, Crosses (F_2/R), Parents, F_2, Reciprocals (R) and Parents Vs. (F_2/R) for these same variables. No significant difference in F_2 Vs Reciprocals was observed for any of the three traits. The Genotype × Years was not significant for the root dry weight, shoot dry weight and the relative root surface area. All the components of the Genotypes × Years interaction, namely, Parents × Years, Crosses × Years and (Parents Vs Crosses) × Years interactions were not significant for all the three traits studied. Similarly, no significant interaction effects were observed in all the components of Crosses × Years interaction (F_2 × Years, Reciprocals × Years and (F_2/R) × Years).

Combining ability analysis

Highly significant GCA mean squares was observed for root dry weight, while the SCA mean squares was negative and not significant (Table 2). Both the GCA and SCA were, however, highly significant for shoot dry weight and the relative root surface area. No significant reciprocal effect was observed for any of the three traits studied.

Parent 5 had the highest (positive) GCA effects for the three traits, while Parent 6 had the next highest (positive) GCA effect for all the traits (Table 3). The remaining four parents had negative GCA effects for all the three traits studied. The least GCA effect was observed in Parent 4 for all the traits.

Mean separation of SCA effects was not carried out for the root dry weight due to non-significance of SCA mean squares. Both negative and positive SCA effects were observed for the shoot dry weight (Table 3). SCA effects for the shoot dry weight ranged from -0.0733 for hybrid 3×4 to 0.1684 for hybrid 5×6. Positive SCA effects were observed for the shoot dry weight in only crosses involving Parent 5 or 6 or both, while all other crosses produced negative SCA effects. The trend in SCA effects for the relative root surface area is similar to that observed for the shoot dry weight. The SCA effects for the relative root surface area ranged from a negative value of -1.0798 for hybrid 3×4 to a positive value of 0.8405 for hybrid 5×6. Positive SCA effects were observed for the relative root surface area in only crosses involving Parents 5 or 6 or both, while all other crosses produced negative SCA effects.

Absolute root dry weight values ranged from 0.2234 g $plant^{-1}$ (Parent 4) to 0.6150 g $plant^{-1}$ (Parent 5) for the Parents and from 0.2925 g $plant^{-1}$ (hybrid 1×4) to 0.7626

Table 2. Mean squares from a combining ability analysis for root and shoot characteristics of an F$_2$ diallel of soybeans grown in acidified aluminium (450 µM Al^{3+}) sand culture.

Source of variation	df	Root dry weight	Shoot dry weight	Relative root surface area
GCA	5	0.1661**	0.5524**	13.6200**
SCA	14	-0.3383	0.2588**	13.6450**
Reciprocal	14	3.9×10^{-8}	8.9×10^{-9}	7.7×10^{-8}
Error	140	0.0074	0.0099	0.1664

*, **: Significant at $P<0.05$ and $P<0.01$, respectively.

Table 3. GCA effects, SCA effects and character means for root and shoot characteristics of an F$_2$ diallel of soybeans grown in acidified aluminium (450 µM Al^{3+}) sand culture.

S/N	Root dry weight	Shoot dry weight	Relative root surface area	Root dry weight(g)	Shoot dry weight(g)	Relative root surface area (g)
	Parents* GCA effects			Character means		
1	-0.0837	-0.0884	-0.4222	0.2868	0.5784	4.8655
2	-0.0495	-0.1260	-0.6251	0.3554	0.5150	4.5650
3	-0.0598	-0.1460	-0.7784	0.3412	0.4750	4.2500
4	-0.1003	-0.1567	-0.8687	0.2234	0.4398	3.9668
5	0.1858	0.3745	1.5868	0.6150	1.0840	7.9300
6	0.1077	0.1425	1.1079	0.5513	0.8698	6.6754
F$_2$ SCA effects						
1×2	-	-0.0392	-0.1969	0.3762	0.6093	5.1720
1×3	-	-0.0100	-0.0874	0.3583	0.6035	5.1282
1×4	-	-0.0198	-0.0608	0.2925	0.5978	5.0650
1×5	-	0.1300	0.6106	0.7196	1.2791	8.1913
1×6	-	0.0659	0.4414	0.6175	0.9829	7.5432
2×3	-	-0.0579	-0.2741	0.3803	0.5330	4.7385
2×4	-	-0.0492	-0.2020	0.3732	0.5310	4.7202
2×5	-	0.1567	0.7302	0.7380	1.2683	8.1081
2×6	-	0.0860	0.5442	0.6340	0.9655	7.4431
3×4	-	-0.0733	-1.0798	0.3548	0.4869	4.3563
3×5	-	0.1552	0.7796	0.7319	1.2466	8.0042
3×6	-	0.0975	0.6039	0.6285	0.9568	7.3496
4×5	-	0.1550	0.7798	0.7011	1.2358	7.9141
4×6	-	0.0976	0.6075	0.6064	0.9463	7.2628
5×6	-	0.1684	0.8405	0.7626	1.3116	8.8704
Critical differences						
SE (g_i)	0.0200	0.0083	0.0616	-	-	-
SE ($g_i - g_j$)	0.0332	0.0129	0.0959	-	-	-
SE (S_{ii})	-	0.0118	0.1960	-	-	-
SE (S_{ij})	-	0.0190	0.0277	-	-	-
SE ($S_{ii} - S_{ij}$)	-	0.0365	0.2715	-	-	-
SE (S_{ij}- S_{ik})	-	0.0289	0.2147	-	-	-
SE ($S_{ij} - S_{kl}$)	-	0.0259	0.1921	-	-	-

*1 = TGX 1873-16E; 2 = TGX 1878-7E; 3 = TGX 1890-7F; 4 = TGX 1891-3F; 5 = TGX 1896-3F; 6 = TGX 1844-18E.

g plant^{-1} (hybrid 5×6) for the crosses (Table 3). The highest and the lowest shoot dry weights of 1.0840 g plant^{-1} and 0.4398 g plant^{-1} were observed for Parents 5 and 4, respectively. Shoot dry weight in the crosses ranged from 0.4869 g plant^{-1} (hybrid 3×4) to 1.3116 g plant^{-1} (hybrid 5×6). Relative root surface area ranged

Table 4. Components of genetic variation for root dry weight, shoot dry weight and relative root surface area from a sand culture diallel experiment.

Variance components	Root dry weight	Shoot dry weight	Relative root surface area
$δ^2_A$	0.3322	1.1048	27.2400
$δ^2_D$	-0.3383	0.2588	13.6450
$δ^2_A : δ^2_D$	1:-1	4:1	2:1

$δ^2_A$ = Additive Variance; $δ^2_D$ = Dominance variance.

Table 5. High parent heterosis (%) for root dry weight, shoot dry weight and relative root surface area in an F_2 diallel of soybeans grown in acidified aluminium (450 µM AL^{3+}) sand culture.

F_2	Root dry weight	Shoot dry weight	Relative root surface area
1×2*	5.9	6.0	6.3
1×3	5.0	5.0	5.4
1×4	2.0	4.0	4.1
1×5	17.0	18.0	8.2
1×6	12.0	13.0	13.0
2×3	7.0	3.5	3.8
2×4	5.0	3.1	4.4
2×5	20.0	17.0	17.0
2×6	15.0	11.0	11.5
3×4	4.0	2.5	2.5
3×5	19.0	15.0	15.5
3×6	14.0	10.0	10.1
4×5	14.0	14.0	14.0
4×6	10.0	8.8	8.8
5×6	24.0	21.0	32.9

*1 = TGX 1873-16E; 2 = TGX 1878-7E; 3 = TGX 1890-7F; 4 = TGX 1891-3F; 5 = TGX 1896-3F; 6 = TGX 1844-18E.

from 3.9668 g $plant^{-1}$ (Parent 4) to 7.9300 g $plant^{-1}$ (Parent 5) for the Parents and from 4.3563 g $plant^{-1}$ (hybrid 3×4) to 8.8704 g $plant^{-1}$ (hybrid 5×6) for the crosses. Crosses involving Parents 5 or 6 or both recorded the highest values for the root dry weight, shoot dry weight and relative root surface area. However, the least root dry weight, shoot dry weight and relative root surface area were observed in crosses involving Parent 4.

Positive values of both the additive and dominance components of genetic variation were observed for all the traits except the dominance component for the root dry weight, where a negative value of -0.3383 was observed for this character (Table 4). However, the additive components of genetic variation for the root dry weight, shoot dry weight and relative root surface area exceeded the dominance components. The additive components were 4 times and 2 times the values of the dominance components for the shoot dry weight and the relative root surface area, respectively.

High parent heterosis

High parent heterosis for the root dry weight ranged from 2.0% for hybrid 1×4 to 24% for hybrid 5×6 (Table 5). All crosses involving Parents 5 or 6 recorded double digit heterosis (10 to 24%), while crosses excluding them recorded single digit high parent heterosis (2 to 7%).

The pattern of high parent heterosis for the shoot dry weight is similar to that observed for the root dry weight. High parent heterosis for the shoot dry weight ranged from 2.5% for hybrid 3×4 to 21% for hybrid 5×6. High parent heterosis for the shoot dry weight was highest in crosses involving Parents 5 or 6 or both, and least in crosses excluding them. The widest range in the high parent heterosis (2.5 to 32.9%) was observed for the relative root surface area. The least high parent heterosis (2.5%) was observed for hybrid 3×4, while the highest high parent heterosis 32.9%) was observed for hybrid 5×6. A narrow range of high parent heterosis (2.5 to 6.3%) was observed in crosses excluding Parents 5 and 6, while a wide range of 8.2 to 32.9% was observed for crosses involving Parents 5 or 6 or both.

DISCUSSION

The highly significant genotypic effects observed for all the traits in both parents and crosses are indications that the diallel population in the current work present genetic variability in response to aluminium stress tolerance. The non-significance of the F_2 Vs Reciprocals is an indication of the absence of maternal effects. This observation is consistent with the findings of Spehar (1999) from a similar diallel experiment on aluminium tolerance in soybean. The highly significant Parents Vs Crosses is an indication of the expression of heterosis which could be exploited in selection work. The non-significance of SCA compared to the highly significant GCA mean squares for root dry weight indicates that selection for this trait should be based on the GCA. Baker (1978) observed that the performance of a hybrid can be adequately predicted on the basis of GCA when SCA is not significant. The highly significant GCA and SCA mean squares for shoot dry weight and relative root surface area is an indication of the presence of both additive and dominance gene action in the control of these traits. The preponderance of additive compared to dominance gene action observed in the combining ability analysis had been previously observed (Spehar, 1999), and it is a favourable phenomenon in a selection work, indicating that pure line selection for aluminium stress tolerance from the genotypes studied is possible. Two genotypes, namely TGX 1896-3F and TGX 1844-18E, were observed as the best combiners in combining ability analysis. The highest GCA effect observed in TGX 1896-3F and TGX 1844-18E, coupled with the highest hybrid values and heterosis in crosses involving these genotypes, make them possible candidates in any selection work on aluminium tolerance. This is because the best performing cross can be obtained by crossing parents with the highest GCA estimates (Ogunbodede et al., 2000). Selection from TGX 1896-3F and TGX 1844-18E and crosses involving these two genotypes on acid soil would enhance a rapid progress in the breeding of aluminium tolerant genotypes of soybeans.

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