

ORIGINAL PAPER

STUDY OF SALT TOLERANCE PARAMETERS IN PEARL MILLET *Pennisetum Americanum* L.**GHULAM MUHAMMAD Ali¹, NAVEED Murtaza^{*2}, J.C. Collins³ and T. McNeilly³**

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ABSTRACT

The genetic basis of salinity tolerance for three parameters Ct, C50 and C0 in *P. americanum* using the diallel analysis was investigated. Tolerance for Ct, C50, and C0 was due to both additive and dominance genetic effects with indication of over-dominance. For these three parameters, dominance is predominantly towards salt sensitivity, but it appears that in different accessions, there are different gene effects for each character. Recessive genes are evident in the salt tolerant line ICMV-94474 for Ct and C50, and in the other tolerant line 10878 are also evident for C50 and C0 for recessive genes.

Salinity data set were found to be adequate totally for C50 and C0, but partially adequate for Ct. It appears in pearl millet that in some accessions recessive genes are responsible for salt tolerance for Ct, C50, and C0, but this trend is not consistent. Different (dominant / recessive) genes control each accession for Ct, C50, and C0. The maximum narrow sense and broad sense of heritability were found for C50 and this suggests that C50 is the best character for selection, rather than absolute root length. C50 is highly correlated with Ct, and C50 is also significantly correlated with C0. These results suggest that the genetic bases of these genes are linked to some degree. These correlations would be of considerable value in breeding for improved salinity tolerance.

KEY WORDS: Pearl millet, *Pennisetum americanum*, salinity, sodium chloride, stress tolerance

INTRODUCTION

Salt tolerance is considered to be a polygenic trait, and its expression is affected by various genetic, developmental, and physiological interactions within the plant, and in addition between genotypes and external environments, Bernstein and Hayward [3] and Shannon [24]. Various crop species have been examined for salt tolerance, which suggests that different genes may be controlling the character, from single major dominant or recessive genes, to QTL control with mainly additive effects, but with some degree of dominance towards tolerance, Azhar and McNeilly [2], Gregoria and Senadhira [9], Lee et al. [19], and Ahsan et al., [1]. An understanding of the genetic basis of desirable attributes, and identification of parent lines which are superior in those attributes, can improve these attributes, and in particular, parent lines for use in achieving such improvements. Genotypic variability of selective traits for seedling resistance to several stress factors has been documented including salinity tolerance in pearl millet, Kebebew and McNeilly [17].

Salt tolerance is a complex character controlled by a number of genes or groups of genes, and involves a number of component traits which are likely to be quantitative in nature, and the importance of salinity as a breeding objective is likely to increase in future, Flower and Yeo [6]. In various studies of different species, tests for salt tolerance have suggested that both additive and non-additive gene effects are important in controlling the expression of tolerance. In rice, seedlings from a 6 x 6 diallel cross indicated that hybridisation breeding based on favourable gene addition is a useful strategy to enhance the resistance of rice to saline stress. Parental general combining ability could be estimated roughly by the salt tolerance levels of varieties used, Gu et al. [10]. During the germination stage mean shoot length of F₁ progeny from eight barley varieties, showed that non-additive genetic variance is greater than additive genetic variance was, and the mean degree of dominance was 1.47, suggesting that salt tolerance at germination is controlled by over-dominant genes, Mano and Takeda [22]. From the information about the diallel genetic information, salinity tolerance could be increased in crops using appropriate breeding methods. The diallel crossing procedure and analysis developed by Hayman [11, 12], Jinks [14, 15] and Mather and Jinks [20] has been carried out using the four most tolerant accessions, and two sensitive accessions.

The objective of this study was to assess the Ct, C50, C0, in diallel analysis where Ct is the threshold concentration at which growth starts to decrease, C50 is the concentration where growth falls to fifty percent of the control and C0, the concentration at which growth

becomes equal to zero, these parameters were analysed by NOPT analysis based on the non-linear least square inversion model developed by Van Gunchen and Hoffman [26]. Replicated data analysed for these three parameters were used in a diallel analysis of variance. Diallel analysis for these parameters could furnish interesting information about type of gene action, which would be helpful in particular situations to understand the type of gene action involved in the expression of a character. It can identify genotypes possessing the most dominant and recessive alleles responsible for the expression of certain character, and also, provide information on narrow and broad sense heritability associated with the characters. This enables breeders to carry out efficient selection in the segregating generations, leading to the improvement of certain characters in breeding populations under stress conditions.

MATERIAL AND METHODS

Selection of parents: Six parents (4 tolerant and 2 sensitive) were chosen from the accessions used for assessment of variability in salinity tolerance. The parental accessions were 25233 (Yemen) and 5960 (Senegal) sensitive, 10878 (Sudan), 18570 (Namibia), ICMV-93753 (India) and ICMV-94474 (India) tolerant.

Crosses: Selected parents were grown using John Innes No. 2 compost in 18 cm plastic pots in a glasshouse. Temperature of the glasshouse was 28 ± 1 °C with 80 % humidity. Sowing was at an interval of 2-3 weeks to ensure synchronisation of flowering. Six parents were crossed in all possible combinations including reciprocal crosses and selfing. The protogynous habit of pearl millet helps the plant breeder to ensure almost 100% cross-pollination without emasculation. Instead of emasculation, heads were enclosed in glassine bags on emergence from the flag leaf sheath, and were examined daily through the glassine bag for the presence of extruded styles. When styles were extruded from floral parts, the head was ready for pollination, Burton [4].

Root length: Six parents and thirty F₁ crosses were tested in five treatments solutions viz. control, 40, 80, 120, and 160 mM NaCl in ½ strength Rorison nutrient solution, Hewitt [13]. Each treatment was replicated thrice in a Completely Randomised Design. Seeds were surface sterilised before sowing for ten minutes with 5% sodium hypochloride solution. Longest root length was measured from ten randomly chosen seedlings from each replication in each treatment after 14 days.

Statistical analysis: After comparing absolute root length means, Ct, C50, and C0 were computed for each parent and hybrids using NOPT Salt Programmes. These

Table 1. Relative root length for six parents and their all crosses, under four NaCl concentrations.

| Parent/ Crosses | 40 mM | 80 mM | 120 mM | 160 mM |
|-------------------------|--------|--------|--------|--------|
| 25233 | 103.17 | 90.47 | 49.69 | 38.86 |
| 5960 | 98.47 | 87.81 | 49.48 | 25.80 |
| 10878 | 103.72 | 98.59 | 84.70 | 61.32 |
| 18570 | 95.41 | 95.99 | 71.56 | 50.84 |
| ICMV-93753 | 103.49 | 114.38 | 75.26 | 50.78 |
| ICMV-94474 | 109.58 | 110.57 | 83.11 | 55.36 |
| 25233 X 5960 | 125.88 | 93.60 | 48.61 | 28.28 |
| 25233 X 10878 | 110.65 | 110.68 | 63.22 | 47.92 |
| 25233 X 18570 | 103.11 | 117.24 | 40.06 | 22.51 |
| 25233 X ICMV-93753 | 120.19 | 135.44 | 77.91 | 50.31 |
| 25233 X ICMV-94474 | 108.03 | 109.03 | 72.51 | 40.90 |
| 5960 X 25233 | 102.04 | 91.07 | 52.61 | 31.46 |
| 5960 X 10878 | 109.50 | 111.57 | 83.93 | 38.89 |
| 5960 X 18570 | 93.44 | 82.03 | 48.48 | 26.33 |
| 5960 X ICMV-93753 | 93.07 | 80.38 | 44.55 | 34.41 |
| 5960 X ICMV-94474 | 83.96 | 76.89 | 38.81 | 26.39 |
| 10878 X 25233 | 99.84 | 119.85 | 72.08 | 44.52 |
| 10878 X 5960 | 101.59 | 104.97 | 36.95 | 20.12 |
| 10878 X 18570 | 98.37 | 98.86 | 47.74 | 41.96 |
| 10878 X ICMV93753 | 107.69 | 87.71 | 53.71 | 27.67 |
| 10878 X ICMV94474 | 92.72 | 93.53 | 50.54 | 30.23 |
| 18570 X 25233 | 109.58 | 110.65 | 78.12 | 35.15 |
| 18570 X 5960 | 95.04 | 95.66 | 52.99 | 30.62 |
| 18570 X 10878 | 113.46 | 107.07 | 66.65 | 36.25 |
| 18570 X ICMV-93753 | 105.74 | 119.95 | 80.49 | 69.50 |
| 18570 X ICMV-94474 | 111.43 | 91.82 | 48.56 | 26.43 |
| ICMV-93753 X 25233 | 119.15 | 117.19 | 80.64 | 39.92 |
| ICMV-93753 X 5960 | 105.12 | 110.63 | 73.50 | 43.17 |
| ICMV-93753 X 10878 | 110.70 | 129.14 | 103.80 | 67.39 |
| ICMV-93753 X 18570 | 119.80 | 102.95 | 63.33 | 45.08 |
| ICMV-93753 X ICMV-94474 | 89.27 | 83.33 | 51.72 | 24.38 |
| ICMV-94474 X 25233 | 120.84 | 117.99 | 86.75 | 53.71 |
| ICMV-94474 X 5960 | 92.81 | 68.17 | 29.82 | 20.61 |
| ICMV-94474 X 10878 | 126.14 | 137.79 | 109.60 | 58.74 |
| ICMV-94474 X 18570 | 100.70 | 105.40 | 65.34 | 39.58 |
| ICMV-94474 X ICMV-93753 | 104.98 | 106.47 | 46.17 | 28.75 |

characters were used to examine the genetic basis of tolerance by Van Genuchten and Hoffman [26]. Diallel analysis based on three components Ct, C50, C0 was performed according to Hayman [11,12].

RESULTS

a. Relative root length: Relative root length decreased as the salinity level increased, the reduction varying among parents and hybrids up to 160 mM NaCl (Table 1), Under 160 mM Hybrids [18570 x ICMV-93753] and [ICMV-93753 x 10878] had higher root length and surpassed the parents with the longest roots. The hybrids [ICMV-93753

x 10878] and [ICMV-94474 X 10878] had the highest root length at all concentration levels. Those with longest relative root length under lower concentrations did not necessarily have the longest roots in more severe salt stress conditions.

b. Mean data for Ct, C50 and C0: Estimates of mean data for Ct, C50, and C0 (Table 2) clearly showed the differences in response of the eight accessions and the F₁ progeny for all three characters in response to NaCl. Estimates of Ct for each of the 30 F₁ progeny, progenies (F₁) ICMV-94474 x 10878, ICMV-93753 x 10878 and 5960 x 10878 had the highest threshold Ct value 111, 110 and 99, respectively among all thirty crosses, while best

Table 2. Mean data of Ct, C50, and C0 for parents and F₁ material.

| Ct | | | | | | |
|-------------------|------------------|---------------|---------------|---------------|-------------------|-------------------|
| | 25233 (M) | 5960 | 10878 | 18570 | ICMV-93753 | ICMV-94474 |
| 25233 (F) | <u>54.75</u> | 49.97 | 74.46 | 78.41 | 79.97 | 90.18 |
| 5960 | 63.05 | <u>60.55</u> | 99.42 | 54.25 | 44.54 | 44.90 |
| 10878 | 81.89 | 73.94 | <u>77.66</u> | 55.45 | 56.03 | 41.32 |
| 18570 | 93.36 | 70.37 | 75.64 | <u>75.71</u> | 87.00 | 57.94 |
| ICMV-93753 | 88.42 | 82.97 | 109.68 | 55.16 | <u>82.25</u> | 58.51 |
| ICMV-94474 | 88.29 | 24.48 | 110.91 | 84.74 | 65.58 | <u>86.61</u> |
| C50 | | | | | | |
| | 25233 (M) | 5960 | 10878 | 18570 | ICMV-93753 | ICMV-94474 |
| 25233 (F) | <u>128.30</u> | 116.39 | 143.08 | 116.80 | 146.92 | 143.47 |
| 5960 | 126.55 | <u>120.51</u> | 147.23 | 116.63 | 118.98 | 111.32 |
| 10878 | 146.99 | 113.90 | <u>181.83</u> | 126.84 | 120.92 | 123.38 |
| 18570 | 141.96 | 129.80 | 135.88 | <u>158.31</u> | 176.53 | 117.78 |
| ICMV-93753 | 143.94 | 146.36 | 166.19 | 133.70 | <u>153.26</u> | 120.44 |
| ICMV-94474 | 155.87 | 97.74 | 158.81 | 140.89 | 119.17 | <u>158.84</u> |
| C0 | | | | | | |
| | 25233 (M) | 5960 | 10878 | 18570 | ICMV-93753 | ICMV-94474 |
| 25233 (F) | <u>212.55</u> | 192.26 | 217.90 | 173.15 | 217.15 | 200.48 |
| 5960 | 198.13 | <u>189.81</u> | 196.17 | 193.21 | 209.51 | 195.12 |
| 10878 | 213.72 | 171.19 | <u>294.01</u> | 212.89 | 194.85 | 208.28 |
| 18570 | 192.86 | 198.61 | 200.52 | <u>245.43</u> | 273.89 | 187.23 |
| ICMV-93753 | 201.17 | 212.47 | 235.71 | 218.35 | <u>229.97</u> | 194.51 |
| ICMV-94474 | 227.72 | 183.68 | 206.33 | 202.89 | 186.27 | <u>236.62</u> |

Female (F): Male (M)

parent ICMV-94474 had 87 Ct. Lowest Ct was found in ICMV-94474 x 5960 (24). For C50, crosses 18570 x ICMV-93753 (177), ICMV-93753 x 10878 (166) and ICMV-94474 x 10878 (159) had greater value, while C0 was higher in 18570 x ICMV-93753 (274) and ICMV-93753 x 10878 (236). Generally, parents and their hybrids were different when ranked for Ct, C50, and C0. Hybrid ICMV-93753 X 10878 had comparatively high values for Ct, C50 and C0. Differences were also found (Table 2) between direct and reciprocal crosses for all these parameters.

c. Diallel analysis for Ct, C50, and C0 for root length:

1. Components of variation for Ct, C50 and C0: The magnitude of the components of genetic variation for each of the three characters are summarised in the form of mean squares, and are given in Table 3. From the mean squares of components of variation for Ct, C50, and C0, the additive effect "a" item is highly significant for Ct, C50, and C0, which suggests the presence of additive gene effects and general dominance effects (b) for three characters are highly significant. Similarly the b₁ item was highly significant for C50 and C0 indicating

the occurrence of variation to directional dominance. Whereas b₁ was non-significant for Ct, the b₂ item was highly significant for Ct and C50, and significant for C0. Thus variation for these character was due to parents containing differing numbers of dominant genes. The b₃ item was significant for C50 and C0, and Ct, suggesting that only certain crosses showed significant deviation from the mid parent (dominance was specific to certain crosses). Maternal effects c, were shown to be highly significant for Ct and C50, and also significant for C0. The highly significant d item revealed the presence of reciprocal differences in the crosses tested for C50 and C0 and significant for Ct characters.

2. Scaling test for adequacy of additive-dominance: The adequacy of the additive-dominance model, and validity of some of three assumptions (no non-allelic interaction, no multiple allelism, and un-correlated gene distribution) were assessed using joint regression analysis, and analysis of variance of (W_r + V_r) and (W_r - V_r). The results of the two tests for each of the three parameters are presented in (Table 4).

2.1. Ct; Thresholds: For Ct the slope of the regression

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Table 3. Mean squares of components of variation in 6-parents diallel cross assessed for Ct, C50, and C0.

| Component of variation | Df | Ct | C50 | C0 |
|---|----|-----------|-----------|-----------|
| Additive effects (a) | 5 | 1275.57** | 2331.14** | 3263.25** |
| General dominance effects (b) | 15 | 917.48** | 1006.38** | 2582.23** |
| Directional dominance effects (b ₁) | 1 | 36.53NS | 4261.53** | 14283.24* |
| Effects due to unequal distribution of dominance (b ₂) | 5 | 948.00** | 843.26** | 2055.61* |
| Effects due to dominance deviation unique to F1's (b ₃) | 9 | 998.41* | 735.29** | 1574.68** |
| Maternal effects (c) | 5 | 2070.86** | 1265.01** | 446.29* |
| Non-maternal reciprocal differences (d) | 10 | 950.48* | 701.92** | 895.16** |
| Error | 70 | 254.46 | 61.24 | 257.05 |

* significant (p<0.05) ** highly significant (p<0.01)

Table 4. Scaling test for adequacy of additive-dominance for 6-parent diallel data for three characters

| Character | Regression analysis | Analysis of variance | | Conclusion |
|------------|---|---------------------------------|---------------------------------|---|
| | | W _r + V _r | W _r - V _r | |
| Ct | b = 0.287 ± 0.277 The slope of the regression line did not deviate significantly from zero. | 1.92NS | 2.78NS | Model was found to be partially adequate for data analysis. |
| C50 | b = 0.493 ± 0.305 The slope of regression line did not deviate significantly either from zero or from unity. | 1.45NS | 1.38NS | Model adequate for data analysis |
| C0 | b = 0.876 ± 0.135 The slope of the regression line deviated significantly from zero but not from unity. | 2.58NS | 2.59NS | Model adequate for data analysis both tests suggested the adequacy. |

Table 5. Estimates of genetic parameters for Ct, C50, and C0

| Components of Genetic Parameters (F ₁ generation) | Ct | C50 | C0 |
|--|------|------|------|
| Mean degree of dominance [(H ₁ /D) ^ ½] | 4.15 | 1.80 | 1.55 |
| Proportion of dominance [H ₂ /4H ₁ (uv)] | 0.23 | 0.20 | 0.20 |
| Narrow sense heritability | 0.21 | 0.25 | 0.16 |
| Broad sense heritability | 0.82 | 0.95 | 0.88 |

line did not deviate significantly ($b = 0.29 \pm 0.28$) from zero (Table 4). The $W_r + V_r$ item was non significant indicating the absence of dominance. However, the mean squares between arrays for $W_r + V_r$ were greater than that within arrays suggesting the presence of dominance, and mean square between arrays for $W_r - V_r$ was non-significant which suggests the absence of non-allelic interaction. From the graphical position (Fig. 1) of W_r on V_r , the regression line passing above the origin indicates over-dominance. As a consequence, analysis of data using the Hayman-Jinks model was partially adequate for Ct.

2.2. C50; salinity level at which root length equal to 50 % control: For C50 the slope of regression line did not deviate significantly either from zero or unity ($b = 0.49 \pm 0.31$) suggesting intra-allelic interaction; this means that genes were distributed independently among the parent lines and were independent in action. The mean squares between arrays for $W_r - V_r$ were non-significant, which showed there is no non-allelic interaction. This also confirms the adequacy of the additive-dominance model. To the analysis of variance of $W_r + V_r$ it can be seen that it is non-significant, and from this evidence, it can be assumed that dominance is not present. But there is no evidence of interaction between non-allelic genes. It may be concluded that although it's not significant by itself, but the higher value for the mean square between arrays for $W_r + V_r$ (Table 4), does in fact reflect dominance, Mather and Jinks [20]. Thus the model was adequate for analysis of the data C50.

2.3. C0; salinity level at which root length equal to zero: For C0, the slope of the regression line ($b = 0.88 \pm 0.14$) deviated significantly from zero, but not from unity (Table 4). This confirmed two things; firstly, the absence of non-allelic interaction, and secondly, independent distribution of gene among parents. The analysis of variance $W_r + V_r$ and $W_r - V_r$ (Table 4) showed another test of dominance. Non-significant differences were found for $W_r - V_r$, suggesting the absence of non-allelic interaction. From results of these two tests it was concluded that the model was adequate for further analysis using the Hayman-Jinks models. From the graphic position, their relationship is examined through the regression of W_r on V_r , which showed that the regression line intercepts the W_r axis below the origin, which indicates over-dominance.

3. Estimates of genetic parameters.

3.1. Ct; Threshold: The heritability narrow and broad sense along with statistical ratios concerning genetic analysis of Ct is given in Table 5, and a regression of variance and covariance are presented in Fig. 1. The regression line of W_r/V_r intersected the y-axis below the origin on negative side which indicated the predominance of over dominance gene action in the expression of C50.

Those parental lines carrying most dominant genes and those possessing maximum recessive alleles, Fig. 1, were identified, the results indicated that accessions 10878, 18570 and ICMV-93753 were close near to the point of origin position, indicating the most dominant alleles, whereas accessions 25233 and ICMV-94474, being away from the origin, appear to contain the most recessive alleles responsible for Ct. The average degree of dominance indicated by $(H_1/D)^{0.5} = 4.15$, was more than unity, suggesting a degree of over-dominance, which was also verified by the position of the intercept of the regression line on the negative side of W_r axis. H_2 is smaller than H_1 , and therefore, there are unequal allele frequencies at all loci (Table 5). Mean value of uv overall all these loci, estimated from the ratio $\frac{1}{4} H_2/H_1 = 0.23$, is less than its maximum value of 0.25 which arises when $u=v=0.5$ at all loci. Narrow sense heritability, was 0.21, whilst for broad sense heritability, the value was 0.82.

3.2. C50; salinity level at which root length equal to 50 % control: Estimates of genetic parameters (Table 5) suggest an active role of dominance compared to additive effects. The average degree of dominance indicated by the $H_1/D^{0.5} = 1.80$, was more than unity, which suggests that dominance tended towards over-dominance. The regression line of W_r/V_r intersected the y-axis above the origin on positive direction, indicating the presence of partial dominance for C50. Comparison of the array distribution in Fig. 1 showed that accessions 5960 and ICMV-93753, which were sensitive and tolerant respectively, possessed the most dominant alleles. Accessions 10878 and ICMV-94474 had the most recessive alleles; both being tolerant accessions, whilst 25233 and 18570 had both type of gene for C50. The estimates of the ratio between H_1 and D showed for over-dominance present. The gene frequencies in the parents were unequal, based upon the ratio of $H_2/4H_1$ which was found 0.20. Narrow and broad sense heritability estimates were 0.25 and 0.95, respectively.

3.3. C0; salinity level at which root length is reduced to zero: There was very little contribution of environmental component of variation for C0, compared with additive and dominance effects. The estimate of the ratio $(H_1/D) = 1.55$, indicating over-dominance gene action for C0. The graphical representation also suggested the presence of over-dominance, the W_r/V_r regression line intersecting the y-axis below the origin. $H_1/D^{0.5} = 1.55$ also indicated over dominance. The most dominant genes were present in the sensitive accessions 5960 and 25233, and tolerant in accessions ICMV-93753 and ICMV-94474. Accession 10878 possessed the maximum number of recessive alleles for C0, and 18570 contained dominant and recessive alleles (Fig. 1). The value of uv (ratio

Table 6. Correlation's for Ct, C50, C0 and 160 mM NaCl concentrations

| | Ct | C50 | C0 | 160 mM NaCl |
|-------------|----|--------|--------|-------------|
| Ct | 1 | 0.68** | 0.08 | 0.48** |
| C50 | | 1 | 0.77** | 0.86** |
| C0 | | | 1 | 0.78** |
| 160 Mm NaCl | | | | 1 |

obtained from dominance effects of genes corrected for gene distribution and dominance effects of genes) over all loci estimated from the ratio $\frac{1}{4} H_2/H_1$, was 0.20, less than its maximum value, which indicated unequal allele frequency. Narrow and broad sense heritability values were 0.16 and 0.88, respectively, again suggesting most dominance effects.

4. Correlation: Ct showed a significant positive correlation with C50 and root length at 160 mM NaCl (Table 6). C50 showed a significant positive correlation with C0 and root length, whereas C0 also showed a significant positive correlation with root length at 160 mM NaCl.

DISCUSSION

A complete diallel set of crosses was analysed using the model of Hayman [11, 12]. Dickinson and Jinks [5] have discussed the tests for linkage, correlated gene distribution, and non-allelic interaction for the heterozygous diallel. No other design includes a test for the presence of these effects, nor do they detect the presence of multiple alleles, Kearsey [16]. The additive-dominance model of Hayman [11] and Jinks [15] was shown to be adequate for analysis of the data obtained from C50 and C0 (Table 4). However, from graphical analysis of diallel data for Ct, a significant deviation of the regression slope from unity, indicated the presence of non-allelic interaction, due to linkage, or non-independent distribution of genes in the parents, as suggested by Mather and Jinks [21]. The data thus showed partial failure to meet the assumptions underlying the model. In the present study the data for Ct, C50, and C0 were analysed to provide information potential value in breeding programmes for improved salinity tolerance in pearl millet (Table 3, 5). This indicated both additive and non-additive gene effects for Ct, C50, and C0. Both additive and non-additive gene effects are important in controlling the expression of salt tolerance. Dominant genes were associated with salt sensitivity, whereas recessive alleles tended to produce greater tolerance in terms of Ct, C50, and C0 (Fig. 1) but not in all parents, such as 18570 and ICMV-93753. The data obtained for Ct and C50, which showed dominance effects that were greater than additive effects, is in agreement with Kebebew and McNeilly [18] findings in pearl millet.

Both additive and dominance gene effects, controlled salt tolerance at both 75 mM NaCl and 175 mM NaCl levels and genes with dominance properties appeared to be more important. For the three characters Ct, C50, and C0, there was a trend towards over-dominance in a barley diallel cross, Mano and Takeda [22], non-additive genetic variance was greater than additive genetic variance for tolerance at germination. The mean degree of dominance was 1.47, suggesting that salt tolerance at germination is controlled by over dominant genes.

The co-variance and variance (W_r , V_r) values satisfied the simple additive dominance model, and therefore, give dominance and recessive relationships of the different accessions for a particular character. Graphical presentation of Ct, C50, and C0, indicated that accession, 5960 (sensitive) had the maximum dominant genes/alleles for C50 and C0, and tolerant lines 10878 for C50 and C0, and ICMV-94474 for Ct and C50 contained recessive genes. Lines 18570 and ICMV-93753 contain both dominant and recessive genes for Ct, C50, and C0. This indicates that in some accessions, Ct, C50, and C0, are governed by recessive alleles and dominant genes are responsible for sensitivity. Dominance is predominantly towards salt sensitivity but it would appear that in different accessions e.g. 25233, 18570, and ICMV-93753, there are different genes affecting each character, which suggested that no general consistency for tolerance was found between the three tolerance traits, Ct, C50, and C0. These results are in accordance with other findings Kebebew and McNeilly [17] in pearl millet. They have found that different genes are responsible for Ct, C50, and C0 between accessions. Mano and Tekada [22] found that in barley, salt tolerance at the germination stage was mainly controlled by recessive genes. In contrast, Lee et al. [19] estimated in japonica rice, more dominant alleles were present in salt tolerant parents.

Some of the F_1 progenies response to salinity (Table 1) differed to that of other progenies. For example the F_1 progenies from crosses involving 25233, which appears to be a sensitive line, showed greater tolerance than progenies of parents which had higher salinity tolerance. In some combinations of ICMV-94474 and ICMV-93753 with 5960, the accessions showed low tolerance, suggesting over-dominance in these combinations, a

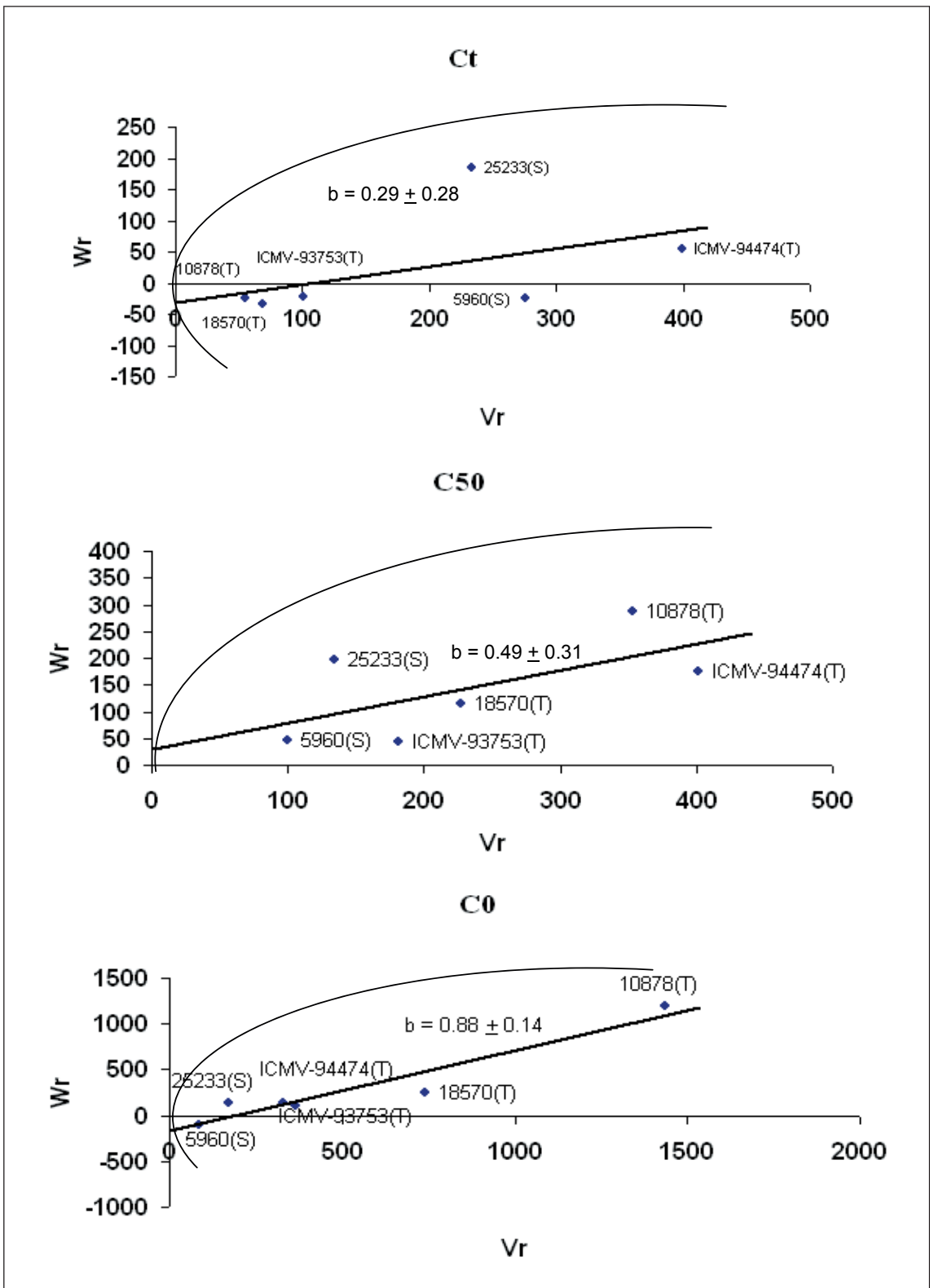


Fig 1. W_r/V_r regression for Ct, C50, and C0 of pearl millet in NaCl from 6 x 6 diallel

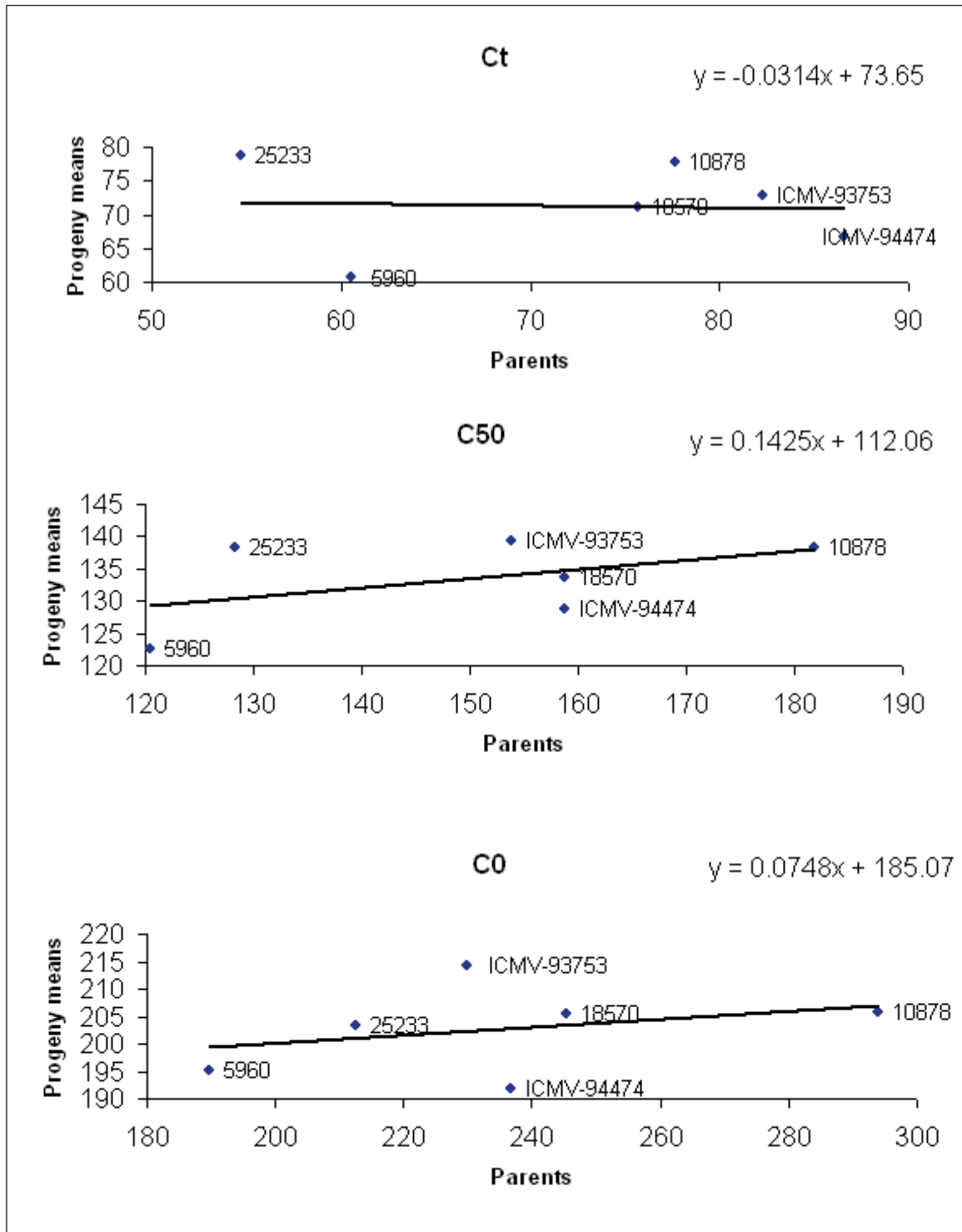


Fig 2. Heritability for Ct, C50 and C0 of pearl millet

phenomenon which had been seen in some sorghum hybrids, Azhar and McNeilly [2].

Narrow sense heritability decreased as salt concentration in rooting media increased progressively, i.e. heritability decreased as stress increased. Thus under higher salt concentration, the selection value of the root length tolerance measurement decreased. Roger et al., [23] and Foolad [8] have shown that selection can be made under salt stress conditions, provided that heritability estimates are high. Maximum narrow as well as broad sense heritability was associated with C50. Under such circumstances it would be feasible to select for C50. Thus C50 is best character for selection in salt stress.

Ct is significantly correlated with C50, and C50 is highly significantly correlated with C0. The genetic basis of Ct, C50, and C0 thus appear to have a common basis. It was suggested by Foolad et al. [7] that in tomato, seed germinating under different cold and salt conditions, expressed the same QTL which controlled, germination under cold stress, or under salt stress, these were called stress specific QTLs. The diallel analysis used in this experiment, for Ct, C50, and C0, also support this suggestion, because the three characters appear to be under the control of over-dominant genes. The correlation between tolerance to low and high salinity conditions, if influenced by the same genes, should be positive, as was suggested by Shannon [25] and it may well be that genes operating for Ct-C50 and C50-C0 are linked or the same (Table 6, Fig. 1).

In this study, results describe here for three characters Ct, C50 and C0, both additive and non-additive genetic affects are present and there is evidence of dominance and over-dominance, tolerance in the main being recessive. Of the character examined, character C50 appears to be the best for selection, rather than absolute root length.

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